

Environmental factors affecting the life-tables of *Tetranychus urticae* (Acari: Tetranychidae). III. Host-plant nutrition

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ABSTRACT

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First, the literature of the last two decades on nutritional effects of host plants on spider mites is briefly reviewed. Second, experiments are described that subjected micro-propagated apple trees to four different levels of each macronutrient N, P and K. Spider mites (*Tetranychus urticae* Koch) feeding on leaf disks of these plants were checked for their developmental time, egg production and longevity. Plant analysis revealed that the concentration of N, P and K corresponded to the respective treatments. The content of phenolic compounds in the leaves increased with N and P deficiency. In the N experiment, spider-mite preimaginal developmental rate and oviposition rate were both positively correlated with leaf N. Often, fecundity was positively correlated with N and carbohydrate content of the leaves, and negatively with the phenolic content. Longevity of the two-spotted spider mite was not significantly affected by any treatment. The K experiments yielded only minor differences in plant contents as well as in spider-mite biology.

From these mite data, life-tables were constructed and statistically analyzed by the Jackknife technique. The life-table analysis showed a gradual decline in the intrinsic rate of natural increase (r_m) with N and P deficiency. With all experiments pooled, r_m was clearly correlated to leaf N and particularly to the content of phenolic compounds in the leaves. Nitrogen shortage had the most distinct influence on mite population growth: in a range of 1.5–3.0% leaf N, r_m increased by a factor of 4, the number of multiplications per generation (R_0) by 11, and the doubling time of the population was prolonged 4-fold on severely N deficient leaves.

INTRODUCTION

The growth of a spider-mite population is modified within a genetically defined spectrum by various environmental factors. Among the environmen-

tal influences are climate, food availability and quality, predation, and inter- and intraspecific competition. The influence of temperature and host-plant condition as affected by water stress have been discussed in previous papers of this three-part series (Wermelinger et al., 1990a,b). Under standard conditions, the developmental rate of the two-spotted spider mite, *Tetranychus urticae* Koch, and its intrinsic rate of natural increase (r_m) were found to be linearly related to temperature in the range between 15°C and 35°C. Generation time gradually declined with increasing temperatures in this range. Temperature increase also turned out to be the most important effect of host-plant water stress; the shortage of water supply caused leaf temperatures to rise, thus decreasing developmental time. The performance of a mite population under water stress was found to be the result of a balance between accelerated development due to higher leaf temperatures and reduced reproduction due to inferior food quality.

The significance of food quality as a further component of environmental influences had been recognized early, and there exist a number of reports on the influence of plant nutrition on spider-mite population development. In most studies, mite densities are related to fertilizer treatments or to the nutrient content of the plant. By way of contrast we seek, in our work, a deeper understanding of this relationship by analyzing the effect of the nutritional status on the mite life-table parameters and their variances, rather than on population densities. This is made possible by recent advances in demographic theory and methodology (Krebs, 1989). In practice, the advent of computers enabled the statistical analysis of life-tables.

Individual single *life-history parameters* (such as developmental time, fecundity, survival) of the spider mites as well as their *life-table parameters* (such as net reproductive rate, intrinsic rate of increase, generation time) are subjected to statistical analyses. The data are related to the physiological state of the plant expressed as contents of macroelements and other nutritionally important compounds. Hereafter, a distinction will be made between two kinds of stress, namely deficiency and excess nutrient supply to the host plant.

LITERATURE REVIEW

The literature on the nutritional effects of food plants on insects has been summarized in elaborate detail by Dale (1988). The specific role of nitrogen was discussed by Mattson (1980). Watson (1964) and Van de Vrie et al. (1972) reviewed the effects of plant mineral nutrition as it concerned spider mites. Van der Geest (1985) summarized the studies that tried to determine the nutritional requirements to rear spider mites on artificial diets. A number of further studies have since been made on how plant nutrition affects tetranychids, and the present synopsis focuses on papers published during the last two decades.

N, P, K nutrition

Nitrogen. Most attention has been given to the effect of host-plant N on spider mites. Many studies investigated its influence on population densities: nitrate fertilization of apple trees led to higher population numbers of *Panonychus ulmi* (Koch), depending on the date of application (Van der Vrie and Delver, 1979). High contents of carbohydrates and insoluble N compounds in the N-deficient treatment were correlated with higher multiplication rates of the same mite species (Fritzsche et al., 1980). On the other hand, carbohydrate contents of different plant lines had a negative effect on *Oligonychus pratensis* (Banks), and the N concentrations in the leaves were not clearly related to mite densities (Perring et al., 1983). Mellors and Propts (1983) found no significant effects of different N fertilization on *T. urticae* in combination with varying soil moisture. A larger population of *Eotetranychus hicoriae* McGregor on N-fertilized pecan was attributed to enhanced reproduction and not to a shorter life-cycle (Jackson and Hunter, 1983). The N content of leaves of various cucurbit varieties positively influenced populations of *T. neocaledonicus* Andre (Sharma and Pande, 1986). Nitrogen fertilization of sorghum and corn only slightly affected *O. pratensis* densities (Archer et al., 1988). Other studies concerned the effects of N on life-history parameters: N fertilization was found to trigger higher levels of amino acids in some vegetables and ornamental plants, and some of the essential amino acids were correlated with elevated fecundity of *T. urticae* (Tulisalo, 1971). Suski and Badowska (1975) reported that increasing N doses shortened developmental time and promoted survival of *T. urticae*. The fecundity of this species was reported to be linearly correlated with N, sugar and water content of apple leaves (Wermelinger et al., 1985). Fecundity and developmental time of *T. pacificus* (McGregor) were favorably influenced by a fertilizer-induced increