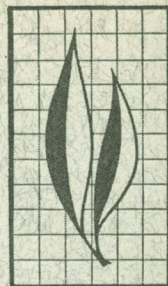# Influence of Host Plant Condition on Population Increase of *Tetranychus telarius* (Linnaeus) (Acarina: Tetranychidae)

Theo F. Watson

Population growth studies were conducted with *Tetranychus telarius* (Linnaeus) on lima beans in the greenhouse. The capacity of populations to increase was studied in relation to host-plant nutrition, leaf age and plant age.

Host-plant nutrition influenced population increase by affecting both longevity and fecundity. Adult female longevity was adversely affected when the mites were confined to plants grown in nutrient solutions deficient in phosphorus, nitrogen or potassium, rather than in full-nutrient solutions. In the host-plant nutrition studies, nitrogen deficiency was most detrimental for survival and phosphorus deficiency least detrimental. Age-specific fecundities were severely reduced when females were confined to plants grown in the deficient solutions. The phosphorus-deficient treatment gave the greatest reduction in total fecundity as well as maximum fecundity attained. This was true for both old and young leaves. The old leaves of the potassium-deficient treatment induced the second greatest reduction in both total and maximum fecundities. The nitrogen-deficient treatment was superior to either mentioned above but significantly inferior to the full-nutrient treatment. The young foliage in the potassium-deficient treatment was somewhat superior to the old foliage in the full-nutrient treatment in both total and maximum fecundities.

Mite populations reared on host plants which received a full nutrient supply showed greater net reproduction rates and intrinsic rates of increase. Phosphorus-deficient plants were the most detrimental to these population attributes. The nitrogen-deficient plants and old leaves of the potassium-deficient plants gave intermediate results, while young leaves of the latter gave results comparable to those obtained on old leaves of the full-nutrient treatment.

Although leaf age had no effect upon adult survival, young leaves, regardless of nutritional treatment, were more favorable for both total and maximum fecundities. Consequently, young leaves enhanced population growth in comparison to old leaves.

Plant age was also found to affect population increase. Fecundity was reduced on older plants but survival was not affected.

THE AUTHOR:

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Influence of Host Plant Condition on Population Increase of *Tetranychus telarius* (Linnaeus) (Acarina: Tetranychidae)[1]

INTRODUCTION

The inherent capacity of a species to increase interacts with numerous environmental factors to cause fluctuations of animal populations in nature. Solomon (1957) states, "The power to increase in favorable conditions, inherent in all living things, is the mainspring of population dynamics." Agricultural entomologists are particularly interested in conditions which permit economic pests to increase to destructive numbers. The effect of certain environmental conditions on the ability to increase has been determined experimentally for many species. For example, the effects of temperature and relative humidity on the development and reproduction of various invertebrate organisms have been explored most extensively. Recent contributions by Andres (1957) and Nickel (1960) evaluated the effects of these two factors upon *Tetranychus telarius* (Linnaeus), which is the test animal in the present work.

The influence of host-plant nutrition on the capacity of phytophagous insects and mites to increase has been the subject of many recent reports. Conflicting reports have been published about the effects of host-plant nutrition on the two-spotted spider mite, *T. telarius*.

Since experimental conditions were apparently similar in these differing reports, undoubtedly something other than host-plant nutrition influenced population increases. Henderson and Holloway (1942) found that more eggs were deposited by the mites *Panonychus citri* (McGregor) [*Metatranychus citri* (McGregor)] on young- and medium-aged leaves than on old leaves. This suggests that differences in the age of leaves sampled could account for some of the variability reported in nutritional studies. They also reported that feeding injuries reduced oviposition by mites. It may be that confining mites to the same area for relatively long periods influences nutritional studies.

Garman and Kennedy (1949) reported that, in the greenhouse, three times as many mites developed on heavily fertilized bean plants as on unfertilized plants. LeRoux (1954) worked with *T. telarius* (*T. bimaculatus* Harvey) on cucumbers grown in the greenhouse on a vermiculite base to which nutrient solutions were added. He reported that high nitrogen and potassium levels were positively correlated with increased fecundity. Phosphorus increased fecundity at certain levels but not at others.

[1] Submitted for publication April 19, 1963.

The findings of LeRoux were not substantiated by those of Fritzche, Wolfgang, and Opel (1957). Working under field conditions with the bean plant, *Phaseolus vulgaris* Linnaeus, and the two-spotted spider mite, *T. telarius* (*T. urticae* Koch), they found that the highest rate of mite increase occurred on potassium-deficient plants, and the lowest on completely fertilized plants. Nitrogen and phosphorus deficiencies seemed to cause a higher rate of increase than did complete fertilization, but these rates were lower than those caused by potassium deficiency.

Rodriguez (1951), working with *T. telarius* (*T. bimaculatus* Harvey) on tomatoes, reported that more than three times as many mites developed on the low-nitrogen foliage as on the high. Absorbed phosphorus was positively correlated with mite populations up to a level of 0.30 per cent dry weight of tomato foliage. Concentrations above that point were correlated with decreased populations. Mite development was positively related to potassium supply but mite populations in different studies were both positively and negatively correlated with absorbed potassium and sodium.

In a more recent study, Rodriguez (1958), working with apple trees under greenhouse conditions, reported that the population size of *T. telarius* was positively correlated with absorbed nitrogen in apple foliage but negatively correlated with increased nitrogen absorption when phosphorus levels were simultaneously increased. Mite populations were positively correlated with phosphorus and potassium absorption. The seemingly contradictory results were explained on the basis of interrelations of ions and different ranges of absorption.

In Nova Scotia, Lord and Stewart (1961) conducted a three-year field study to determine the effects on mite and predator populations of increasing the absorbed nitrogen in apple leaves. They found that the number of *Panonychus ulmi* (Koch) remained very low despite the difference in leaf nitrogen content resulting from fertilizer treatments. Populations of *Bryobia arborea* M & A and the eriophyids [probably *Vasates schlechtendali* (Nalepa)] were considerably higher but there was no significant difference in the numbers present under high and low nitrogen fertilization. The same was true for populations of the predacious typhlodromid mites and various predacious insects.

Henneberry (1960), working in the greenhouse with phosphate-resistant and nonresistant strains of *T. telarius*, showed that they produced more progeny when the inorganic nitrogen supply of lima beans was increased. Higher reproductive rates were correlated with absorbed nitrogen. Population growth of both strains was accelerated by increases in total water-soluble carbohydrates. When phosphorus supplies were increased, progeny of the nonresistant strain also increased. The resistant strain produced more progeny on plants supplied with high potassium. Phosphorus and potassium supplies with certain combinations of nitrogen affected the soluble carbohydrate content of leaf tissue. High phosphorus levels with low or intermediate nitrogen resulted in decreased soluble carbohydrate content of the leaf tissue. Low nitrogen and potassium supplies resulted in a decrease of total carbohydrate.

A subsequent investigation by Henneberry (1962), in which he again studied *T. telarius* and lima bean plants, showed that more progeny were produced on plants supplied with high nitrogen than on those supplied with low nitrogen. Also, more progeny were produced on second, third, or fourth trifoliate leaves than were produced on the first trifoliates regardless of nitrogen supply.

Hampstead and Gould (1957), working in the Cumberland-Shenandoah fruit area over a period of two seasons, showed that populations of *Panonychus ulmi* (Koch) [*Metatranychus ulmi* (Koch)] and *T. telarius* in apple or-

chards were substantially greater in plots with the highest leaf nitrogen. The seasonal mite peak followed closely after the seasonal leaf-nitrogen peak. The authors stated that, other factors being equal, high leaf-nitrogen appeared to be a factor that could cause a benign mite population to become destructive and difficult to control.

Morris (1961), working in the greenhouse with the clover mite, *Bryobia praetiosa* Koch, on bush lima beans, found that increasing the supply of nitrogen, phosphorus, and potassium increased the leaf content of these elements. He showed that about six times as many mites developed on medium-nitrogen plants as on low-nitrogen plants, and about eleven times as many developed on high-nitrogen plants. Larger mite populations developed with medium-phosphorus or potassium supplies than at lower or higher levels of these elements. Morris also found that low levels of nitrate-free nitrogen in the foliage adversely affected adult longevity, the duration of oviposition, the number of eggs laid, and the total number of mites to reach maturity.

Since most of these investigations dealt with groups of mites, it was thought that data from individually caged mites would be more informative, and that construction of life-fecundity tables as described by Birch (1948) would give a more precise picture of actual responses to the different nutritional treatments.

The above mite-nutrition studies demonstrate that results are not only variable but completely contradictory in certain cases. Numerous factors may have produced these differences. In field studies, predation or changes in the microhabitat as a result of fertilizer practices may have influenced population growth. In the greenhouse studies, methods of handling the test plants as well as the mites may have been partially responsible for the variable results. For example, failure to ensure that all females were of a uniform age and fertilized would have significant effects on the size of the developing population.

Since plants exhibit different growth characteristics in response to various nutritional treatments, the optimum area for the mites on different plants may vary. Unless absolute numbers are sampled from entire plants of each treatment, difficulties may arise in determining appropriately comparable sampling areas. This might have influenced the results obtained in previous studies.

In the present study, the effect of host-plant nutrition upon the capacity of a mite population to increase was the primary concern, but the effects of leaf age and plant age were also investigated as possible influencing factors. Life-fecundity tables were constructed for the populations of mites that developed under the various treatments. Utilizing the data in the life-fecundity tables, the intrinsic rates of increase were calculated for the populations. This statistic was determined for use as an index in evaluating the effects of leaf age, plant age and host-plant nutrition on population increase.

METHODS

Establishment of the Mite Colony

The mites used in these studies were the progeny of one adult female which was obtained from a greenhouse colony infesting alfalfa plants at Berkeley, California. Eggs deposited in a 24-hour period by this female were placed in a constant-temperature cabinet for propagation of the stock culture. The temperature cabinet was a modified 7-cubic-foot refrigerator with six 15-watt daylight fluorescent lamps providing continuous illumination. The temperature was maintained at 75° F by means of a thermostat and a small circulating fan.

Once the mites were established, the stock culture was reared on rapidly growing baby lima bean plants of the Henderson variety. The bean plants were potted in vermiculite and supplied with sufficient quantities of Hoagland's (1950) nutrient solution to maintain good growth.

Growing and Handling of the Test Plants

One lot of baby lima bean seeds was purchased initially in sufficient quantity to ensure uniformity of the test plants throughout the investigations.

Test plants were germinated in vermiculite and transplanted to one-half gallon mason jars after the primary leaves had expanded. The jars were coated with black asphaltum paint and then sprayed with a light coat of aluminum paint. A large cork was placed in each jar top to support a plant. The roots of the seedlings were inserted through a hole in the cork into the nutrient solution. Nonabsorbent cotton was then wrapped around the stem to support the plant and minimize water loss by evaporation. Only tap water was added to the vermiculite while the plants were in the germinating flat. Therefore, except for the food stored in the cotyledons, no nutrients were available to the bean plants until they were transferred to the mason jars. The various salt solutions were pipetted to the test jars individually. Distilled water was used in all nutrient solutions.

Aeration was provided for the plants in nutrient solutions by a small portable air compressor. A slow, but continuous bubbling of air was maintained in all solution jars. In addition to the compressor, the system consisted of two rows of small ⅛-inch iron pipes, sixty air jets with .0135-inch openings, rubber tubing, and glass rods for the individual nutrient jars. The pipes extended the length of the greenhouse table with the air jets fitted into the pipes at regular intervals. The rubber tubing connected the air jets with the glass rods which were dropped into the solution jars via a small hole near the periphery
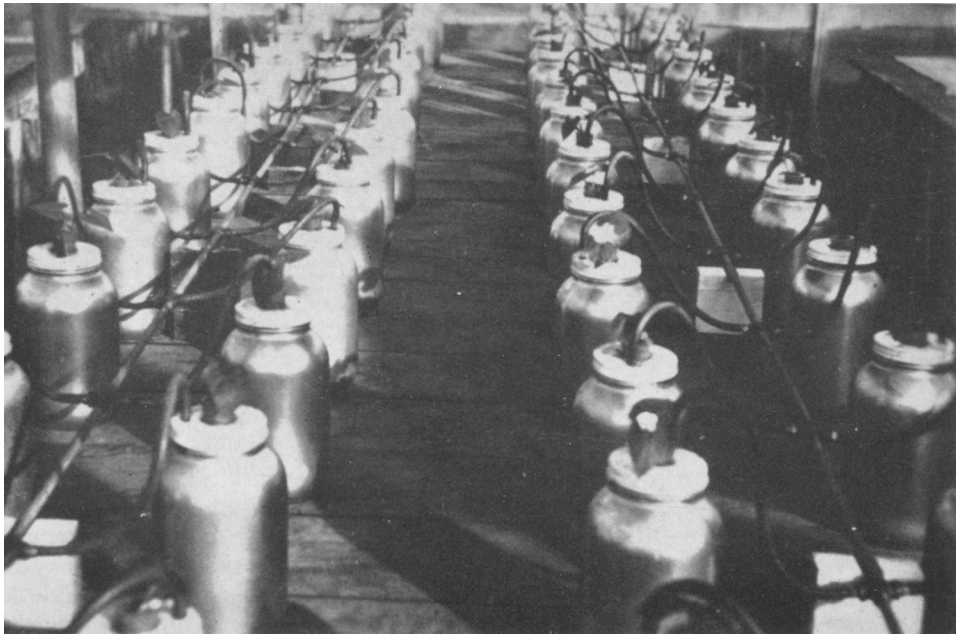

Fig. 1. A typical experimental arrangement showing nutrient solution jars, newly transplanted seedlings, and the aeration system.
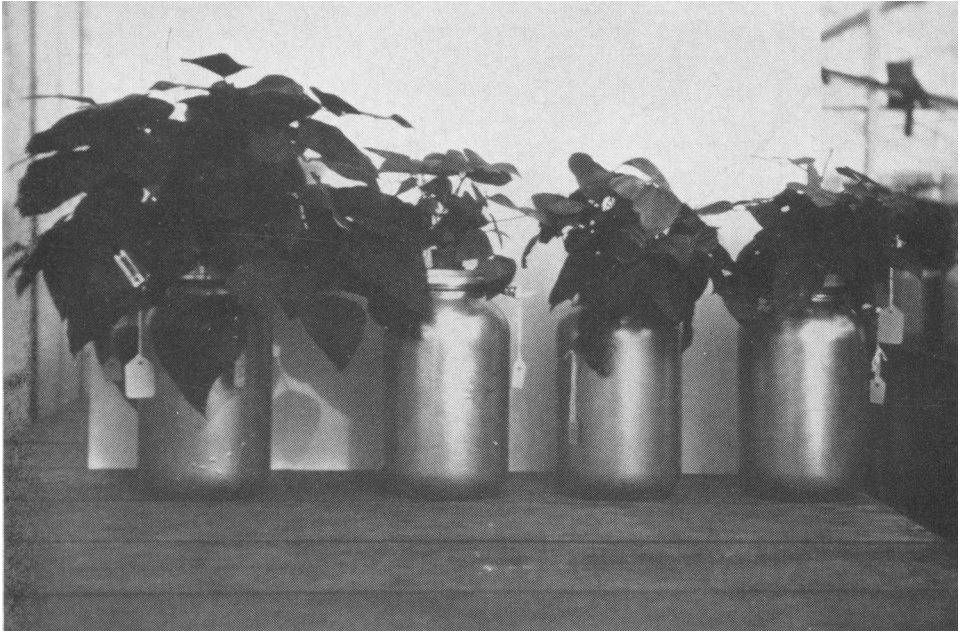
Fig. 2. Lima bean plants after 52 days in (left to right) full-nutrient, low-nitrogen, low-potassium and low-phosphorus solutions.

of the jar lid. Figure 1 shows the physical arrangement of the experimental set-up at the beginning of an experiment.

In order to avoid major effects of bias due to location of plants within the greenhouse room, equal numbers of replicates of each treatment were located in each quadrant of the table. This necessitated a systematic arrangement of treatments rather than complete randomization.

Generally, four nutritional treatments were used in each experiment. The control consisted of plants grown in Hoagland's complete nutrient solution. The other treatments were maintained as similar solutions except that one of three nutrient elements—nitrogen, phosphorus, potassium—was either supplied in low quantity or completely eliminated. In every experiment, 15 plants—one per jar—were used for each nutritional treatment. Figure 2 shows a typical plant from each nutritional treatment after an advanced state of deficiency had been effected.

Experimental Procedures

The mite investigations were conducted in a greenhouse provided with a light coating of whitewash. Physical conditions were not constant and, consequently, hygrothermograph records were kept throughout all test periods to provide a basis for comparison of conditions from test to test.

A group of test mites of comparable age was obtained by placing adult females from the stock culture onto detached leaves for oviposition. After a 24-hour period, the females were removed and destroyed. Eggs deposited by these mites eventually produced the females that were used in the tests. After adult females emerged, they were placed in individual leaf cages. The cages (figure 3), similar to those described by Noble (1958), were constructed from modified hair clips and small cylinders of polyethylene tubing which were covered with cellophane sheeting perforated to allow for ventilation. The cages were attached to leaves
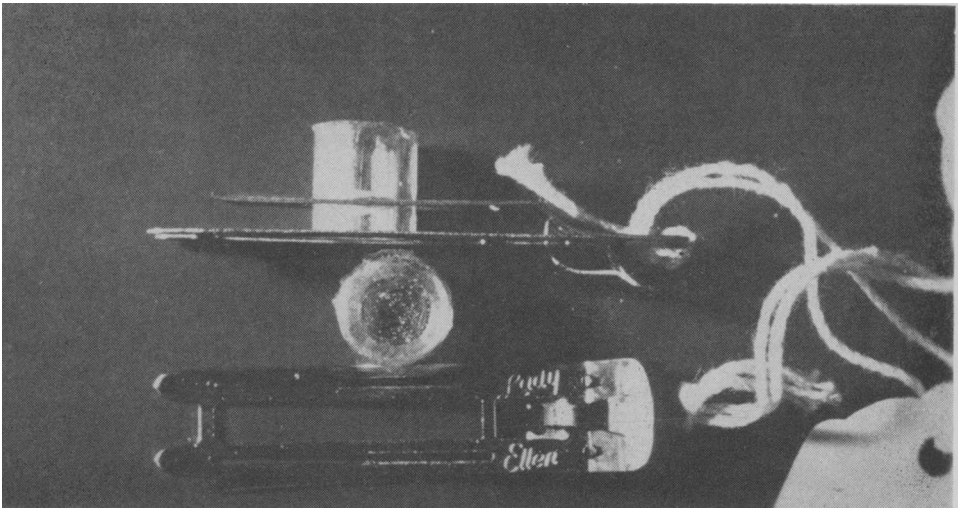
Fig. 3. Leaf cages used to confine individual females of *Tetranychus telarius* on the leaves of experimental plants.

of test plants, and daily egg counts were made by placing the test plants beneath a binocular microscope mounted on a flexible arm. The eggs were removed and the cages transferred to a new location on the lower surface of the leaf every other day.

Records were kept for four individual mites on each plant from the time adult females emerged until death. This provided data for 60 females from each nutritional treatment. To study the effect of leaf age on the mites, two females per plant were maintained throughout their lives on the primary leaves while the other two were placed on opposite leaflets of the youngest trifoliate. As new growth appeared, the cages were transferred up the plant. Daily egg production was averaged for each treatment according to the number of females alive at the beginning of each day. The cohort for the life tables consisted only of those females that presumably died a natural death; accidental deaths and escapes were not included in the l_x column.

In the last test, mites used for life-table studies were conditioned to the various nutritional treatments by undergoing their entire immature de-velopment on their respective host plants, rather than being placed on them as adults. Since plants completely lacking nitrogen, phosphorus, or potassium will survive for only approximately 4 weeks, it was necessary to precondition a substitute set of plants which could be used when the original plants were no longer in a favorable condition for mite feeding.

Preliminary work was conducted with mites reared on detached leaves from plants receiving full nutrients and those receiving a low level of phosphorus. Although data were collected and differences observed, the method of detached leaf culture was determined to be unsatisfactory for this investigation primarily because the number of mites lost by unnatural means was excessive. In addition, the use of leaf cages maintains the mite on the growing plant under more natural conditions.

Construction of Life Tables and Calculation of Intrinsic Rate of Natural Increase

Life-fecundity tables are used extensively in the present study and the basic

ecological parameter, the intrinsic rate of increase, is calculated as an index to evaluate population responses to varying conditions. Birch (1948) describes a method for calculating the intrinsic rate of natural increase, and Andrewartha and Birch (1954) discuss the use of life tables in calculating such growth rates. In the latter paper, they define the intrinsic rate of natural increase as the actual rate of increase of a population under specified constant environmental conditions in which space and food are unlimited. This growth rate is expressed as r_m in the formula $dN/dt = r_m N$. The increase in numbers of individuals (dN) with time (dt) is equal to the growth rate (r_m) multiplied by the numbers already present (N). This growth rate, r_m, can also be expressed in the following derived formula:

$$N_t = N_0 e^{r_m t}$$

With this latter formula it is possible to calculate the actual numbers occurring at some future time, t, based on the numbers at present, N_o, and the growth rate, r_m. In this formula, e is the base of the Naperian, or natural logarithms. An accurate estimate of r_m may be determined from the quantitative pattern by which mortality and fecundity of the organisms in the population vary with the age of the individuals under the specified environmental conditions. These data are best provided in the form of a combined life-fecundity table.

In such a life table, data are presented for survival and fecundity of a given initial number of individuals as these individuals develop from newly laid eggs through immature development to adulthood and eventual old age. Naturally, as the age of the sample increases, the proportion surviving gradually decreases from 1.0 to 0.0. On the other hand, fecundity does not appear until the individuals mature, starting out

with low values per unit of time, rising rather rapidly to a peak, and then declining less swiftly to zero again. In the life table, x is the age of individuals in appropriate units of time, l_x is the proportion of individuals still alive at age x, and m_x is the number of female offspring produced per female in the age interval x.

The intrinsic rate of increase is computed from the data of the life table according to the following formula:

$$\sum e^{-r_m x} l_x m_x = 1$$

The main problem encountered in applying this formula is in the calculation of the value for $e^{-r_m x}$. With the usual values for r_m and x encountered in the present research, this negative exponent of e lies outside the limits of the tables in most available mathematical handbooks. Therefore, it was more convenient to multiply both sides of the equation by a factor of e^k in order to work with powers of e which lie in the more detailed parts of the table. Thus, as in Birch's study, K was taken as 7.

$$e^7 \sum e^{-r_m x} l_x m_x = e^7$$

$$\sum e^{7-r_m x} l_x m_x = 1,096.6(1097)$$

Once r_m has been calculated, a more easily visualized term for the growth of animal populations can be computed. This term is the finite rate of increase (λ) which is the multiplication per female per unit of time which a population would have when increasing in a constant environment in which food and space were unlimited. It is derived from the formula $\lambda = $ antilog $e \ r_m$.

In the present study, each treatment consisted of a population of 30 individual females. These mites were followed individually from the period of newly emerged adulthood until death occurred. The average number of eggs produced per female was computed from

the total number of mites alive in each treatment at the beginning of the day that counts were made. For the purposes of this work the sex ratio was considered as unity. The m_x column is comprised of the mean number of female eggs produced in each unit of time, expressed as days. The total number of mites used to calculate the l_x column (survivors) was based only upon those considered to have died a natural death, that is, a cohort of 1 was based on the proportion of the original 30 mites in each treatment that presumably died a natural death. Natural death was considered to have occurred in all cases except where the mites were lost or crushed. Based on preliminary laboratory studies, it was shown that immature mortality under greenhouse conditions was negligible. Therefore, immature mortality was ignored in the life tables and in all cases the first day of adult life consisted of a cohort of 1.0.

In utilizing the formula

$$\sum e^{7-r_m x} l_x m_x = 1,097$$

trial values of r_m were sought which would make the left-hand side of the equation equal to 1,097. It was decided that r_m would be computed to three decimal places in order to reveal the differences occurring in the different treatments. Therefore, two trial r_m's were needed for this computation, one giving a value of slightly less than 1,097 and the next lower r_m (2 decimal places) which would give a higher value than 1,097 in the $e^{7-r_m x} l_x m_x$ column. With these two provisional r_m's (0.20 and 0.21) interpolation yielded the third place figure, or 0.208 in the example below. The following example illustrates this technique in its entirety.

A brief description of how each of the columns is derived should clarify the example below. The first row of figures (adjacent to the figure 13, that is, 13th

day of life, in the age or x column) will be used as an illustration. The number 1.00—l_x column—is the proportion of the initial population still alive at age x (in this case the 13th day). The figure 3.15 (m_x) indicates the mean number of female eggs produced at this age interval. Multiplying the two figures together gives the $l_x m_x$ value, 3.15. A trial r_m must then be selected which is presumed to fit closely the organism when living under the specified conditions. This trial value (for example, $r_m = 0.21$) is multiplied by each of the numbers in the x column to give the figure in the $r_m x$ column (for example $0.21 \times 13 = 2.73$). Each of the figures in the $r_m x$ column is then subtracted from the number 7. The reason for using 7 was discussed above. The figures in the $e^{7-r_m x}$ column are obtained by consulting a table of exponential functions for each of the figures in the $7^{-r_m x}$ column; for example, the exponential function of 4.27 is 71.52. The figure 71.52 ($e^{7-r_m x}$) is multiplied by the figure 3.15 ($l_x m_x$ column) to yield the figure 225.29 ($e^{7-r_m x} l_x m_x$). This figure of 225.29 and each subsequent figure in the $e^{7-r_m x} l_x m_x$ column when compared to the column total is the ratio of the populations' total contribution for the particular age group being examined.

Once the two provisional r_m's have been calculated, as shown in table 1, graphic interpolation yields the accurate r_m. The method of interpolation is illustrated in figure 4.

The vertical axis encompasses the range between the two provisional r_m's. The horizontal axis shows the range of possible values obtained from the $e^{7-r_m x} l_x m_x$ column while striving for the desired value of 1,097. The $e^{7-r_m x} l_x m_x$ values of the two provisional r_m's are plotted on the horizontal axis opposite their respective provisional r_m's. A line connecting the points representing these

two values intersects with the vertical line representing the value (1,097) of the accurate r_m. The point of intersection is the accurate r_m to the third decimal place.

A modified life-fecundity table, as shown in table 1, was constructed for every group of test mites in each experiment. Subsequent calculations were made to determine their intrinsic rates of natural increase (r_m), net reproduction rates (R_o), and mean generation times (T). These ecological parameters, thus calculated, were summarized in tabular form and inserted in the body of the text. Detailed life tables from which these summaries were made are given by Watson (1962).

TABLE 1

A TYPICAL LIFE-FECUNDITY TABLE SHOWING CALCULATIONS
WITH TWO PROVISIONAL r_m's

| x | l_x | m_x | $l_x m_x$ | Provisional r_m's | | | | | | | |
| | | | | 0.21 | | | | 0.20 | | | |
				$r_m x$	$7 - r_m x$	$e^{7 - r_m x}$	$e^{7 - r_m x} l_x m_x$	$r_m x$	$7 - r_m x$	$e^{7 - r_m x}$	$e^{7 - r_m x} l_x m_x$
0-12	....	....	....	....	....	......	....	....	....	.....	....
13	1.00	3.15	3.15	2.73	4.27	71.52	225.29	2.60	4.40	81.45	256.57
14	1.00	3.22	3.22	2.94	4.06	57.97	186.66	2.80	4.20	66.69	214.74
15	1.00	4.49	4.49	3.15	3.85	46.99	210.99	3.00	4.00	54.60	245.15
16	1.00	3.40	3.40	3.36	3.64	38.09	129.51	3.20	3.80	44.70	151.98
17	0.79	3.25	2.57	3.57	3.43	30.88	79.36	3.40	3.60	36.60	94.06
18	0.79	2.04	1.61	3.78	3.22	25.03	40.30	3.60	3.40	29.96	48.24
19	0.79	2.07	1.64	3.99	3.01	20.29	33.28	3.80	3.20	24.53	40.23
20	0.75	2.65	1.99	4.20	2.80	16.45	32.74	4.00	3.00	20.09	39.98
21	0.75	2.64	1.98	4.41	2.59	13.33	26.39	4.20	2.80	16.45	32.57
22	0.75	4.50	3.38	4.62	2.38	10 81	36.54	4.40	2.60	13.46	45.49
23	0.75	2.67	2.00	4.83	2.17	8.76	17.61	4.60	2.40	11.02	22.04
24	0.63	2.50	1.58	5.04	1.96	7.10	11.22	4.80	2.20	9.03	14.27
25	0.63	2.50	1.58	5.25	1.75	5.75	9.09	5.00	2.00	7.39	11.68
26	0.58	1.65	0.96	5.46	1.54	4.66	4.47	5.20	1.80	6.05	5.81
27	0.54	1.91	1.03	5.67	1.33	3.78	3.89	5.40	1.60	4.95	5.10
28	0.46	1.22	0.56	5.88	1.12	3.06	1.71	5.60	1.40	4.06	2.27
29	0.25	0.55	0.14	6.09	0.91	2.48	0.35	5.80	1.20	3.32	0.46
30	0.25	0.59	0.15	6.30	0.70	2.01	0.30	6.00	1.00	2.72	0.41
31	0.21	0.50	0.11	6.51	0.49	1.63	0.18	6.20	0.80	2.23	0.25
32	0.13	0.40	0.05	6.72	0.28	1.32	0.07	6.40	0.60	1.82	0.09
33	0.13	0.67	0.09	6.93	0.07	1.07	0.10	6.60	0.40	1.49	0.13
34	0.13	0.34	0.04	7.14	−0.14	0.87	0.03	6.80	0.20	1.22	0.05
35	0.04	0.17	0.01	7.35	−0.35	0.70	0.01	7.00	0.00	1.00	0.01
36	0.04	0.00	0.00	....	....	.....	....	....	....	.....	......
37	0.00	0.00	0.00	....	....	.....	....	....	....	.....	......
	$R_o = 35.73$ $r_m = 0.208$ $T = 17.19$			Total......... 1,068.8				Total......... 1,231.6			

THE EXPERIMENTS

The experimental results reported in this paper were obtained from five separate tests. Preliminary studies were conducted to determine growth characteristics of the bean plant when grown with different nutritional treatments. Nitrogen- and phosphorus-deficient plants were much smaller, having not only smaller leaves but many fewer leaves per plant. Table 2 describes the appearance of the plants after 12 days of growth in their respective nutrient solutions.

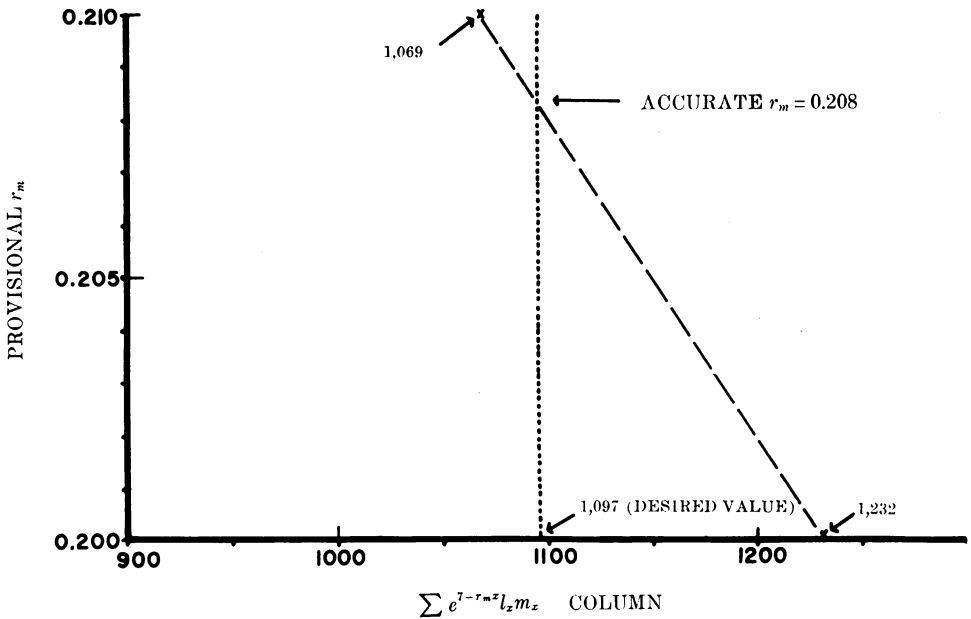Leaf measurements in the prelimi-

Fig. 4. Method of utilizing two provisional r_m's to interpolate the
accurate r_m to three decimal places.

TABLE 2

GROWTH CHARACTERISTICS AND PLANT COLOR OF LIMA BEAN PLANTS
AFTER TWELVE DAYS OF GROWTH IN FOUR TYPES OF NUTRIENT SOLUTIONS

Treatment	Number of plants	Number of trifoliates	Terminal runners	Plant color			
				Normal	Dark green	Pale green	Chlorotic and necrotic tissue
Full nutrient....	15	5	15	14	0	1	0
Low P..........	15	2	1	0	15	0	0
Low N..........	15	1	0	0	0	15	0
Low K..........	15	4	13	0	0	0	15

nary work showed that all trifoliates grew at approximately the same rate with a time interval of 3 to 4 days between production and expansion of leaves. With this information mite development could be synchronized with plant growth for the desired combination.

Experiment 1

In this experiment the mortality and fecundity rates were determined for mites caged on old and young leaves of lima bean plants grown under four types of nutritional treatment—full nutrients, low phosphorus, low nitrogen, and low potassium. There were 15 plants in each treatment, with one plant per jar. Data pertaining to the nutrient solutions are given in table 3.

Host plants used in this experiment were placed in their respective nutrient solutions on February 5, 1961. One week later, the test mites were placed on all plants. Four newly emerged adult females were placed in individual leaf-cages on each plant, two on the primary leaves and one each on opposite leaflets of the youngest expanded trifoliate. Daily fecundity and mortality records were kept for each mite.

Experiment 1 was in progress from

TABLE 3

NUTRIENT SOLUTION SUPPLIED TO LIMA BEAN PLANTS USED IN
EXPERIMENT 1 (FEBRUARY 12 TO MARCH 30, 1961), IN EXPERIMENT 2
(MARCH 11 TO APRIL 27, 1961) AND ON THE OLD PLANTS IN
EXPERIMENT 3 (APRIL 6 TO JUNE 4, 1961)

Date added	Full nutrient		Low phosphorus		Low nitrogen		Low potassium	
	Salt	Milliliter per liter	Salt	Milliliter per liter	Salt	Milliliter per liter	Salt	Milliliter per liter
2-5-61	M/1 MgSO₄	2	M/1 MgSO₄	2	M/1 MgSO₄	2	M/1 MgSO₄	2
	M/1 KH₂PO₄	1	M/1 KNO₃	6	M/20 Ca(H₂PO₄)₂	10	M/20 Ca(H₂PO₄)₂	10
	M/1 KNO₃	5	M/1 Ca(NO₃)₂	4	M/2 K₂SO₄	5	M/1 Ca(NO₃)₂	5
	M/1 Ca(NO₃)₂	5	M/2 Na₂SiO₃	1	M/100 CaSO₄	200	M/2 Na₂SiO₃	1
	M/2 Na₂SiO₃	1	M/1 NaCl	1	M/2 Na₂SiO₃	1	M/1 NaCl	1
	M/1 NaCl	1	A₅	1	M/1 NaCl	1	A₅	1
	A₅	1	Fe	1	A₅	1	Fe	1
	Fe	1			Fe	1		
2-8-61	None		M/10 KH₂PO₄	1.25	M/1 Ca(NO₃)₂	0.5	M/20 K₂SO₄	1.25
2-25-61	M/1 MgSO₄	1	M/1 MgSO₄	1	M/1 MgSO₄	1	M/1 MgSO₄	1
	M/1 KH₂PO₄	1	M/1 KNO₃	6	M/20 Ca(H₂PO₄)₂	10	M/20 Ca(H₂PO₄)₂	10
	M/1 KNO₃	5	M/1 Ca(NO₃)₂	4	M/2 K₂SO₄	5	M/1 Ca(NO₃)₂	5
	M/1 Ca(NO₃)₂	5						
2-27-61	None		None		M/100 CaSO₄	100	None	
					M/1 Ca(NO₃)₂	0.5		
3-2-61	None		None		None		M/20 K₂SO₄	1.25
3-7-61	None		None		M/1 Ca(NO₃)₂	0.5	M/20 K₂SO₄	1.25
					M/100 CaSO₄	100		
3-10-61	None		M/10 KH₂PO₄	0.63	None		None	
3-21-61	M/1 MgSO₄	2	M/1 MgSO₄	2	M/1 MgSO₄	2	M/1 MgSO₄	2
	M/1 KH₂PO₄	1	M/1 Ca(NO₃)₂	4	M/20 Ca(H₂PO₄)₂	10	M/20 Ca(H₂PO₄)₂	10
	M/1 KNO₃	5	M/1 KNO₃	6	M/2 K₂SO₄	5	M/1 Ca(NO₃)₂	5
	M/1 Ca(NO₃)₂	5			M/100 CaSO₄	100		
4-4-61	M/1 KH₂PO₄	1						
	M/1 KNO₃	5						
	M/1 Ca(NO₃)₂	5	Terminated		Terminated		Terminated	
	M/1 MgSO₄	2						
	M/2 Na₂SiO₃	1						
	M/1 NaCl	1						
	A₅	1						
	Fe	1						

February 12 until the last female died on March 30, 1961. Since test plants utilized in Experiment 1 were also to be used in Experiment 2, it was decided that low amounts of the deficient salts should be placed in their respective solutions. This was necessary to maintain the deficient plants in a satisfactory condition for completing both experiments. Additions of other salts were made often enough to prevent those elements from becoming deficient. The results of Experiment 1 are illustrated by pictorial life tables in figures 5 and 6.

Experiment 2

In this experiment the mortality and fecundity were determined for mites caged on old and young leaves of the host plants utilized in Experiment 1. The objectives of inoculating these plants with a new group of test mites
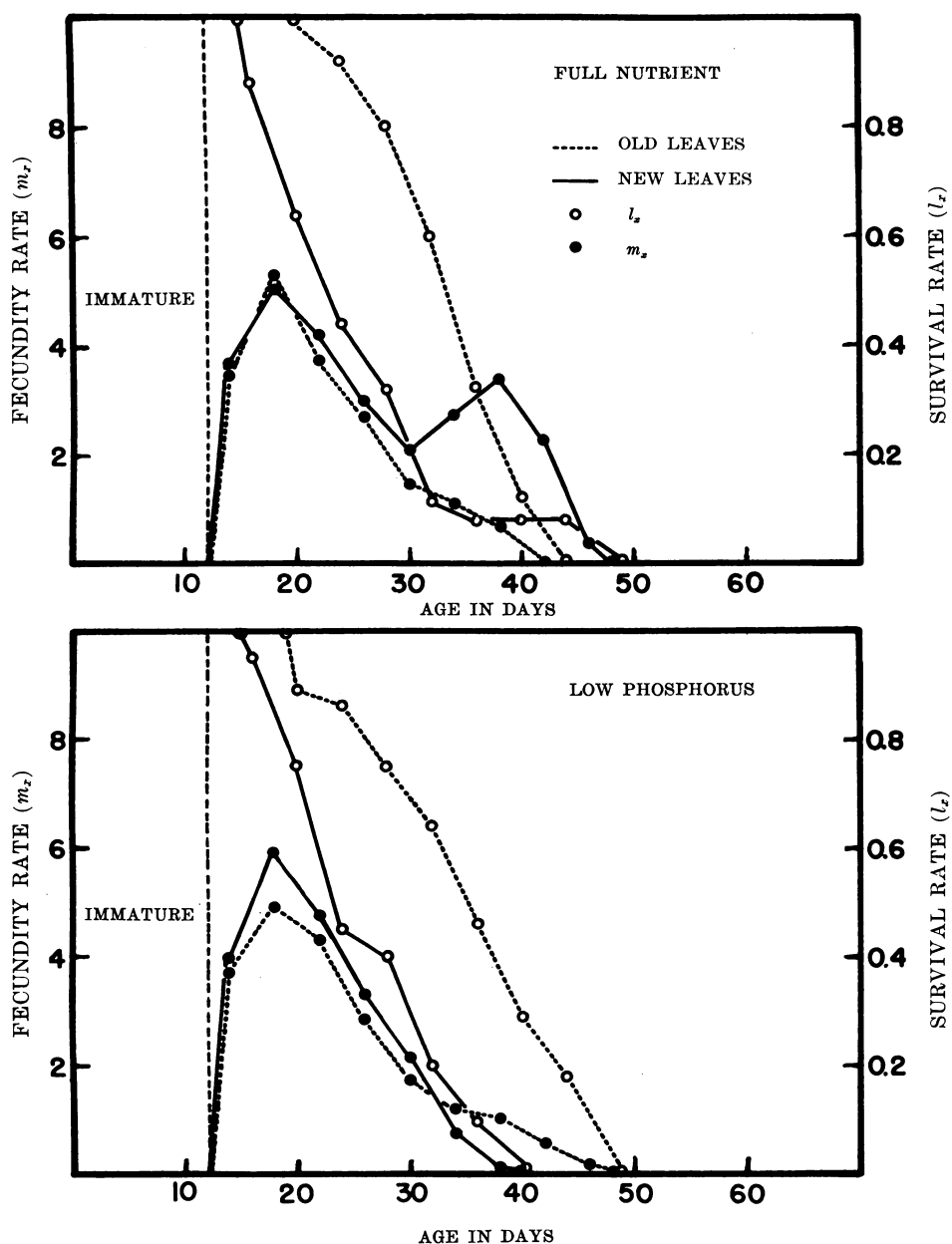
Fig. 5. Experiment 1. Longevity and age-specific fecundity of adult *Tetranychus telarius* females on old and young leaves of lima beans. Upper: Full-nutrient solution. Lower: Low-phosphorus solution.

were (1) to continue the study of host plant nutrition as it affected the mites and (2) to determine the effects of plant age upon the reproducing females. Newly emerged females were placed on the plants on March 11 in the same manner as described in Experiment 1.

Because the primary leaves began dropping from the deficient plants, females from these leaves had to be transferred to the oldest trifoliate leaves to complete the experiment. Fruit for-
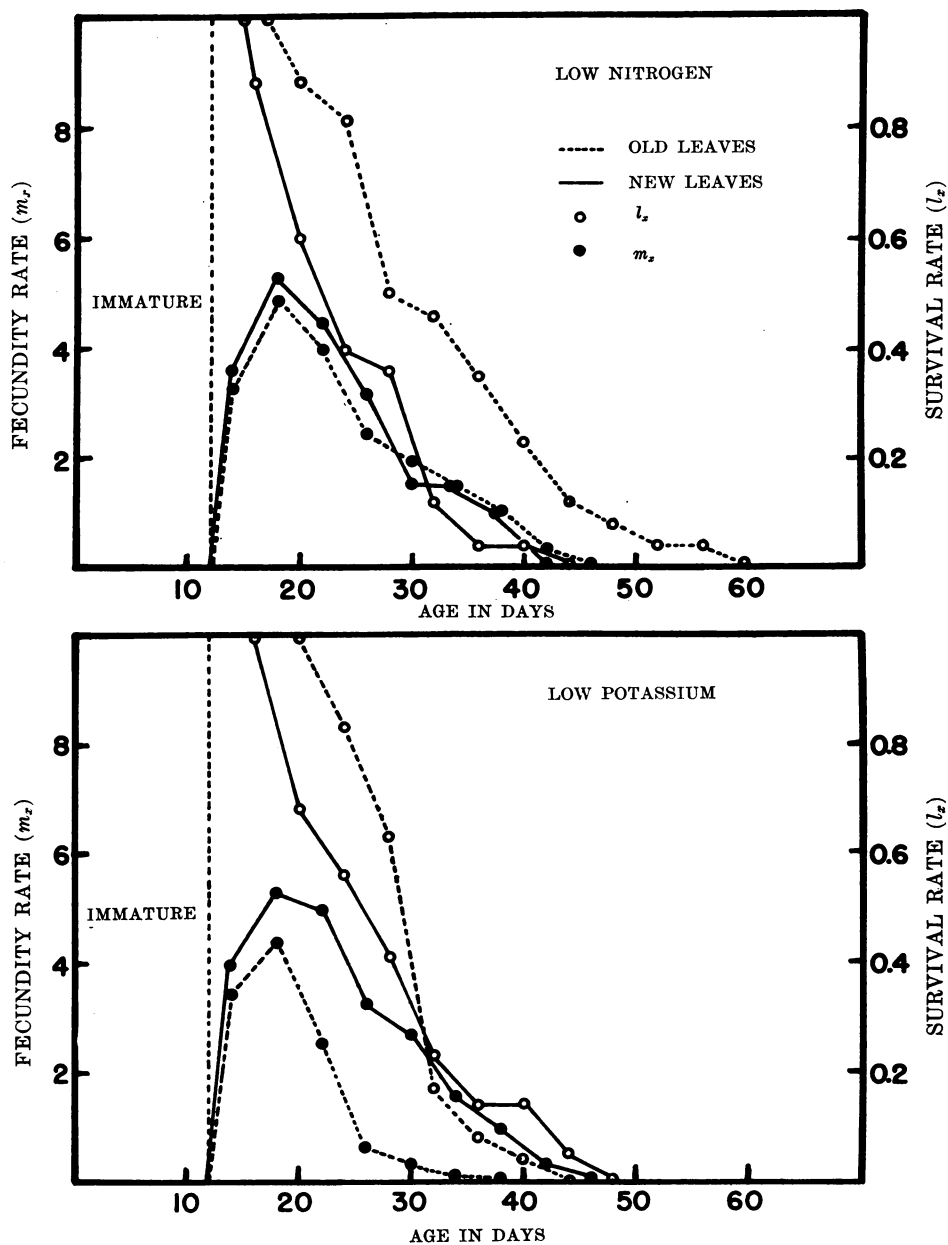
Fig. 6. Experiment 1. Longevity and age-specific fecundity of adult *Tetranychus telarius* females on old and young leaves of lima beans. Upper: Low-nitrogen solution. Lower: Low-potassium solution.

mation was occurring throughout the course of this experiment, which was completed on April 27.

As can be seen from the above dates, there was an overlap between the two experiments. Salt additions made during the course of Experiment 2 are given in table 3. The results of Experiment 2 are illustrated by pictorial life tables in figures 7 and 8.
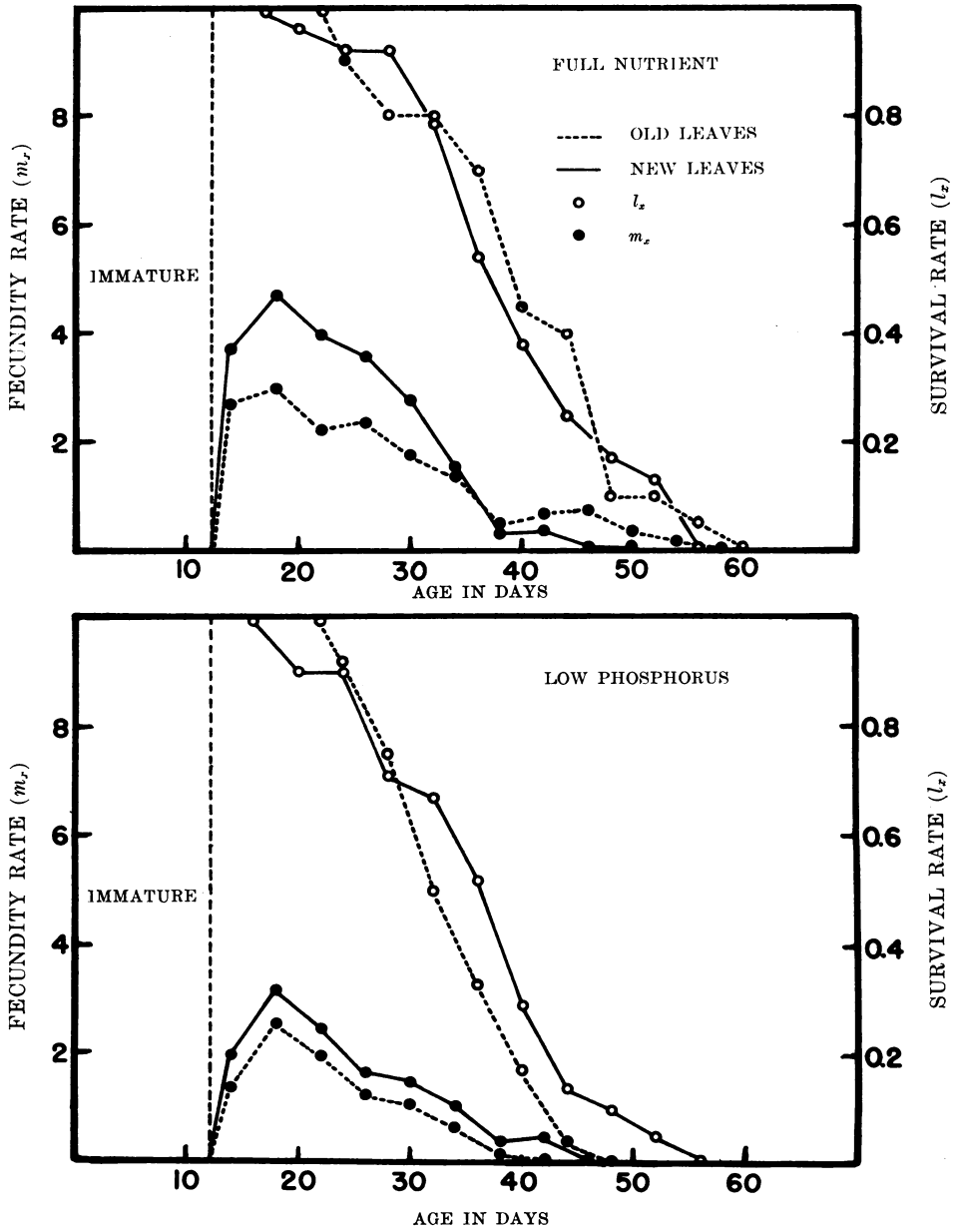
Fig. 7. Experiment 2. Longevity and age-specific fecundity of adult *Tetranychus telarius* females on old and young leaves of lima beans. Upper: Full-nutrient solutions. Lower: Low-phosphorus solution.

Experiment 3

This experiment was designed to confirm the indication from Experiment 2 that the plant age did affect the ability of a mite population to increase. Only plants receiving a full-nutrient supply were used. The old plants receiving full nutrients which were utilized in Experiments 1 and 2 comprised one-half of the experiment. At this time, maturation of the bean pods was occurring and production of new growth had ceased.
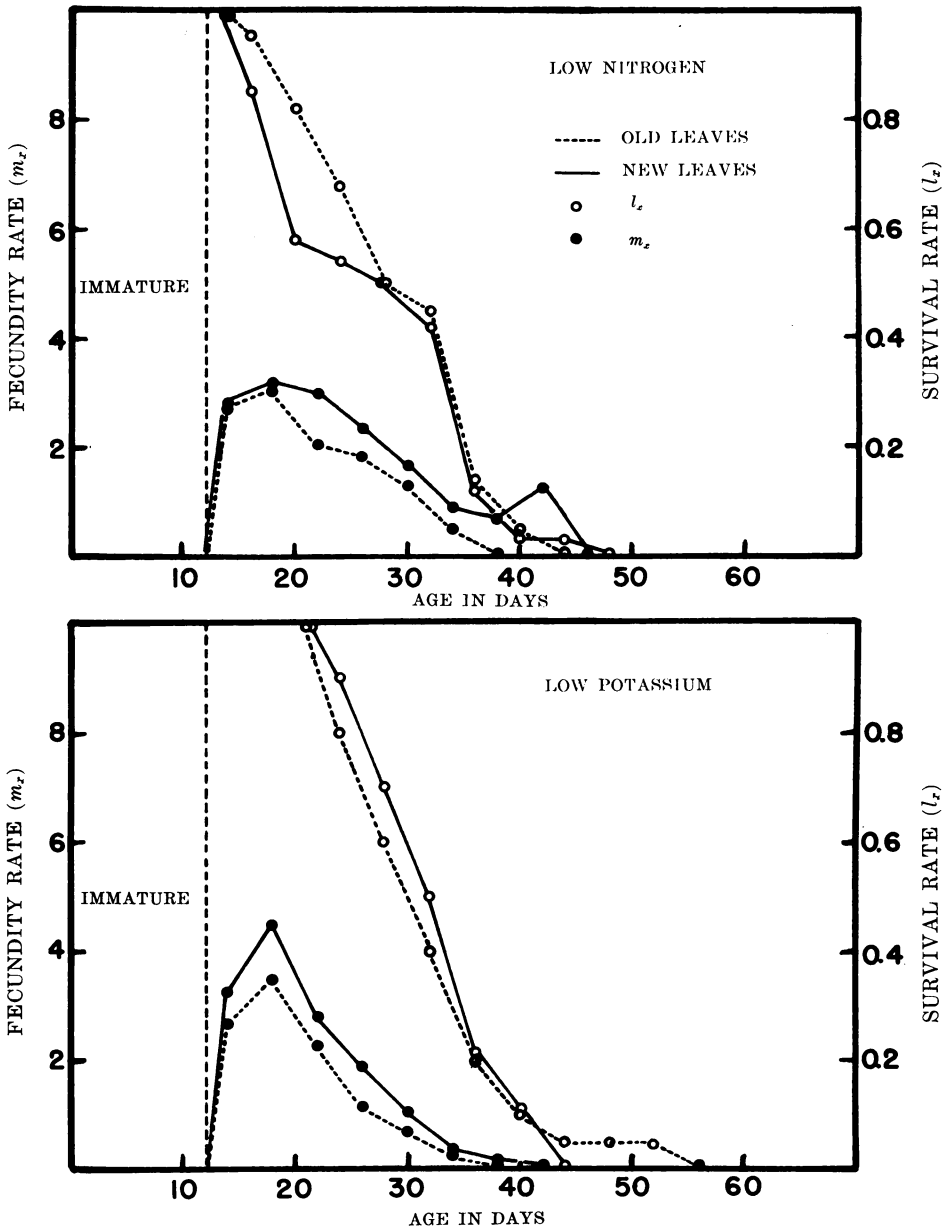
Fig. 8. Experiment 2. Longevity and age-specific fecundity of adult *Tetranychus telarius* females on old and young leaves of lima beans. Upper: Low-nitrogen solution. Lower: Low-potassium solution.

However, toward the latter part of the experiment, a new flush of growth appeared. Newly emerged plants similar to those used in the initial experiment were used for the other half of the experiment. Solutions were identical to those utilized in the full-nutrient treat-ment in Experiment 1, table 3. Both groups of plants were treated identically. Mite inoculation occurred on April 6. The experiment was terminated on June 4 because mite populations outside the cages on the old plants had reached densities sufficient to create ad-

ditional problems. However, the major contribution of the test mites had been achieved before the "wild" population had reached such densities. The life tables constructed from data obtained in this experiment show only 4 weeks of oviposition, but this period was sufficient to calculate the intrinsic rate of increase. These findings are illustrated by the pictorial life table in figure 9.
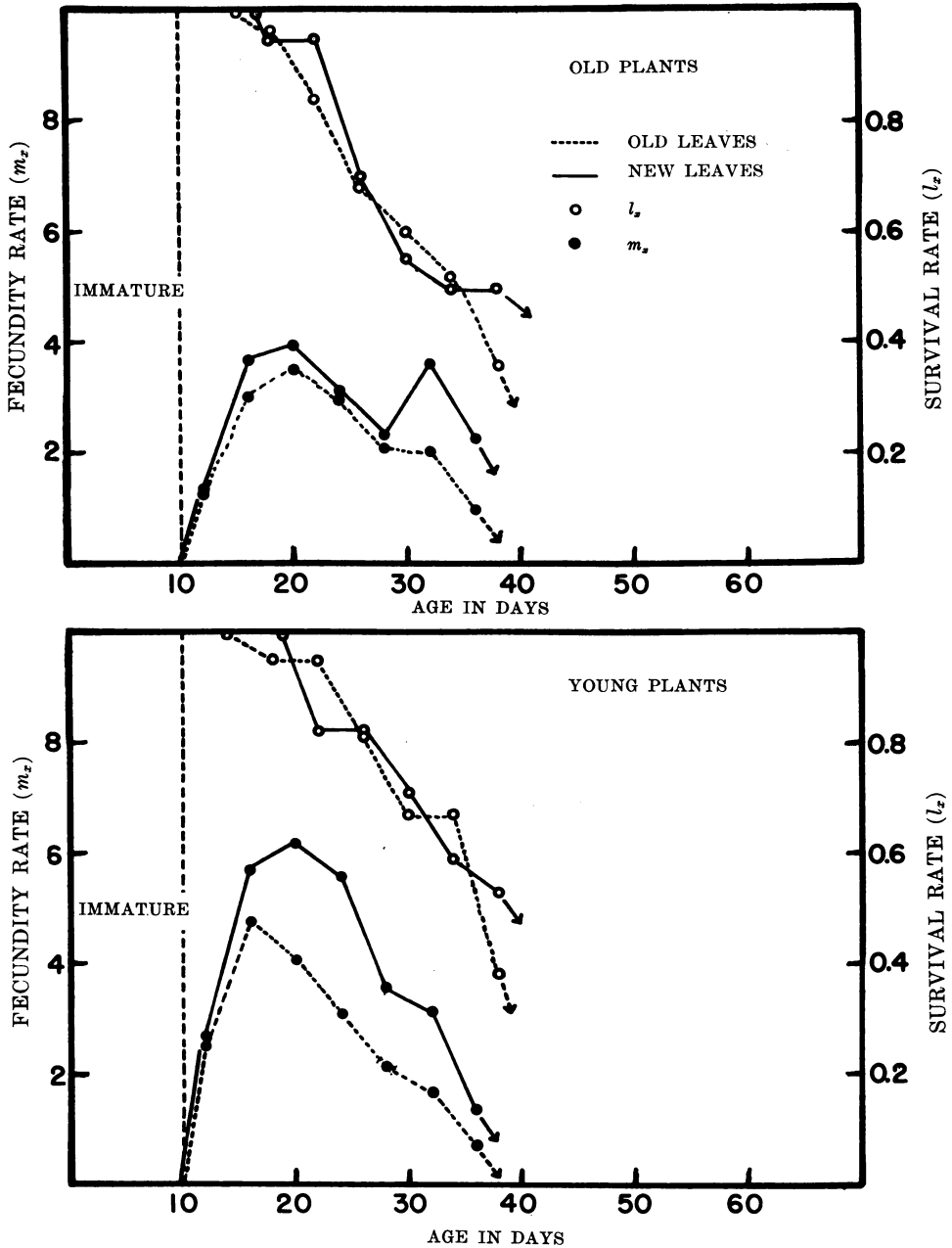
Fig. 9. Experiment 3. Longevity and age-specific fecundity of adult *Tetranychus telarius* females on old and young leaves of lima beans grown in full-nutrient solutions. Upper: Old plants. Lower: Young plants.

Experiment 4

In this experiment the plant nutrient solutions were modified by completely deleting the elements N, P, and K in their respective treatments. The experiment also differed from the previous tests in that the females were placed on the host plants only one day after the plants had been placed in the solutions. As a result, the peak period of egg laying had already been achieved before the plants began showing deficiency symptoms. The test extended from May 16 to June 19. Nutrient solutions supplied to plants in this experiment are given in table 4. Results of this test are illustrated by pictorial life tables in figures 10 and 11.

Experiment 5

This test was essentially a duplication of Experiment 4 with one major exception. Here, the experimental mites were reared from eggs on their respective treatments. When adult females emerged, they were caged individually and placed back on the same plants that had harbored them during their immature stages. By this time, plant nutrient deficiencies were quite evident. The plants were in their respective nutrient solutions on June 26 and adult females were caged July 9. The last females died August 28. In order to conduct such an experiment, substitute host plants were needed since deficient plants were suitable for mite feeding for only approximately 4 weeks. Substitute plants were preconditioned for 10 days in the same types of nutrient solutions as supplied for the test plants. These were then transferred to the original solution jars to replace the older plants. The solutions were discarded and new solutions, identical to those at the start of the test, were utilized.

The results of Experiment 5 are illustrated by pictorial life tables in figures 12 and 13.

Temperature and relative humidity data as well as initiation and termination dates for all experiments are presented in table 5. The temperature and relative humidity data were obtained from hygrothermograph charts. The hygrothermograph was placed at the center of the greenhouse table and sheltered from the direct rays of the sun by an aluminum shade-screen. Periodic laboratory calibration of the hygrothermograph assured the reliability of the readings. As indicated in table 5, the average temperature and humidity conditions varied little from test to test.

TABLE 4

NUTRIENT SOLUTIONS SUPPLIED TO LIMA BEAN PLANTS USED IN
EXPERIMENT 4 (MAY 16 TO JUNE 19, 1961)

Treatments							
Full nutrient		Lacking phosphorus		Lacking nitrogen		Lacking potassium	
Salt	Milliliter per liter	Salt	Milliliter per liter	Salt	Milliliter per liter	Salt	Milliliter per liter
M/1 KH₂PO₄	1	M/1 Ca(NO₃)₂	4	M/2 K₂SO₄	5	M/1 Ca(NO₃)₂	5
M/1 KNO₃	5	M/1 KNO₃	6	M/1 MgSO₄	2	M/1 MgSO₄	2
M/1 Ca(NO₃)₂	5	M/1 MgSO₄	2	M/20 Ca(H₂PO₄)₂	10	M/20 Ca(H₂PO₄)₂	10
M/1 MgSO₄	2	M/2 Na₂SiO₃	1	M/100 CaSO₄	100	M/2 Na₂SiO₃	1
M/2 Na₂SiO₃	1	M/1 NaCl	1	M/2 Na₂SiO₃	1	M/1 NaCl	1
M/1 NaCl	1	A₅	1	M/1 NaCl	1	A₅	1
A₅	1	Fe	1	A₅	1	Fe	1
Fe	1			Fe	1		

PLANTS NOT PRECONDITIONED

Fig. 10. Experiment 4. Longevity and age-specific fecundity of adult *Tetranychus telarius* females on old and young leaves of lima beans. Upper: Full-nutrient solutions. Lower: Solutions lacking phosphorus.

PLANTS NOT PRECONDITIONED

Fig. 11. Experiment 4. Longevity and age-specific fecundity of adult *Tetranychus telarius* females on old and young leaves of lima beans. Upper: Solutions lacking nitrogen. Lower: Solutions lacking potassium.

Fig. 12. Experiment 5. Longevity and age-specific fecundity of adult *Tetranychus telarius* females on old and young leaves of lima beans. Upper: Full-nutrient solutions. Lower: Solutions lacking phosphorus.
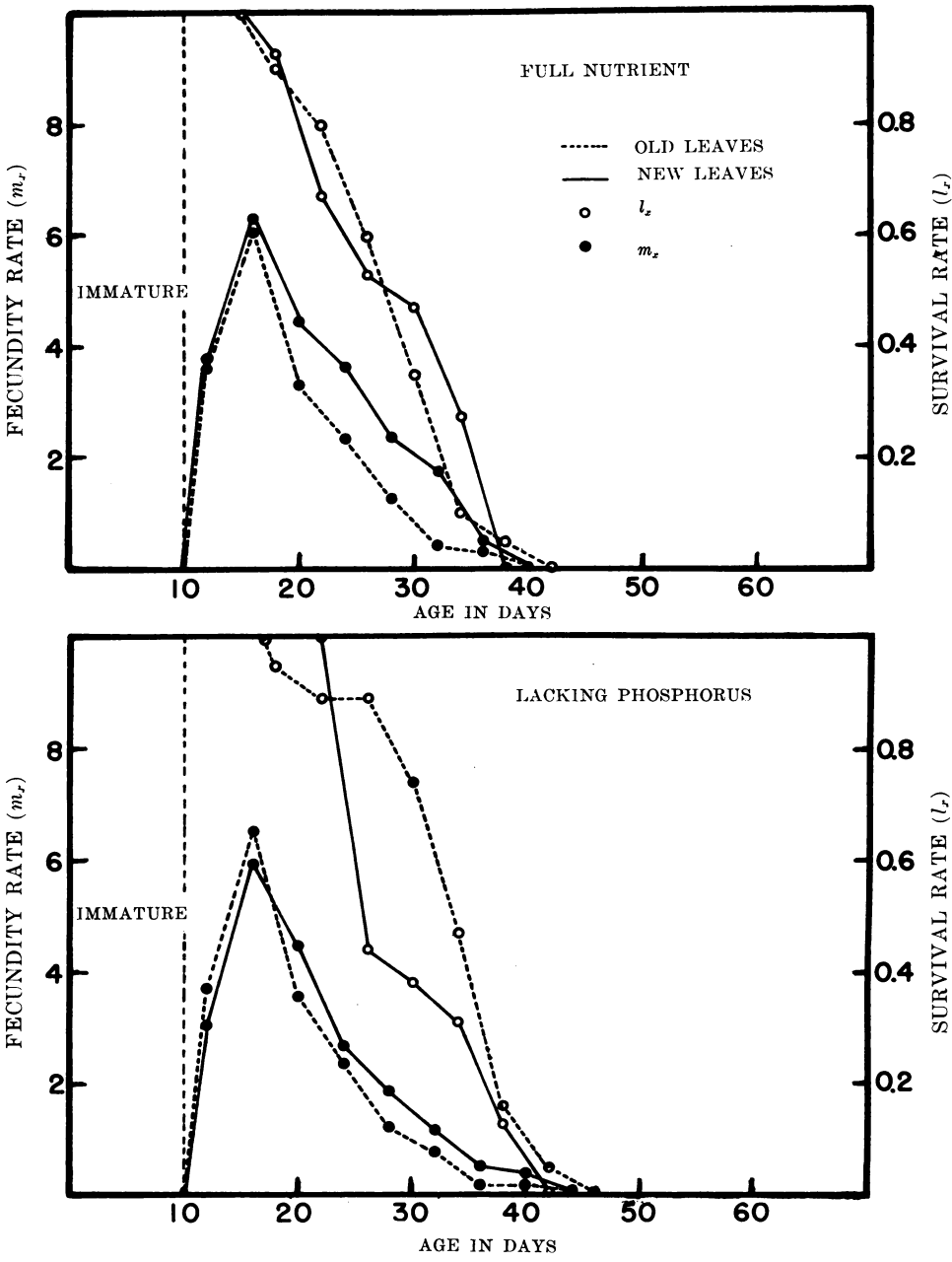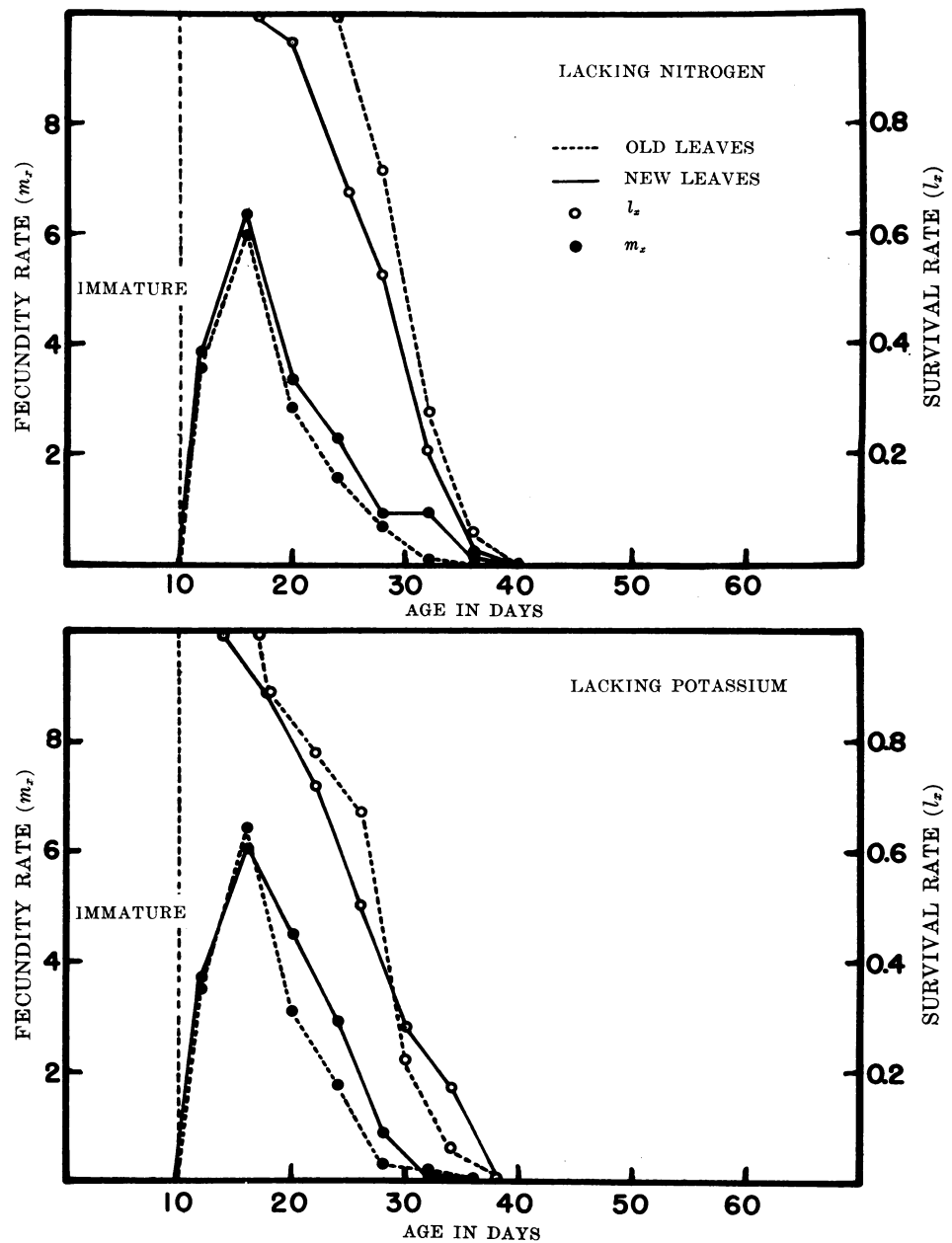
Fig. 13. Experiment 5. Longevity and age-specific fecundity of adult *Tetranychus telarius* females on old and young leaves of lima beans. Upper: Solutions lacking nitrogen. Lower: Solutions lacking potassium.
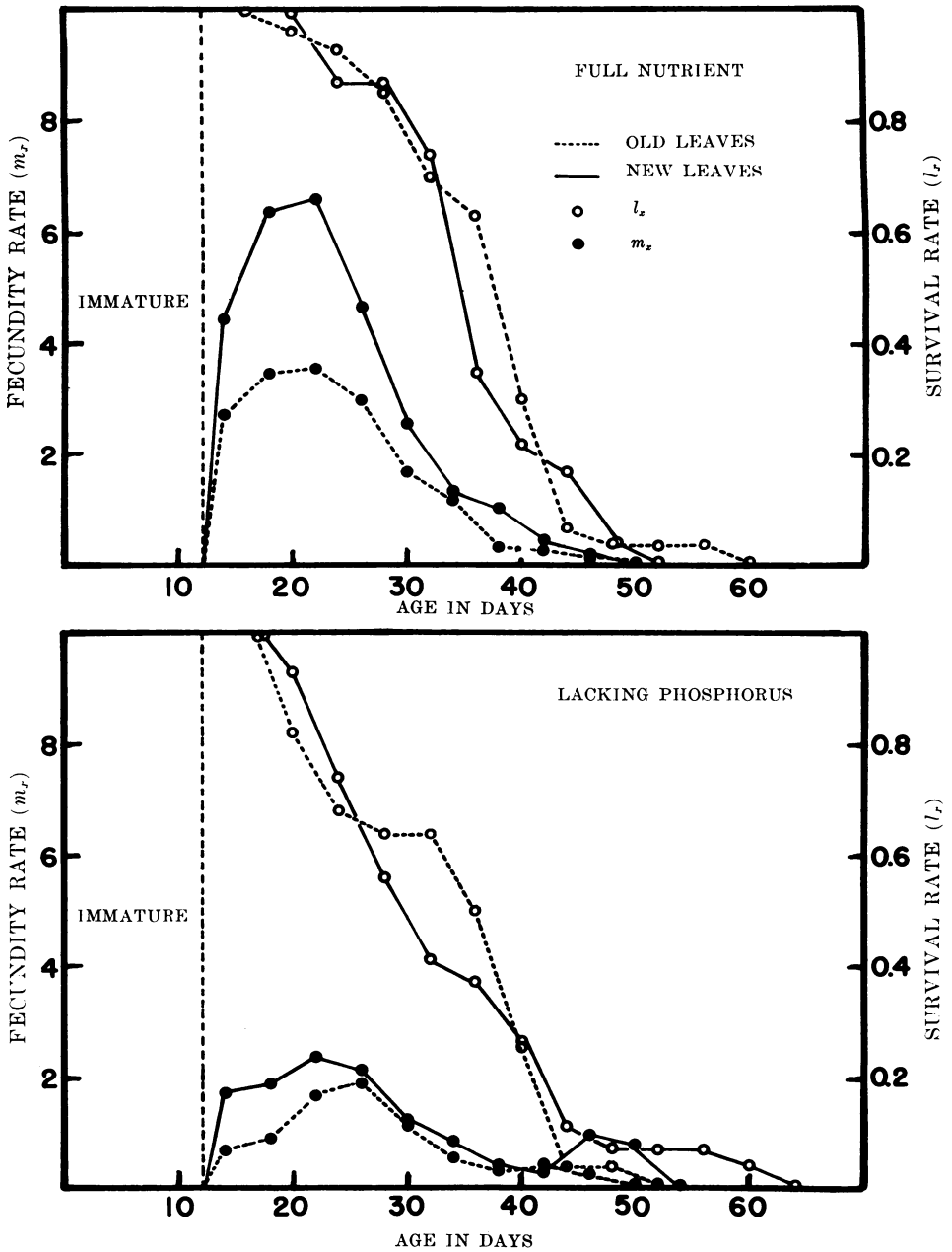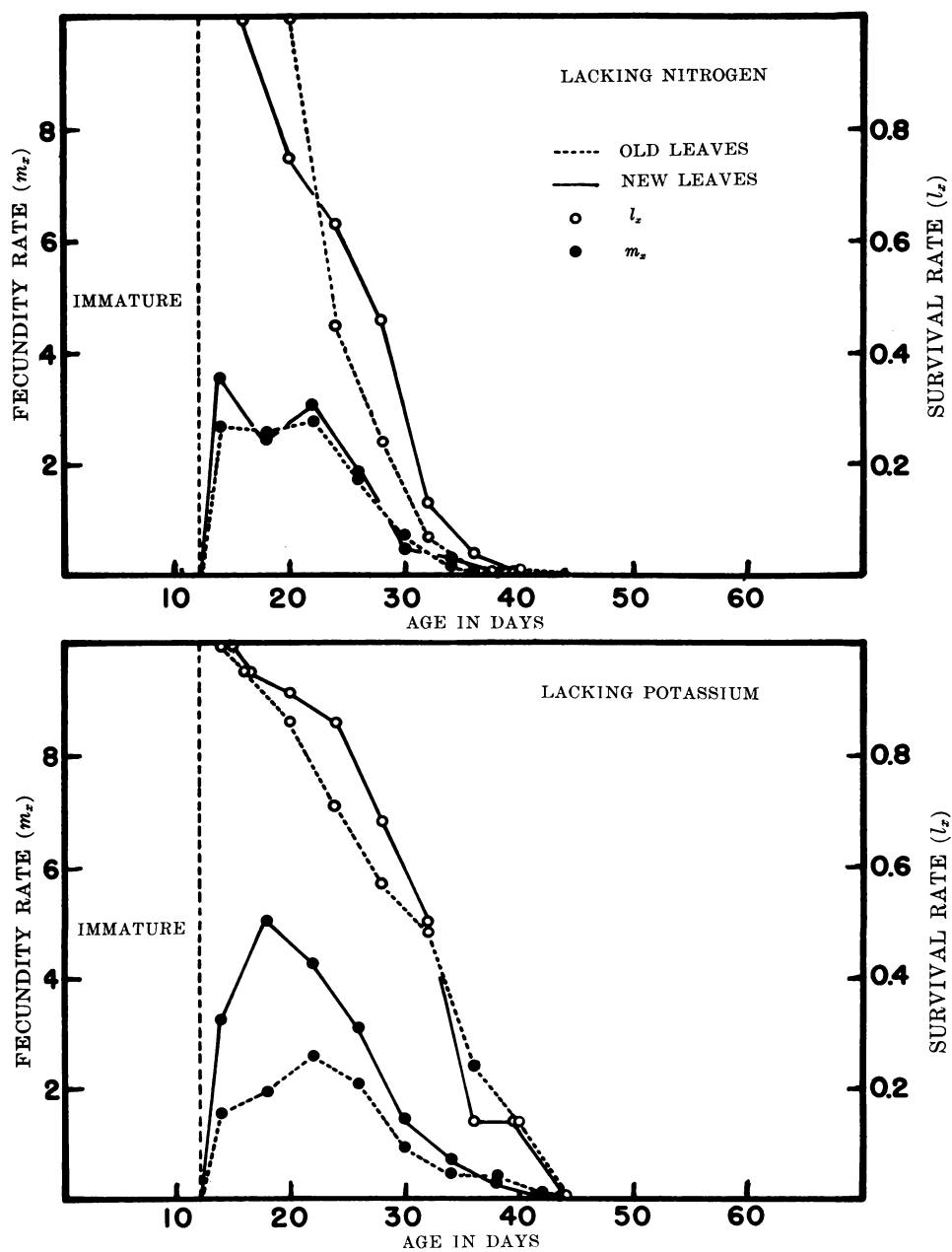
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TABLE 5

TEMPERATURE AND RELATIVE HUMIDITY ON GREENHOUSE BENCH
DURING COURSE OF EXPERIMENTS

</div>

Experiment	Time period	Temperature			Relative humidity		
		Mean maximum	Mean minimum	Mean mean	Mean maximum	Mean minimum	Mean mean
		degrees F	*degrees F*	*degrees F*	*per cent*	*per cent*	*per cent*
1	February 12 to March 30	82.7	71.2	76.95	58	42	50
2	March 11 to April 27	84.8	70.1	77.45	62	44	53
3	April 6 to May 4	85.4	68.5	76.95	61	43	52
4	May 16 to June 19	85.2	68.6	76.90	65	43	54
5	July 9 to August 28	87.8	67.1	77.45	65	36	51

RESULTS AND DISCUSSION

INFLUENCE OF LEAF AGE

Although the primary concern of these investigations was to study the effects of host-plant nutrition upon two-spotted spider-mite populations, the influence of leaf age was also studied. The findings demonstrated that leaf age did exert an influence on the capacity of the mite population to increase.

Effect on Longevity

To determine why population growth was enhanced when mites fed on young leaves, longevity of mites living on both young and old foliage was compared. Two arbitrary levels of survival were selected for analysis—the 75 per cent and 50 per cent levels—and the number of days required for each mite population to decrease to these two levels was ascertained.

Because leaf-age effects differ with each nutritional treatment, the treatments will be considered separately. Experiment 1 will not be considered in this discussion because an unexplained heavy early mortality occurred on the young leaves. A disease hypothesis to explain the results seems rather doubt-

ful since the mortality occurred only in the young leaf treatments of the first experiment. The fact that all mites in the experiment were obtained from a common source would also tend to rule out disease. A more plausible explanation would be that some type of incompatibility, unique to this experiment, existed between the mites and the substrata upon which they fed.

Experiment 4 must also be eliminated from this discussion since all test mites were confined to the primary leaves for the first 9 days of the experiment. Shortly after the females originally designated to feed on the young leaves were transferred to that site, their mortality rate greatly accelerated. This may have been caused by the sudden change from primary to trifoliate leaves.

The times required for populations to decline to the 75 per cent and 50 per cent survival levels in the experiments used for this comparison are shown in table 6. The age of foliage in the full-nutrient treatment and in the phosphorus-deficient treatment had very little effect upon longevity of the mites. Old and young leaves both favored survival at different times.

The mites on the nitrogen-deficient plants were affected by leaf age. In Experiments 2 and 5, survival was greater on the old foliage than on the young foliage at the 75 per cent survival level. However, in Experiment 5 survival was greater on the young foliage at the 50 per cent level. This suggests that some type of conditioning is necessary before young leaves are favorable for survival of *Tetranychus telarius*.

In both Experiments 2 and 5, where extreme potassium deficiencies existed, survival was greatest on the young foliage at both the 75 and 50 per cent levels. Mites on the young leaves required 3 days longer to reach the 75 per cent level and 2½ days longer to reach the 50 per cent level. Since the old leaves suffer from potassium deficiency first (Arnon and Hoagland, 1943), this would indicate that either potassium enhances survival directly or that the microenvironmental conditions created by the presence of potassium were more favorable for survival.

Effect on Fecundity

Regardless of the nutritional treatment, leaf age had a profound effect upon egg production. This was in contrast to the erratic effects that leaf age has on longevity. Figures 5 through 13 show that age-specific fecundities are

definitely favored when mites are located on the young leaves.

In the full-nutrient treatments, mites on the young foliage normally produced more eggs per day than those on the old. Exceptions to this did occur, but only once did the reversal take place early in the reproductive cycle. Figure 5 (full-nutrient treatment) shows that during the period of maximum age-specific fecundity, mites on the old foliage exhibited an m_x (fecundity rate) of 5.27 compared to 5.18 for those on the young. As can be seen from the m_x curves of this figure, differences were small at any time during the first two weeks of oviposition, and it is probable that normal variation accounted for the reversal noted above. A reversal of the two m_x curves also occurred in Experiment 2 (figure 7) in the latter phase of the experiment. No significance can be attributed to this since the numbers involved in each population were low and daily egg production had decreased to such a low level that small changes effected considerable differences in daily averages. The bimodal m_x curve shown in figure 9 (old plants), Experiment 3, presents an interesting demonstration of leaf-age effect. The production of new foliage had ceased on this group of plants with the maturation of a bean crop. Consequently, leaf differences—

TABLE 6

DAYS REQUIRED FOR POPULATIONS OF ADULT *TETRANYCHUS TELARIUS* FEMALES TO REACH 75 PER CENT AND 50 PER CENT SURVIVAL LEVELS ON BOTH OLD AND YOUNG FOLIAGE IN EXPERIMENTS 2, 3 AND 5

Experiment	Treatment	Days to reach 75 per cent survival level		Days to reach 50 per cent survival level	
		Old foliage	Young foliage	Old foliage	Young foliage
2	Complete	23	21	27	25
	Low P	16	15	20	24
	Low N	9	5	16	16
	Low K	13	11	18	20
3	Complete (old plants)	13	11	24	24
	Complete (young plants)	17	18	26	27
5	Complete	19	20	26	23
	− P	9	12	24	16
	− N	10	8	12	15
	− K	10	15	17	20

old and young—were not so great as in other tests. This resulted in m_x curves that followed parallel courses. However, after 18 days and the maturation of the bean crop, a new flush of growth appeared. Mites on the younger leaves were subsequently transferred to this new growth. The resultant effect was a sharp rise in age-specific fecundities of this group of mites. Simultaneously, the age-specific fecundities of mites on the old leaves continued in a steady decline. This is a clear demonstration that young leaves increase fecundity. When test mites were caged on their hosts soon after the young plants had been placed in nutrient solutions, the separation of the m_x curves came about slowly as shown in figures 5 and 10 (full nutrients). But, with older plants, the initial separation occurred early and increased to a greater degree than on the young plants. This can be seen in figures 7 and 12 (full nutrients). There were considerably lower maximum fecundities with females on the old leaves of the older plants.

The age-specific fecundity curves were higher, in most cases, on the young foliage in all the other nutritional treatments. Again, during the latter phase of several tests, as shown in figures 5 (low phosphorus), 6 (low nitrogen), 11 (low potassium), 12 (low phosphorus), and 13 (low nitrogen and low potassium), the m_x curves reversed. This, too, is considered to be a chance effect because of the low numbers of mites still ovipositing. Those deviations which should be of concern are the reversals that occurred early in the reproductive period. This happened in the phosphorus and potassium treatments of Experiment 4—figures 10 (low phosphorus) and 11 (low potassium), respectively. A relatively simple explanation for these two small deviations can be given. As stated earlier, the test mites were caged on the primary leaves at the initiation of this experiment—before trifoliates were produced. Those mites originally assigned to the old leaves had

slightly greater age-specific fecundity rates. As soon as trifoliates appeared, the mites designated to feed on young leaves were transferred to the new trifoliates and at no subsequent time did age-specific fecundity rates fall below those on the old leaves.

Another exception where young foliage was not superior occurred in the nitrogen treatment of Experiment 5 (figure 13—low nitrogen). Initially, the young foliage gave higher age-specific fecundity rates. But, from the fifth day on, the fecundity rate of females on young foliage occasionally dropped below that on the old leaves. Thus, with the alternating positions of the two m_x curves, no significant differences could be shown. No explanation is offered for the bimodal peaks in this treatment.

Figures 5 to 13 reveal that age-specific fecundities changed over a period of time in a somewhat characteristic manner depending upon the nutritional treatments. In the full-nutrient treatments (figures 7 and 12), differences in the m_x values can be noted rather early in the reproductive period with a gradual separation occurring. Generally, the greatest separation occurs at approximately the time when maximum age-specific fecundity is reached. A gradual closing of the two curves takes place near the termination of oviposition. This is true to varying degrees in all of the full-nutrient treatments except in Experiments 1 and 4. As noted earlier, some separations occurred late in the reproductive period and reasons for this have been discussed.

The difference between the m_x curves in the phosphorus-deficient series seemed to be relatively constant with no great separation occurring between the two at any time. However, in Experiment 5, where severe stresses were placed on both plants and mites, a wide initial separation occurred. The maximum age-specific fecundity for the mites on young leaves was reached much earlier than for those on the old. The m_x curve, figure 12 (low phosphorus), for

the young foliage was on the decline before that for the old had reached its maximum. A wide separation persisted between the two for approximately 14 days.

The m_x curves in the nitrogen-deficient series followed a more parallel and closer pattern than any of the others. The gradual increase and decline along with the same peak period indicated that mites were responding quite similarly to both leaf ages regardless of time. Again, an exception must be pointed out. In Experiment 5, figure 13 (low nitrogen), the m_x curve of mites on young leaves was bimodal. This was true also for the m_x curve from the old leaves but not to the extent of that on young foliage. This gave a somewhat wider separation of the two curves early in the reproductive period.

The potassium-deficient treatments present the most interesting aspect of leaf-age effect with time. In Experiment 1, figure 6 (low potassium), the m_x curves began a gradual separation which continued until the end of the test. This is believed to be directly related to host-plant nutrition as it affected the leaves at the different ages. Figure 8 (low potassium), Experiment 2, again shows the initial separation which reached its maximum during the period of maximum age-specific fecundity. After that, the two curves traveled a parallel course until the end of the test. This was probably due to the shortage of potassium in all the leaves at this time regardless of leaf age. Figure 11 (low potassium) shows that very little difference occurred between the m_x curves of old and young foliage until after the maximum age-specific fecundity rates had been achieved. This was expected since all test mites were on the primary leaves until this time. When mites were transferred to the young leaves, a separation in the curves began and continued until oviposition ceased. In figure 13, Experiment 5 (low potassium) showed the greatest effect of time on the difference between leaf-age ef-

fects. The m_x curve from old foliage shows a comparatively slow rise to its peak, followed by a leveling off and then a gradual decline. However, the m_x curve from young foliage rises sharply to its maximum, followed by a faster rate of fall until its approximates the m_x curve from older foliage near the end of the test.

Another important aspect of leaf-age effect is the higher daily fecundity of mites on young leaves. Probably the most striking feature in such comparisons is the maximum age-specific fecundity that each group of mites achieved. Table 7 shows the maximum age-specific fecundity for each group of mites in all experiments except Experiment 4, which was omitted because data were obtained when all mites were still on the primary leaves. Table 7 shows that young leaves favored maximum age-specific fecundities in all cases.

After trifoliates were produced in Experiment 4, the mites originally designated to feed on the young leaves were placed on the new growth. Maximum age-specific fecundities attained after this transfer showed that young foliage was superior in all treatments.

That leaf age does affect fecundity can best be demonstrated by a comparison of the total average number of eggs produced per female on both young and old foliage where nutritional factors should play no part—on those plants receiving full nutrient solutions. The combined results of the five separate tests with full nutrients show that an average of 116 eggs per female was produced on old foliage compared to 160 on young foliage.

A comparison of total fecundities of females on old and young leaves is graphically depicted in figures 14 through 18 which show the frequency distribution of fecundities. An examination of the full-nutrient treatment of each test shows that a higher percentage of the population on young leaves produced at the high production end of the scale. This is not entirely true

<div align="center">TABLE 7</div>

MAXIMUM AGE-SPECIFIC FECUNDITIES OF MITE POPULATIONS ON LIMA BEAN PLANTS RECEIVING DIFFERENT NUTRITIONAL TREATMENTS

Experiment	Treatment	Maximum age-specific fecundities	
		Old foliage	Young foliage
1	Full nutrient........	6.28	6.37
	Low phosphorus....	5.75	7.43
	Low nitrogen	6.25	6.26
	Low potassium...	5.27	6.54
2	Full nutrient....	3.57	5.09
	Low phosphorus....	2.72	3.36
	Low nitrogen....	3.67	3.90
	Low potassium...	4.23	4.67
3	Full nutrient—old plants...	5.06	6.16
	Full nutrient—young plants.	6.12	9.16
5	Full nutrient....	4.72	8.29
	Lacking phosphorus...	2.58	3.32
	Lacking nitrogen.	3.80	4.50
	Lacking potassium.	3.28	6.62

Fig. 14. Experiment 1. Frequency distribution of fecundities of *Tetranychus telarius* individuals on old and young leaves of lima bean plants grown in four types of nutrient solutions.
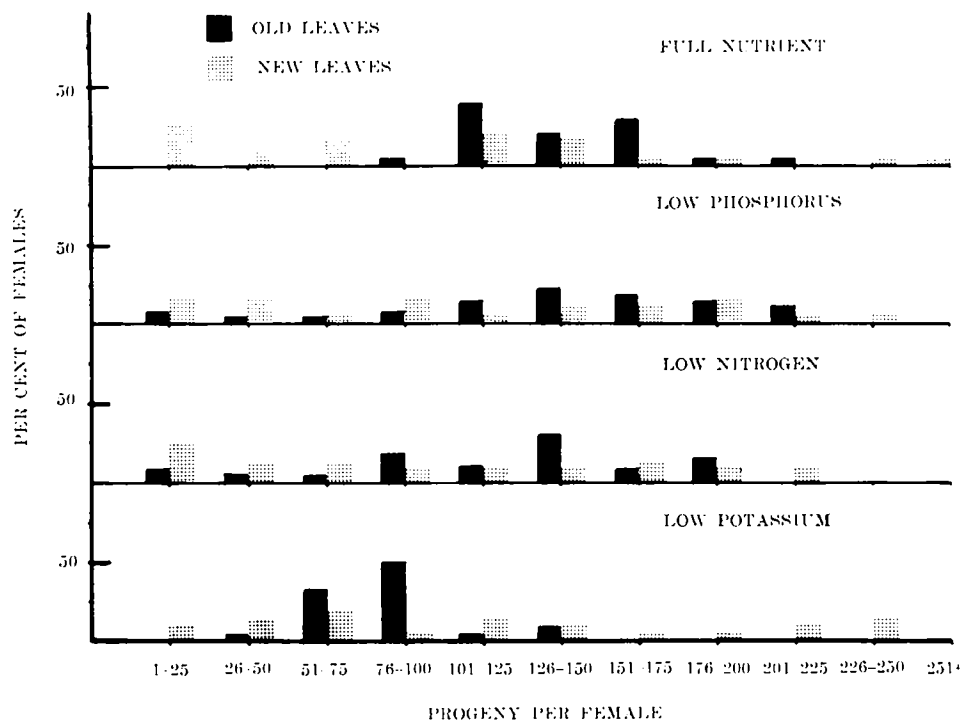
Fig. 15. Experiment 2. Frequency distribution of fecundities of *Tetranychus telarius* individuals on old and young leaves of lima bean plants grown in four types of nutrient solutions.

Fig. 16. Experiment 3. Frequency distribution of fecundities of *Tetranychus telarius* individuals on old and young leaves of lima bean plants grown in full-nutrient solutions.

Fig. 17. Experiment 4. Frequency distribution of fecundities of *Tetranychus telarius* individuals on old and young leaves of lima bean plants grown in four types of nutrient solutions.
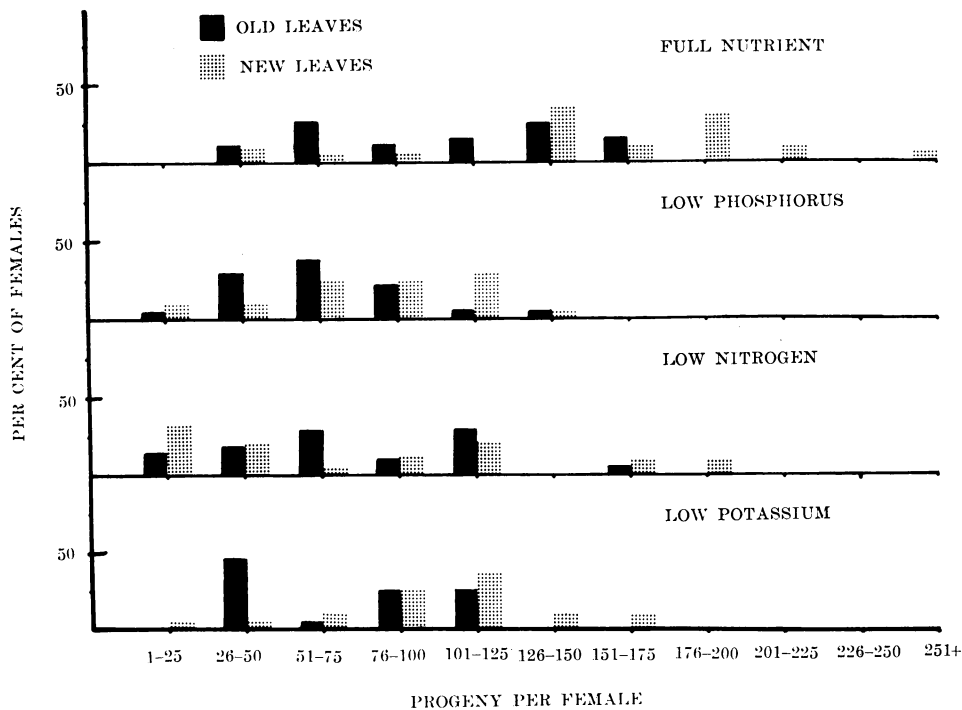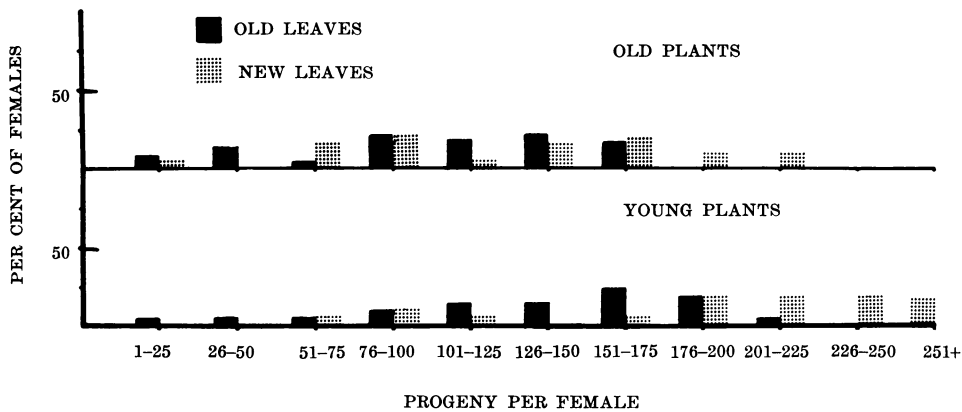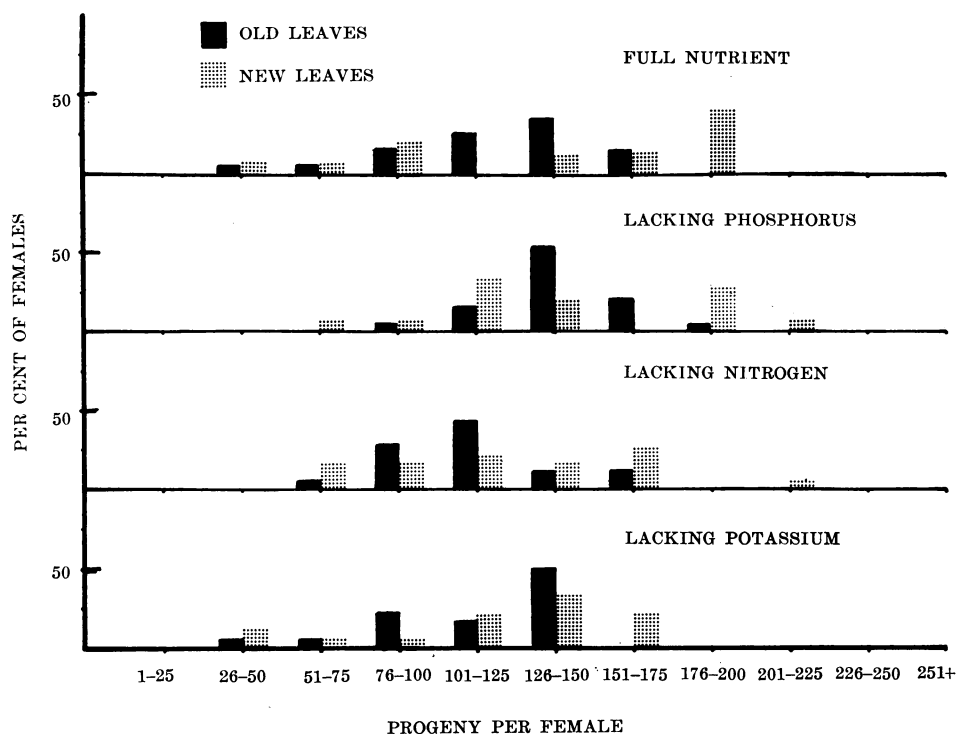
in Experiment 1 but individual females producing the maximum number of eggs were located on the young leaves.

The effect of leaf age also varies considerably according to the degree of mineral deficiency that the mites encounter in the particular test plants. A comparison of Experiments 1 and 2 (figures 14 and 15) demonstrates leaf-age effects. In the latter experiment host plants were subjected to more severe deficiencies. Figures 5 and 6 show age-specific fecundity rates for Experiment 1. The m_x curves in the full-nutrient treatment were similar throughout the first half of the test. In the phosphorus treatment, even the low level of phosphorus appeared to be sufficient until late in the test, although separations occurred during the maximum period of egg production. The degree of nitrogen deficiency seemed to have very little effect upon the importance of leaf

age. However, the potassium treatment definitely showed the effects of leaf age as the deficiency became more severe. In this case, as seen in figure 6 (low potassium), the m_x curves showed a gradual separation in favor of the young leaves as the deficiency became greater.

When total fecundities of females in each treatment of Experiments 2, 3, and 5 were examined, a pattern of distribution emerged which indicated the level of egg production achieved by a majority of the females and the extremes reached. This facilitated the construction of a graph depicting the frequency distribution of fecundities. Such a graph, figure 19, shows the effect of leaf age on the frequency distribution of fecundities when all nutritional treatments were combined. From this figure, it can be seen that more females on young foliage are represented at the high end of the fecundity scale—175
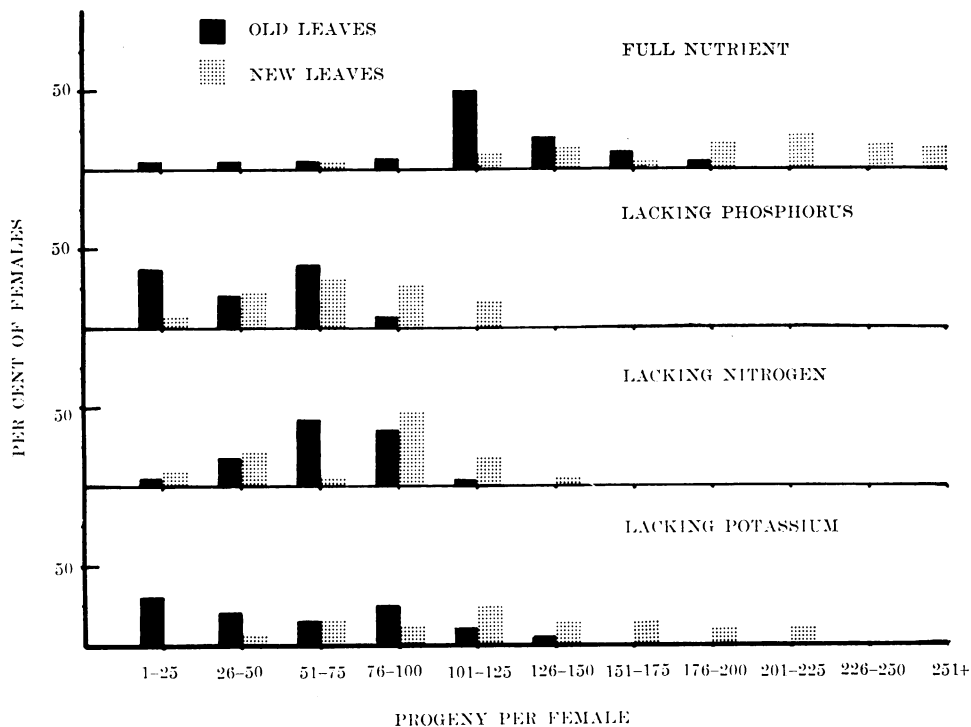
Fig. 18. Experiment 5. Frequency distribution of fecundities of *Tetranychus telarius* individuals on old and young leaves of lima bean plants grown in four types of nutrient solutions.
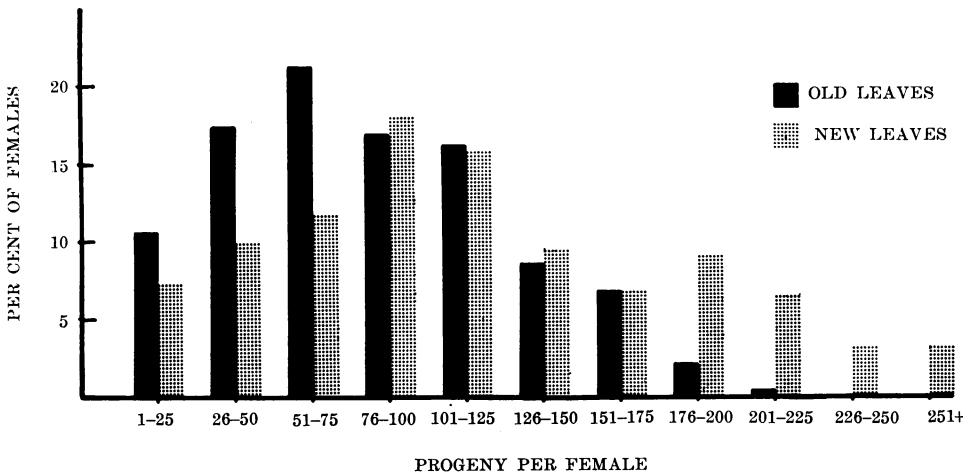

Fig. 19. Experiment 2, 3, and 5. Frequency distribution of fecundities of *Tetranychus telarius* individuals on old and young leaves of lima bean plants where data of all nutrient treatments were combined.

eggs per female and higher—in comparison to those on old leaves.

Effect on Population Increase

Population increase is dependent upon more than just total offspring produced. A combination of factors may determine how successful a species may be or how rapidly it may increase or decline in numbers. Not only are we concerned with numbers produced per female but also with the age-specific fecundity schedule during the life of the reproducing female. It can readily be shown that eggs laid early in the female's life contribute much more to population increase than those appearing later.

Survival of the offspring also determines to a large extent the capacity of a population to increase. Because of the importance of offspring produced early in the female's life, early mortality exerts a more severe effect on population at this time. In Experiment 1 (figures 5 and 6) the treatments involving full-nutrient, low-phosphorus, and low-nitrogen supply showed the greatest population increase on old foliage because of the greater mortality on the young leaves. The low-potassium treatment in this experiment demonstrated the same type of early mortality on the young leaves. But daily fecundity was so much greater on these leaves that it overshadowed the effects of mortality. When life tables were constructed and the intrinsic rates of increase calculated, it was evident that young foliage favored population increase in spite of the greater mortality. This serves to demonstrate the interaction of both survival and fecundity in determining population increase. The ensuing presentation of results obtained from the full-nutrient series emphasizes the importance of leaf age upon population increase.

Data presented earlier showed the effects of leaf age upon survival and age-specific fecundity rates. These two population characteristics can now be

integrated to yield the most meaningful attribute—population increase. Because of the interaction of mineral deficiencies and leaf age, only treatments involving a full-nutrient supply will be considered in making this comparison. The net reproduction rates (R_o), mean generation time (T), and intrinsic rates of increase (r_m) of mites reared on plants receiving full-nutrient supplies are summarized in table 8 for all experiments. An examination of the section comparing the R_o's shows that young foliage was superior to the old in all experiments except the first. An earlier discussion pointed out that abnormal early mortality of mites on the young leaves was responsible for the reversal shown in this experiment. Had this not occurred, the R_o would probably have been similar to those in Experiments 3b and 5 (95.54 and 96.35, respectively). The nutritional treatment of the host plants in these three experiments was similar and the R_o's of mites on the old leaves indicate like similarities (65.69, 65.78 and 57.87, respectively). Experiment 4 demonstrates a very small difference in the R_o's— 58.08 on old foliage and 67.62 on young. Again, it must be pointed out that all mites were maintained on the primary leaves in the experiment through the first 9 days of oviposition—by far the most important period when evaluating population increase. The R_o contribution of both populations during these first 9 days was very much the same— 40.94 to 42.36. The greater part of the separation between the two groups occurred after the mites assigned to feed on young leaves were transferred to that feeding site.

The difference in mean generation times (T) of mites on old and young leaves was so small that the trend pointed out for the R_o's in the above discussion remained consistent for the intrinsic rates of increase (r_m). As can be seen in table 8, a comparison of the r_m's reveals the same advantage of young over old leaves. Again, Experi-

RELATION OF LEAF AGE TO NET REPRODUCTION RATES (R_o), MEAN
GENERATION TIME (T), INTRINSIC RATE OF INCREASE (r_m) OF
TETRANYCHUS TELARIUS ON LIMA BEANS RECEIVING
FULL NUTRIENT SUPPLY

Population attribute	Experiment	Old foliage	Young foliage
R_o	1	65.69	47.83
	2	52.14	75.23
	3a	49.16	62.47
	3b	65.78	95.54
	4	58.08	67.62
	5	57.87	96.35
T	1	18.68	17.99
	2	19.57	19.29
	3a	18.91	19.14
	3b	17.52	18.28
	4	15.99	16.46
	5	19.42	19.03
r_m	1	0.224	0.215
	2	0.202	0.224
	3a	0.206	0.216
	3b	0.239	0.250
	4	0.254	0.256
	5	0.209	0.240

3a = old plants in Experiment 3.
3b = young plants in Experiment 3.

ment 1 produced the lower r_m with mites on young leaves. Experiment 4 showed only a very slight advantage to the mites on young leaves, 0.256 compared to 0.254 for those on old. The reason for this was pointed out above.

An examination of the figures representing full nutrients in each of the experiments shows that in all cases the mean number of eggs per female per day was greatest on the younger foliage. This, however, does not necessarily mean that population increase was also greater. For instance, figure 5 (full nutrient) shows that even though average daily egg production was greater on the young leaves, the population that contributed most to succeeding generations was located on the old foliage. The net reproduction rates of the mites on both old and young leaves were 66 and 48 respectively. The intrinsic rate of increase was greater on old leaves than on the young leaves. Other experiments showed that leaf age had no significant effect upon survival. Here the small differences resulted in much greater net

reproduction rates $(R_o$'s$)$. It also resulted in a higher intrinsic rate of increase (r_m), even though mean generation time (T) was generally a little greater on the young foliage. The slightly longer generation time would tend to minimize the r_m. It may also be noted that the r_m is influenced quite strongly by a relatively small change in generation time. For example, on the old leaves of Experiment 1 (full nutrient) and on the old leaves of the young plants in Experiment 3, the R_o's are practically the same—65.69 and 65.78. But, since mean generation time in Experiment 1 (old plants) exceeds mean generation time in Experiment 3 (young plants) by 1.16 days, the r_m increases from 0.224 on old plants to 0.239 on the young.

Discussion

That leaf age affects the longevity and fecundity of the two-spotted spider mite seems to be substantiated by data presented in the foregoing section. As pointed out earlier, Henderson and Hol-

loway (1942) showed that citrus red mites produced significantly greater numbers of eggs on young and medium-aged leaves than on older ones. Various aphids have also been investigated from the standpoint of leaf-age effects. Kennedy, Ibbotson and Booth (1950), working with *Myzus persicae* (Sulzer) and *Aphis fabae* Scopoli on sugar beets and spindle showed that growing leaves were more susceptible to colonization than maturing, mature and dying leaves. Essentially the same results were reported in other contributions of Kennedy and Booth (1951) and of Ibbotson and Kennedy (1950). Paschke (1959), working with the spotted alfalfa aphid, *Therioaphis maculata* (Buckton), concluded that leaf age had no apparent effect on the type of progeny produced by the apterae during their feeding period. He also concluded that age of the leaves did not in any way affect the progeny after they were deposited. Kessler and Swikski (1958) induced metabolic changes in apple leaves by treating the leaves with caffeine. These induced changes resemble those found in aging leaves in nature, where the ribonucleic and deoxyribonucleic acid ratio increases. They showed that the apple aphid, *Aphis pomi* DeGeer, developed to a much lesser extent on mature leaves and leaves pretreated with caffeine than on younger leaves.

The present work does not explain why leaf age affects *T. telarius* but does point out that young leaves enhance age-specific fecundity schedules although neither young nor old foliage greatly affects adult longevity. This suggests that under favorable conditions for new plant growth, population explosions would be more likely than under conditions unfavorable for new growth. Conversely, population explosion would seem less likely on older foliage but such foliage would be advantageous from the standpoint of species perpetuation.

INFLUENCE OF PLANT AGE

Effect on Longevity

In the previous section, leaf age was shown to have little effect on longevity of reproducing females but did greatly affect age-specific fecundities. These same population attributes were investigated to determine the possible effects of plant age. Experiment 3 was designed to test the hypothesis that plants differing in age would exercise some influence on the mites.

Plants utilized in this experiment were grown in identical nutrient solutions and inoculated with newly emerged adult females from a common source. The main variable introduced into this experiment was plant age; one group of plants was 60 days older than the other. An examination of the l_x curves in figure 9 indicates that no significant variation occurred with mites on the different plants. The survival pattern on the old plants in Experiment 3 (Figure 9), is similar to the pattern produced by the same plants during Experiment 1 (figure 5—full nutrients), with the exception of the young foliage, where abnormal early mortality occurred.

Effect on Fecundity

The age-fecundity schedules of two successive groups of test mites living on the same set of host plants showed considerable reductions in the second group regardless of the nutritional treatment. This indicates, perhaps, that as the plant ages, it becomes less favorable for mite reproduction. To avoid becoming involved with the changes occurring in the host plant due to nutrient deficiencies, only the full-nutrient series in Experiments 1, 2 and 3 (figures 5, 7, and 9) will be discussed. Age-fecundity schedules of both old and young foliage were combined for purposes of this discussion.

When comparing the results of Experiments 1, 2, and 3, it must be remem-

bered that greenhouse conditions may have changed slightly from test to test. Table 5 shows the temperature and relative humidity summaries for the experiments. The mean temperatures for Experiments 1, 2, and 3 are approximately the same; to the nearest whole degree, all are 77° F. However, when temperature differences between the daily maximums and minimums were calculated, more variation occurred between the experiments than was indicated by the overall means. The mean daily differences between high and low in Experiments 1 and 2 were 12° and 15° F, respectively. But in Experiment 3, the mean daily difference was 17° F. The wider fluctuations in daily temperatures in Experiment 3 may have had greater effects upon the mites than the relatively more constant ones in Experiments 1 and 2.

A comparison of the age fecundity schedules for Experiments 1, 2, and 3 indicates that plant age may affect the mites in several ways. First of all, the maximum age-specific fecundity was shown to be considerably reduced in the second experiment. Figure 20 illustrates this point clearly. On the other hand, the maximum fecundity rate in Experiment 3 (old plants) was slightly greater than in Experiment 2. Nevertheless, it did not attain the height that the fecundity curve did in Experiment 1. This increase in Experiment 3 over 2 may have been due to the greater fluctuations in daily temperatures. According to Dick (1937), there is evidence that a short period at low temperature may result in an increased rate of egg-production on return to a higher temperature. The control, that is, mites on young plants, conducted simultaneously with the test on old plants in Experiment 3 showed a higher maximum fecundity than was achieved on similar young plants during Experiment 1.

Because Experiment 3 was terminated after 4 weeks, figure 20 shows
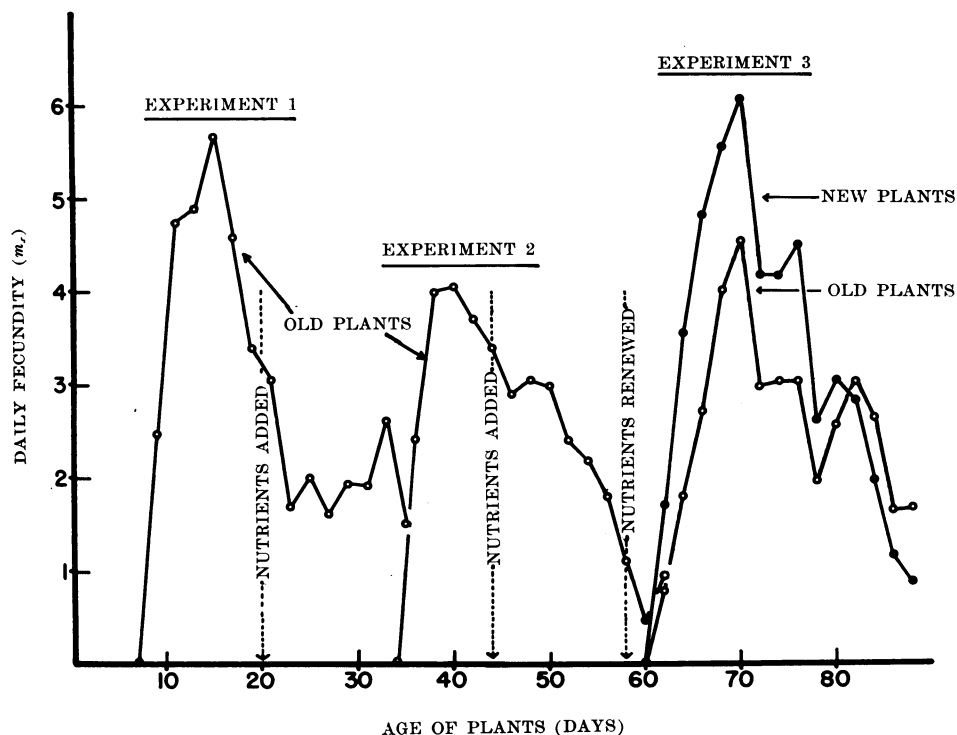

Fig. 20. Experiments 1, 2, and 3. Effect of plant age on daily fecundity of *Tetranychus telarius* where results of both old and young foliage are combined.

only the first 4 weeks of the age-fecundity schedules in each experiment. This was considered sufficient since the major part of the population contribution has been made by the end of 2 weeks. Each point on the m_x curves in figure 20 represents the mean number of female eggs per day when results from both old and young foliage were combined. A comparison of the first point on each curve shows very little difference between Experiments 1 and 2. But, in Experiment 3 the fecundity rate for that age group was approximately one-third as high as the other two. Each successive age interval (2-day intervals in figure 20) showed a uniform increase in age-fecundity rates in Experiment 3 (old plants) until the maximum was reached on the 10th day. This pattern of increase was quite different from that in Experiments 1 and 2. The pattern of age-fecundity schedules was very similar in these two experiments for the first 6 days. Even though the patterns were similar, the magnitude reached at each age interval in Experiment 1 was greater than in Experiment 2. After 6 days, the age-fecundity rate in Experiment 2 started the characteristic decline normally exhibited once the peak was reached. However, the peak was not reached until the 8th day in Experiment 1. The latter phase of the m_x curves in Experiments 1 and 2 differed in the pattern of decline. The curve in Experiment 1 had a faster rate of decline initially but then leveled off, whereas that in Experiment 2 showed a rather consistent, steady decline.

Since the young leaf treatments in Experiment 1 resulted in abnormal mortality which in turn reduced the total fecundities, evaluation of plant-age effects on total fecundity was based only on the old foliage. Results from the old foliage in Experiments 1, 2, and 3 show that total fecundities were reduced by 22 per cent in Experiment 2 and by 24 per cent in Experiment 3. But, it must be pointed out that the reduction of 24 per cent would not have been

quite as great had the experiment not been artificially terminated at the end of 4 weeks. Another interesting feature that emphasizes plant-age effect on total fecundity was found upon reviewing both age-groups of plants in Experiment 3. When total fecundities were compared between mites on old foliage of old plants, and those on old foliage of young plants, the reduction imposed on the mites feeding on the old plants again amounted to 22 per cent. This is a valid comparison since results were obtained concurrently and both tests terminated at the same time. A contrast can also be made in this experiment between total fecundities of mites on the young foliage of plants of different ages. Total fecundity of the mites on young foliage of old plants was reduced by 36 per cent as opposed to that on the young plants.

It might be noted that total fecundities of mites on old foliage in the deficient treatments were also reduced in Experiment 2 when compared to the first. Potassium-deficient plants yielded the smallest reduction of total fecundity, nitrogen deficiency was intermediate and phosphorus deficiency exhibited the greatest reduction. The reductions in Experiment 2 compared to Experiment 1 were 16 per cent, 42 per cent, and 53 per cent respectively. Results obtained in Experiment 3 corroborate the inferences shown in Experiments 1 and 2.

As previously demonstrated, *T. telarius* females, when confined to leaves of different ages on the same plant, yielded different results. It was also pointed out in the preceding paragraph that leaves of the same age on plants of different ages will give dissimilar results. Experiment 3 illustrates both points mentioned. Figure 9 shows the findings in a full nutrient test involving two groups of plants different in age by 60 days. As indicated in figure 9, smaller differences occurred between young and old foliage on the older plants than between the two on younger

plants. Nevertheless, figure 9 does show that some differences occurred. The fecundity rates remained very close until the 18th day of egg production. At that time there was a sudden acceleration in the rate of fecundity with the mites on the younger leaves. This can be explained by the growth characteristics of the plant and the handling of the test mites. During the time prior to the accelerated rate, new leaf formation had ceased during the maturing of the bean crop. But, once the beans were mature, a new flush of growth appeared and the mites were subsequently transferred to the new growth. Figure 9 shows the results of the young set of plants, both old and young foliage. This demonstrates that even the mites on the old leaves produced more than did those on the young leaves of the older plants. An even greater increase occurred on the young leaves of the young plants.

When total fecundities of each female involved in the various experiments are viewed, there are indications that a great deal of variation took place within the same treatments. As a means of classifying females according to total fecundity, an arbitrary division separated them into two major groups—those demonstrating high fecundities (females producing over 125 eggs) and those demonstrating low fecundities (females producing 125 eggs or less). Figures 14 through 18 show the frequency distribution of fecundities for the various experiments and treatments with the arbitrary division into high and low fecundity categories. Calculations were made to show the percentage of each population producing in the high and low fecundity categories. An earlier comparison of mean total fecundities for each population showed that host-plant age affected the mites. When individual mites were separated into high and low fecundity groups, plant age again demonstrated its effect. By comparing the effects of old foliage in the full-nutrient treatments in Experiments 1, 2, and 3, it is shown that the

percentage of high-producing females declined as plant age increased. Individual records of 25, 20, and 24 females in Experiments 1, 2, and 3 respectively, showed percentages of 56, 40, and 37 females producing in the high category. An examination of the results obtained with mites on old foliage in the deficient treatments of Experiments 1 and 2 reveals a more severe reduction in the percentage of high-producing females than observed in the full-nutrient treatment. It is believed that the aging plants were responsible for some of this decrease but, undoubtedly, host-plant nutrition also played a part in the reduction.

Effect on Population Increase

The influence of plant age on *Tetranychus telarius* is most readily shown when comparisons are made of population attributes derived from plants of different ages. The statistics from the full-nutrient treatments in Experiments 1, 2, and 3 are shown in table 9. As discussed earlier, Experiments 1, 2, and 3 (old plants) were conducted on plants increasing in age in like sequence. By comparing results from the old foliage, the net reproduction rates are shown to decline with increased plant age—66, 52, and 49 respectively. Failure of the r_m's to decrease in a similar manner can probably be attributed, at least in part, to experimental procedures. The generation time in Experiment 3 would have been longer had the test gone to completion. With a longer generation time, the intrinsic rate of increase would have been reduced to coincide with the decline in the net reproduction rates. It was also postulated earlier that a difference in greenhouse temperature may have been partially responsible for the higher intrinsic rate of increase when comparing results in Experiments 2 and 3 (old plants).

The abnormal findings obtained on young foliage in Experiment 1 makes a direct comparison between the three experiments extremely difficult. How-

ever, if the results of very similar experiments (Experiments 3b or 5—full nutrient) were substituted for those obtained on young foliage in Experiment 1, the decline of R_o's and r_m's experienced on old foliage would likewise follow the pattern for young foliage. In this instance, the R_o's would decrease from 96 (young plants, Experiment 3) to 75 (older plants, Experiment 2) to 62 (oldest plants, Experiment 3). In like manner, the r_m's would be 0.250, 0.224, and 0.216 on the oldest plants. There appeared to be no consistent pattern or trend in the mean generation times. This seems logical since, as mentioned earlier, plant age had no apparent effect upon longevity.

The results obtained in Experiment 3 indicate that older plants are inferior to younger plants with regard to population increase. Furthermore, the older leaves, regardless of the age of the plant, are less favorable than younger leaves on the same plant. Findings in this experiment are given in figure 9 and are summarized in table 9. It is interesting to note that the R_o of mites on old leaves of young plants was only slightly greater (65.78 to 62.47) than the R_o of mites on young leaves of older plants. However, because of a shorter mean generation time (T) of mites on young plants, the r_m was considerably higher—0.239 to 0.216. When comparing the effects of old versus young plants, it can also be seen that smaller differences occurred between the old leaves of young and old plants ($R_o =$

65.78 to 49.16) than occurred between the young leaves of young and old plants ($R_o = 95.54$ to 62.47). The r_m's of mites on both old and young foliage from young plants were also greater than on either old or young foliage from old plants. This indicates conclusively that older plants adversely affect population increase of *T. telarius*.

From the results obtained with the old versus young plants in full-nutrient solutions, inferences can be made about the effects of plant age in the nitrogen-, phosphorus-, and potassium-deficient treatments in Experiments 1 and 2. An examination of table 10 shows that populations found on the older plants were decidedly limited in growth as compared to those on the younger plants. In all cases the multiplication per generation was considerably reduced on the older plants. The R_o's were reduced as much as one-half in certain cases. The r_m's were also greatly reduced even though the mean generation times (T) were longer. Had the mean generation time been the same in each test, there would have been an even greater reduction of the intrinsic rates of increase on the older plants.

The potassium treatment also presents an interesting picture of plant-age effects. Figure 6 (low potassium) shows a gradual change in the fecundity rates of mites on both the old and young foliage, an indication that a faster decline occurs with the mites on the old leaves. Figure 8—low potassium—(Experiment 2, identical to Ex-

TABLE 9

NET REPRODUCTION RATES (R_o), MEAN GENERATION TIMES (T), AND INTRINSIC RATES OF INCREASE (r_m) OF *TETRANYCHUS TELARIUS* ON LIMA BEAN PLANTS GROWN IN FULL NUTRIENT SUPPLY

Experiment number	Number of days plants were in nutrient solution when inoculated	R_o		T		r_m	
		Old foliage	Young foliage	Old foliage	Young foliage	Old foliage	Young foliage
1.................	7	65.69	47.83	18.68	17.99	0.224	0.215
2.................	34	52.14	75.23	19.57	19.29	0.202	0.224
3a (old plants).....	60	49.16	62.47	18.91	19.14	0.206	0.216
3b (young plants)..	2	65.78	95.54	17.52	18.28	0.239	0.250

TABLE 10

RELATION OF PLANT AGE TO NET REPRODUCTION RATES (R_o), MEAN GENERATION TIME (T), AND INTRINSIC RATES OF INCREASE (r_m) OF *TETRANYCHUS TELARIUS* ON LIMA BEAN PLANTS GROWN IN NITROGEN-, PHOSPHORUS-, AND POTASSIUM-DEFICIENT SOLUTIONS

Statistic	Age of plants at time of inoculation (days)	Old leaves			Young leaves		
		Low phosphorus	Low nitrogen	Low potassium	Low phosphorus	Low nitrogen	Low potassium
R_o	7	67.08	58.20	42.52	51.99	45.38	57.19
	34	31.28	34.15	37.41	40.94	34.52	50.37
T	7	18.86	18.73	17.52	17.88	17.74	18.15
	34	19.45	18.01	17.93	19.33	18.35	18.23
r_m	7	0.223	0.217	0.214	0.221	0.215	0.223
	34	0.177	0.196	0.202	0.192	0.193	0.215

periment 1 with the exception of the use of older host plants) initially continues to show the separation but then seems to stabilize with the younger foliage maintaining the advantage. The overall age-fecundity schedule in Experiment 2 manifests quite a reduction over that in Experiment 1 (younger plants). On the other hand, in the case of the deficient treatments, it would be impossible to make a definite statement concerning plant age when nutritional status of the plant undoubtedly played at least some part and perhaps the major role in the subsequent reduction.

Discussion

These data show the effect of aging plants upon the capacity of spider mites to increase. A comparison between the deficient treatments of Experiments 1 and 2 for purposes of explaining plant-age effect would be erroneous unless analyses were available to show that the nutritional deficiencies had not increased accordingly. This type of information was not obtained in these experiments and it may very well have been nutritional changes rather than age which adversely affected fecundity rates.

Ulrich and Berry (1961), working with a phosphorus series on lima beans (*Phaseolus limensis* MacF.) showed that identical plant parts of different physiological age vary in their phosphate-phosphorus concentrations. They also found that young leaves have the highest concentrations under deficient conditions and the old leaves the highest when there is an abundance of phosphorus. According to Meyer and Anderson (1956), phosphorus is readily redistributed in plants from one organ to another. In growing plants, phosphorus is most abundant in meristematic tissues, where it is utilized in the synthesis of nucleoprotein and other phosphorus-containing compounds. It was also stated that a very large proportion of phosphorus in a mature plant is located in the seeds and fruit, accumulating there during the period of their development. This may offer some explanation as to why differences were observed in daily fecundities between old- and young-leaf treatments in Experiment 1 but practically no differences were noted in Experiment 2. It was probably significant that at the time Experiment 2 was being conducted, fruit formation was occurring on the plant and the low level of phosphorus was being utilized in the formation of beans.

Other essential elements have also been shown to be redistributed during the process of plant growth. According to Arnon and Hoagland (1943), potassium is highly mobile in plants. Internal redistribution of this element occurs

readily and more or less continuously during the life history of the plant. Older leaves and other organs frequently lose potassium, which is translocated to growing regions. Arnon and Hoagland also found that those tissues of the plant that are undergoing the most active growth appear to have the greatest capacity for accumulating potassium in contrast to cells that are physiologically less active. Thus, as can be seen in Figure 8 (low potassium), the gradual separation of daily fecundities between old and young treatments is not directly a result of plant age but probably due to the concentration of potassium in the young foliage. The latter is probably the result of the aging plant and the low initial level of potassium.

While elements such as potassium have been shown to be translocated in ionic form, redistribution of others seems to occur only in a combined state. Meyer and Anderson (1956) state that nitrogen, phosphorus, and sulfur probably move out of leaves at least partly in organic combinations, whereas potassium, magnesium and chloride move out mostly in the form of inorganic ions. The present investigation demonstrated that mites were adversely affected by low nitrogen levels and if translocation of the element did occur, it was in such small quantities that the mites were not influenced. With increasing plant age, however, mites were affected. This was probably due to the decreasing availability of nitrogen in the older plants rather than translocation. Meyer and Anderson state that inorganic nitrogen compounds are readily absorbed and accumulated in plant tissues when available phosphates are low, but on the other hand, when available phosphates are abundant, and nitrogen is relatively low, the absorption of nitrogen is depressed. It is believed that sufficient phosphorus was available and that reductions imposed on the mites were due to insufficient nitrogen.

Comparisons were made between the full-nutrient series of Experiments 1, 2, and 3. In these tests nutrients were renewed (table 3) frequently enough to prevent the occurrence of deficiencies. This series indicated that with increased plant age, a reduction in fecundity occurred in spite of full-nutrient treatment.

Aging plants were shown to be less favorable for spider-mite development. Even though longevity was not affected, fecundity was reduced by a considerable degree. It is postulated that this was due to a physiological change in the leaves as well as nutritional changes.

INFLUENCE OF HOST-PLANT NUTRITION

Much of the variation in spider-mite population increase in this study could be explained in terms of the effects of both leaf age and plant age. Since host-plant nutrition varies with the age of leaf or plant, it was possible to determine its influence on mite population increase.

Effect on Longevity

In the previous sections, it was shown that neither leaf age nor plant age has significant effects upon the ability of *T. telarius* to survive. However, each factor affected population increase by its direct influence upon the age-fecundity schedules. When one considers the influence of host-plant nutrition, it becomes necessary to assess the relative effects that longevity and fecundity have upon the capacity of the population to increase.

Since it was shown that leaf age had little if any effect upon survival, both old and young leaf-age treatments were combined within each nutritional treatment. Therefore, comparisons between the four nutritional treatments for their effects on survival include the females on both old and young leaves of each treatment. Figure 21 shows survivorship curves based on all experiments for each nutritional treatment. Table 11 demonstrates the number of days
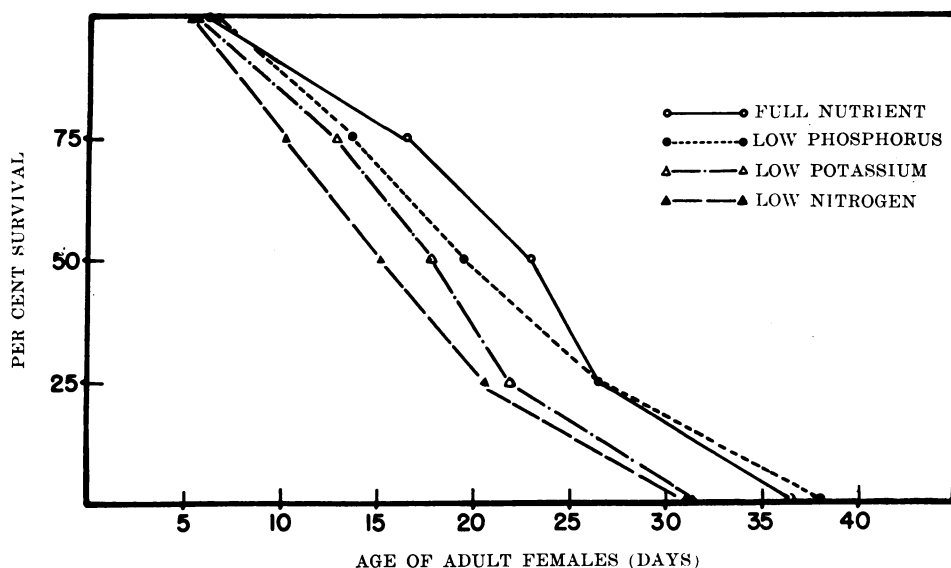
Fig. 21. All experiments. Survival rates of adult *Tetranychus telarius* females on host plants grown in four types of nutrient solutions: full nutrient, phosphorus deficient, nitrogen deficient, and potassium deficient.

TABLE 11

RELATIONSHIP BETWEEN HOST-PLANT NUTRITION AND DURATION OF SURVIVAL (DAYS) OF *TETRANYCHUS TELARIUS* WHEN ALL EXPERIMENTS ARE COMBINED

Per cent survival	Survivorship schedule—in days			
	Complete nutrient	Low phosphorus	Low nitrogen	Low potassium
All females alive	6.15	6.65	5.65	5.75
75	16.50	13.65	10.15	12.90
50	23.00	19.50	15.25	17.90
25	26.50	26.50	20.55	21.90
0	37.40	36.40	31.25	31.30

that had elapsed when each survival point was reached.

As shown in figure 21, no significant differences occurred between treatments to the point where mortality began. The greatest separation between treatments occurred at the 75 per cent and 50 per cent survival points. Full-nutrient solutions favored greatest survival while nitrogen deficiency favored survival least. At the 75 per cent point, the mites on normal plants survived 6.35 days longer than those on nitrogen-deficient plants, with a 7.75 day spread separating the two groups at the 50 per cent point. Similar curves

are to be found in figure 22 which represents the data obtained in Experiment 5. This test should give the best indication of the effect of nutrition upon survival since both plants and mites were placed under greater stress. These plants were preconditioned in their respective solutions and the test mites were reared to adulthood on them. The results shown in figure 22 exaggerate the differences shown where results of all experiments were grouped. The number of days required for each population to reach specific survival points is shown in table 12. At the 75 per cent point, mites on normal plants survived
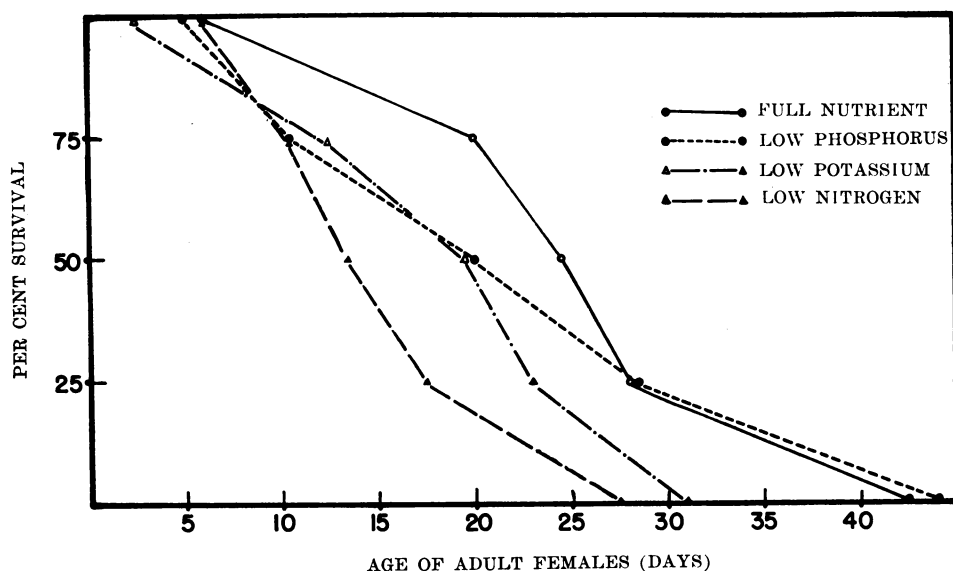
AGE OF ADULT FEMALES (DAYS)

Fig. 22. Experiment 5. Survival rates of adult *Tetranychus telarius* females on host plants grown in four types of nutrient solutions: full nutrient, phosphorus deficient, nitrogen deficient, and potassium deficient.

TABLE 12

RELATIONSHIP BETWEEN HOST-PLANT NUTRITION AND DURATION OF
SURVIVAL OF *TETRANYCHUS TELARIUS* IN EXPERIMENT 5

Per cent survival	Survivorship schedule—in days			
	Complete nutrient	Low phosphorus	Low nitrogen	Low potassium
All females alive......................................	6.0	5.0	6.0	2.5
75..	20.0	10.5	10.5	12.5
50..	24.5	20.0	13.5	19.5
25..	28.0	28.5	17.5	23.0
0..	42.5	44.5	27.5	31.0

almost two times longer than all others. The results strongly indicate that when females of *T. telarius* are confined to host plants suffering from major nutrient deficiencies, such as N-P-K, survival is adversely affected.

Effect on Fecundity

To define clearly the influence of host-plant nutrition upon fecundity of *T. telarius,* several aspects of fecundity must be viewed concurrently. These are the age-specific fecundity schedules, maximum fecundity rates, and total fecundity. All of these should be considered when evaluating population increase.

As pointed out earlier, the eggs laid early in the life of a reproducing female are more important to a population in terms of increase than those laid later. Thus, a situation can easily be visualized in which a population with a greater maximum rate of fecundity, greater total fecundity, or even both, might conceivably contribute less to population increase than one which laid the majority of its eggs early in the reproductive period.

An examination of the age schedules of fecundity in Experiment 5 indicates that highly significant differences were obtained between nutritional treatments. In this experiment the plants

were subjected to greater stress in the form of nutrient deficiencies before test mites were introduced. In addition, females were reared from eggs on their respective host plants. Examination of the frequency distribution of total fecundities in figure 18 shows the reduction of oviposition in the nitrogen and phosphorus treatments as well as on old foliage in the potassium treatment. Females were grouped into three total-fecundity categories—high, medium, and low. Table 13 shows the percentage of each population that falls into each category.

This table also summarizes the information depicted graphically in figure 18. Although variation of total fecundities occurred between individuals within the same treatment, it is apparent that distinct trends did exist. Females from only two treatments were found in the high-fecundity category: 52 per cent of the females on young foliage with full nutrients and 9 per cent of those on young leaves in the potassium-deficient treatment. Most of the females (81 per cent) on old leaves of the full-nutrient treatment produced in the intermediate category, with the remainder (19 per cent) falling into the low production group. Also, 59 per cent of the females on young leaves of the potassium-deficient treatment fell into the intermediate group. A majority of females from both leaf ages in the phosphorus and nitrogen treatments and those on old leaves in the potassium-

deficient treatment were found in the low-fecundity category. It is of interest to note that 100 per cent of the females on old foliage of the phosphorus-deficient plants and 97 per cent of those on old foliage of the nitrogen-deficient plants were in the low-fecundity category.

Experiment 2 (figure 15 and table 14) likewise demonstrates the effect of host-plant nutrition on total fecundity. The plants had been growing in their respective solutions for 34 days and a definite degree of deficiency had been attained. It should be remembered from an earlier discussion that plant age does affect total fecundity. Females living on plants in complete-nutrient solutions in Experiment 2 showed reductions in total fecundity when compared to younger plants such as those in Experiment 5. But, comparable reductions did not occur with females on plants in the deficient treatments of these two experiments. If plant age alone were responsible, reductions should have occurred. Instead, total fecundity was greater in Experiment 2. An explanation of this seems to stem from the nutrition of the host plants. Low levels of the deficient salts were supplied to the host plants in Experiment 2 but omitted completely in Experiment 5. Thus, even though the plants were younger in Experiment 5, the reductions in fecundities were greater. Table 14 shows the percentage of each population in Experiment 2 which produced in the low,

TABLE 13

EFFECTS OF HOST-PLANT NUTRITION AND LEAF AGE UPON TOTAL
FECUNDITY OF *TETRANYCHUS TELARIUS* (EXPERIMENT 5)

Treatment	Type foliage	Percentage of population		
		Low 0–100	Medium 101–200	High 201–300
Full nutrient	Old leaves	19	81	0
	Young leaves	5	43	52
No phosphorus	Old leaves	100	0	0
	Young leaves	85	15	0
No nitrogen	Old leaves	97	3	0
	Young leaves	79	21	0
No potassium	Old leaves	86	14	0
	Young leaves	32	59	9

TABLE 14

EFFECTS OF HOST-PLANT NUTRITION AND LEAF AGE UPON TOTAL
FECUNDITY OF *TETRANYCHUS TELARIUS* (EXPERIMENT 2)

Treatment	Type foliage	Percentage of total population		
		Low	Medium	High
Full nutrients	Old leaves...............................	45	55	0
	Young leaves...........................	17	71	12
Low phosphorus	Old leaves...............................	92	8	0
	Young leaves...........................	67	33	0
Low nitrogen	Old leaves...............................	68	32	0
	Young leaves	65	35	0
Low potassium	Old leaves...............................	75	25	0
	Young leaves...........................	45	55	0

medium, and high categories. Again, as shown in figure 15 and table 14, the phosphorus and nitrogen treatments as well as old foliage of the potassium-deficient treatment had the greatest effect on reducing total fecundity.

Experiment 4 (figure 17) demonstrates that even though plants may be growing under different nutritional conditions, it does not necessarily follow that sufficient stress has been placed upon the plants to affect a phytophagous pest feeding on them. In this test the plants were infested with the test mites one day after they were placed into their respective nutrient solutions. Figure 17 shows that total fecundity was affected little by the different nutritional treatments.

When considering the influence of host-plant nutrition on maximum fecundity, Experiment 5 illustrates the close relationship of total fecundity to maximum age-specific fecundity. Table 15 shows that nutritional effects produced the same trend with maximum

age fecundity as demonstrated when comparing total fecundities.

An examination of figures 12 and 13 shows the age schedule of fecundities of the different nutritional treatments. Age-fecundity schedules of the full-nutrient and potassium treatments showed a uniform and rapid rate of increase until the peak was reached. This was followed by a similar rate of decline. On the other hand, the phosphorus- and nitrogen-deficient treatments exhibited entirely different types of age-fecundity schedules. In the case of the phosphorus treatment the mites on the old foliage showed a slow rate of increase until the peak was reached about midway in their reproductive life. But, with mites on the young leaves, there was an initial sharp rise to the peak followed by a slow rate of decline. The nitrogen treatment exhibited an even more peculiar response in the form of bimodal curves for both the old and young leaves. The first peak on both old and young leaves came rather early, fol-

TABLE 15

MAXIMUM AGE-SPECIFIC FECUNDITY AND MEAN TOTAL FECUNDITY OF
TETRANYCHUS TELARIUS IN EACH NUTRITIONAL TREATMENT
(EXPERIMENT 5)

Treatment	Maximum age-specific fecundity		Mean total fecundity	
	Old leaves	Young leaves	Old leaves	Young leaves
Full nutrient.........................	4.72	8.29	116	193
Lacking phosphorus..................	2.58	3.32	41	64
Lacking nitrogen.....................	3.80	4.50	67	75
Lacking potassium....................	3.28	6.62	59	125

lowed by a decline and then another peak. No explanation of this interesting feature can be offered at this time.

The irregularities shown in the phosphorus and nitrogen treatments of Experiment 5 were not demonstrated in Experiment 2. In fact the pattern of reproduction (figures 7 and 8) was very similar in all treatments except for one phase of the reproduction pattern in the nitrogen and one in the potassium treatment. In the deficient nitrogen treatment, even though the peak period of oviposition was the same as in the other treatments, the initial rate of fecundity approached the peak almost immediately. In other words, females on the nitrogen-deficient plants seem to show a faster initial rate of fecundity, in relation to the maximum attained, than those on the other treatments. In the case of the potassium-deficient plants, similarities with the other treatments were observed until after the peak had been achieved. At this point, the m_x curves show a faster rate of decline than any of the others. A good indication of the influence of potassium on the fecundity of *T. telarius* is gained by observing both figures 6 and 8 (low potassium) together. In these tests low amounts of the deficient salts were added to the solution as indicated in table 3. Since potassium is translocated from old to young leaves as growth continues and deficiencies become more severe, it is probable that mites feeding on young leaves were not subjected to as high a deficiency stress as those on the older foliage. Figures 6 and 8 show an interesting trend in age-specific fecundity rates which is believed to be due to the gradual change in the nutritional status of the host plant. With the very small amount of potassium incorporated in the solution of the potassium series, noticeable deficiency symptoms began showing rather early. As this condition progressed, the older leaves suffered more than did the younger ones, resulting in a gradual separation of the fecundity curves. In Experiment 2 there was the initial separation of the m_x curves, but following the peak period, the curves moved closer together again as in figure 8 (low potassium). Both showed a faster rate of decline than those in the other three treatments.

Because of irregularities in Experiment 1, there is little value in discussing the influence of host-plant nutrition upon the age schedules of fecundity. However, since the irregularities in the low-potassium treatment (figure 6) were minimal, this treatment was considered in evaluating the influence of host-plant nutrition on fecundity.

Effect on Population Increase

Population changes occur because of the interactions of many factors. By excluding some of these factors, such as parasitism, predation, or shortage of food, any of which may occur in nature, it is possible to evaluate introduced variables in terms of their effects on population increase. The effects of host-plant nutrition and the location of mites on the plants were the primary factors under consideration in this investigation.

As mentioned above, both adult longevity and age-specific fecundity schedules were affected by the nutritional treatment of the host plant. Since population increase is directly dependent upon both of these characteristics, it is necessary to consider the interaction of both when evaluating their importance to the population. Neither should be treated alone when making such an evaluation. The life-table and age-specific fecundity curves shown in figures 5 through 13 provide all the information necessary for calculating the intrinsic rates of natural increase for populations involved in the nutritional studies.

Examination of the pictorial life tables in Experiments 2 and 5 (figures 7, 8, 12, and 13) gives a clear indication of the effects of host-plant nutrition upon population increase. Conversely, Experiments 1 and 4 (figures 5, 6, 10,

and 11) show how little populations are affected if mineral deficiencies have not yet been effected in the host plants.

A close examination of Experiments 2 and 5 shows that once deficiencies have been established, population increase is greatly retarded. Populations of mites on the young foliage of full-nutrient plants have much greater net reproduction rates than the populations on deficient plants (see table 16). The same is true when mites on young foliage are compared to those on old foliage of the full-nutrient plants. Also, the intrinsic rate of increase was greatest in this treatment. It might be pointed out that even though the R_o was slightly smaller with the population on the young foliage in the potassium series of Experiment 2 compared to the one on the old foliage of full-nutrient plants, the intrinsic rate of increase (r_m) was greater. This is due to the difference in mean generation time (T), which was 1.34 days shorter in the potassium-deficient treatment. In the same experiment, a comparison of the effects of old versus young foliage in the nitrogen treatment reveals that the young foliage enhances R_o whereas old foliage is more favorable to r_m. This is due to the shorter mean generation time on old leaves.

In Experiment 5 the same general trends occurred. From the standpoint of net reproduction rate, all three deficient treatments caused relatively large reductions as compared to the full-nutrient solution. However, this is

shown only in the old foliage in the potassium treatments. This is not surprising since both tests show that the R_o's on the young foliage correspond very closely to those on the old foliage of the full-nutrient plants. The intrinsic rates of increase were affected differently from the R_o's. Here, the differences in the mean generation time were responsible for more variation in the r_m's than the R_o's would indicate. For example, in general the phosphorus-deficient plants had a longer mean generation time and the nitrogen-deficient plants a shorter one than did those on full-nutrient plants. The r_m's in the nitrogen treatment were elevated to almost equal those on the old foliage of the normal plants even though the R_o's were only half as great.

Another important factor is the pattern of reproduction. In Experiment 5 there was not a great deal of difference in the age schedule of fecundities (figures 12 and 13) during the early part of the reproductive period, but those on old foliage of normal plants maintained a higher average for a longer period of time. The latter was important in contributing to the R_o but made very little contribution to r_m.

Even though Experiments 2 and 5 showed definite responses of *T. telarius* to changes in host-plant nutrition, other experiments failed to confirm this evidence. Experiments 1 and 4 (see table 17) demonstrated little, if any, difference. Since plants in these experiments had achieved practically no deficiencies

TABLE 16

EFFECTS OF HOST-PLANT NUTRITION AND LEAF AGE UPON R_o, T, AND r_m OF
TETRANYCHUS TELARIUS (EXPERIMENTS 2 AND 5)

Statistic	Experiment number	Complete		Low phosphorus		Low nitrogen		Low potassium	
		Old leaves	Young leaves	Old leaves	Young leaves	Old leaves	Young leaves	Old leaves	Young leaves
R_o	2..............	52.14	75.23	31.28	40.94	34.15	34.52	37.41	50.37
	5..............	57.87	96.35	20.13	31.29	31.78	35.73	29.36	60.04
T	2..............	19.57	19.29	19.45	19.33	18.01	18.35	17.93	18.23
	5..............	19.42	19.03	21.76	19.45	17.56	17.19	19.40	18.70
r_m	2..............	0.202	0.224	0.177	0.192	0.196	0.193	0.202	0.215
	5..............	0.209	0.240	0.138	0.177	0.197	0.208	0.174	0.219

compared to those in Experiments 2 and 5, this does not invalidate the results of Experiments 2 and 5 but rather adds support to the importance of phosphorus, nitrogen, and potassium as necessary components in the host-plants of two-spotted spider mites. Results with females on young leaves of all nutritional treatments in Experiment 1 must be disregarded because of abnormal mortality. However, a comparison of all the old-leaf treatments in this experiment reveals some interesting points. Examination of the net reproduction rates shows that the phosphorus treatment resulted in no reduction compared to the full-nutrient treatment. A low level of phosphorus was provided in this treatment and deficiency symptoms did not appear until much later. It seems likely that this generation of mites had passed most or all of its reproductive period on the plants before they became deficient in phosphorus. As shown in table 17, the R_o's in the nitrogen- and potassium-deficient treatments were lower than those on full-nutrient or the phosphorus-deficient treatments. Deficiency symptoms also appeared earlier in these two treatments than in the case of phosphorus. The intrinsic rate of increase in the full-nutrient treatment was slightly greater than in the low-phosphorus group even though the R_o's were somewhat lower. This was due to a slightly longer generation time in the phosphorus-deficient group. On the other hand, the generation times were very similar for full-

nutrient and nitrogen-deficient treatments. Consequently, T values exercised very little influence upon the differences shown in the r_m's. Therefore, the lower r_m in the nitrogen test was primarily a reflection of the lower net-reproduction rate. In the potassium treatment, the R_o was substantially reduced as compared to the full-nutrient treatment. In spite of the shorter generation time of 1.16 days, the r_m was considerably lower than that in the full-nutrient treatment. This tends to indicate that phosphorus was supplied in sufficient quantity to prevent deficiency whereas nitrogen and potassium, even though supplied at low levels, became deficient in time to exert a small degree of influence upon the mites feeding on the plants in those two treatments.

In contrast to the first experiment, Experiment 4 demonstrated no differences from the standpoint of nutritional treatments. This suggests that the greater part of the mite's contribution to population increase had already been made when the plants became conditioned to their respective treatments. Had the plants been allowed to grow somewhat longer before the mites were introduced, presumably quite different results would have been obtained. This was verified in Experiment 5. Nevertheless, an absolute comparison cannot be made since not only were the plants in Experiment 5 placed under greater stress, but the females also passed their immature stages on their respective nutritional treatments.

TABLE 17

EFFECTS OF HOST-PLANT NUTRITION AND LEAF AGE UPON R_o, T, AND r_m OF
TETRANYCHUS TELARIUS (EXPERIMENTS 1 AND 4)

Statistic	Experiment number	Full nutrient		Low phosphorus		Low nitrogen		Low potassium	
		Old leaves	Young leaves	Old leaves	Young leaves	Old leaves	Young leaves	Old leaves	Young leaves
R_o	1	65.69	47.83	67.08	51.99	58.20	45.38	45.52	57.19
	4	58.08	67.62	67.70	65.39	56.99	58.76	55.33	60.30
T	1	18.68	17.99	18.86	17.88	18.73	17.74	17.52	18.15
	4	15.99	16.46	16.34	16.72	15.85	15.79	15.86	16.14
r_m	1	0.224	0.215	0.223	0.221	0.217	0.215	0.214	0.223
	4	0.254	0.256	0.258	0.250	0.255	0.258	0.253	0.254

Discussion

When studying the relationship of two biological entities such as a phytophagous pest and its host plant, many interesting facets may be discovered that otherwise go unnoticed when considering only one. On the other hand, the interpretation of data regarding these relationships may be extremely difficult on account of the complexities involved in either organism as well as the combination of both.

Various insects and mites have been studied in relation to the nutrition of their host plants as it affects some of their innate characteristics. Evans (1938), working with the cabbage aphid, *Brevicoryne brassicae* (Linnaeus), showed that the higher the percentage of total nitrogen, the greater the number of young produced. He found a negative correlation in this same case with winged forms.

Coon (1959), working with the apple grain aphid, *Rhopalosiphum fitchii* (Saunderson), showed similar results; that is, the population potential was significantly greater when more nitrogen was available. Daniels and Porter (1956) showed a positive correlation between nitrogen supply and a greenbug population, *Toxoptera graminum* (Rondani). Maltais (1951) has shown a high-nitrogen content of pea plants to be positively correlated with a high degree of susceptibility to the pea aphid, *Macrosiphum pisi* (Harris). Barker and Tauber (1951*b*) presented data indicating greater fecundity of pea aphids on pea plants growing in a complete-nutrient diet than on plants deficient in nitrogen, phosphorus, potassium, calcium or magnesium. Other workers were unable to show any responses of their test organisms to changes in the nutritional status of their host plants. Taylor, Apple, and Berger (1952), working with the potato aphid, *Aphis fabae,* and the pea aphid, *Macrosiphum pisi,* and Barker and Tauber (1951*a*), working with *Myzus persicae,* represent such examples. On the other hand, negative responses to increased fertilization have been reported by Daniels (1957), Arant and Jones (1951), Haseman (1946) and Smith (1960).

Results of nutritional studies on various spider mites were reported in the introduction. The present work reveals definite responses of the two-spotted spider mite to nutritional changes of the host plant. The components necessary to calculate population increases—survival and age-specific fecundity—were both affected by nutritional treatments. Survival of adults was greatest on normal plants; survival decreased on plants deficient in phosphorus, potassium, and nitrogen, in that order. As shown in figures 14 and 15, nitrogen deficiency reduced longevity quite severely. Figures 7, 8, 12, and 13 show the effects of the various treatments on age-fecundity schedules. The rates of fecundity were drastically reduced when mites were allowed to feed on plants suffering from nitrogen, phosphorus or potassium deficiencies.

It is readily evident that normal plants gave higher fecundities than any of the deficient series. However, it must be stated that the type of foliage in each treatment yielded marked differences except in the nitrogen-deficient treatments. Phosphorus deficiency appeared to give the greatest reduction in oviposition, with old foliage of the potassium-deficient and nitrogen-deficient treatments following in that order. From the standpoint of population increase, nitrogen-deficient plants were superior to old foliage, potassium-deficient treatments and old and young phosphorus-deficient treatments because of shorter mean generation time. Old leaves deficient in potassium and young leaves deficient in phosphorus gave practically the same results. Young leaves deficient in potassium were superior to old leaves on the normal plants.

The data clearly indicate that there is an interaction between the type of

foliage and nutritional treatments as it affects the two-spotted spider mite. A full nutrient supply is most favorable for population increase with definite reductions being imposed by deficiencies of nitrogen, phosphorus, and potassium.

In the preceding sections, the discussion was restricted to the effects of longevity and fecundity on population increase. Many other factors undoubtedly enter into this phenomenon, especially under field conditions. Perhaps the eggs from females on nutrient-deficient plants are affected to the point of altering population growth trends. Although no data were obtained to substantiate this, it seems plausible to think that nutrient deficiencies might affect viability of eggs, survival of the offspring, and other population attributes in subsequent generations.

Even though it was shown that population increase was greatest on well-fed plants, it should not necessarily be implied that these plants would suffer more damage than nutrient-deficient plants. It is not inconceivable that plants receiving a full nutrient supply, although more favorable for population growth, could produce sufficient, luxuri-

ant growth to escape the severe effects that would be imposed on plants suffering from some nutrient deficiency.

Another important aspect that should not be overlooked is the effect of the microenvironment on the organisms. Examination of figure 1 reveals striking differences in the size, form and color of bean plants grown under different nutritional treatments. Obviously, temperature and relative humidity would differ in the microenvironments of such plants. Under field conditions, air movements would also differ markedly at the leaf surfaces. In addition to the obvious effects on temperature, relative humidity, and leaf transpiration, wind dispersal of the organisms would alter the density of the population and consequently the amount of competition encountered.

The above speculation merely serves to point out that numerous factors may be involved in explaining a given phenomenon. Generally, many of these factors are controlled or excluded from the experiment but complete understanding of the final results, when allowed to exist under natural conditions, is seldom achieved.

SUMMARY

Population growth studies were conducted with *Tetranychus telarius* (Linnaeus) on lima beans in the greenhouse. The capacity of populations to increase was studied in relation to the nitrogen, phosphorus, and potassium nutrition of the host plants. In addition, the effects of both leaf age and plant age on the rates of increase were studied.

Host-plant nutrition influenced population increase by affecting both longevity and fecundity. When compared to mites on plants in full-nutrient solutions, adult female longevity was adversely affected when the mites were confined to plants grown in nutrient solutions deficient in phosphorus, nitrogen or potassium. Of the three deficiency treatments mentioned, phospho-

rus deficiency was least detrimental for survival and nitrogen deficiency most detrimental. Age-specific fecundity schedules were significantly reduced when females were confined to plants grown in the nitrogen-, phosphorus-, or potassium-deficient solutions. The phosphorus-deficient treatments gave the greatest reduction in total fecundity and maximum fecundity attained, even though ultimate survival of the populations was least affected. This was true for both old and young leaves. The old leaves of the potassium-deficient treatments induced the second greatest reduction in both total and maximum fecundities. The nitrogen-deficient treatments were superior to either mentioned above but yielded significant reductions

when compared to the treatments involving a full nutrient supply. The young foliage in the potassium-deficient treatments was somewhat superior to the old foliage in the full-nutrient treatment in both total fecundity and maximum fecundity.

Plants grown in a full nutrient supply resulted in greater reproduction rates and intrinsic rates of increase. Phosphorus-deficient plants were the most detrimental to these population attributes. Old leaves of the potassium-deficient plants and nitrogen-deficient plants gave intermediate results and young leaves of the potassium treatment gave comparable results to those obtained on old leaves of the full-nutrient treatment.

Evidence was accumulated which showed that host plants must be conditioned in mineral-deficient solutions for a period of time before the mites respond to the various treatments.

Young leaves, regardless of nutritional treatment, were more favorable for both total and maximum fecundity. There was no significant difference in adult survival with different leaf ages. Consequently, young leaves enhanced population growth in comparison to old leaves. The differences were not significant, however, in the nitrogen-deficient treatment.

Plant age was also found to affect population increase. Again, no differences were noted in survival of adult females on plants of different ages, but data obtained from experiments involving plants grown in full-nutrient solutions showed that as the plants aged, fecundity was reduced. This was also true in the deficient treatments. However, this involved an interaction of nutritional deficiencies which undoubtedly were changing as the plants aged. Thus, both factors were probably involved in causing the reductions.

ACKNOWLEDGMENTS

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[3] Microfilm copies may be purchased from the University of California Library Photographic Service, Berkeley, California 94720.

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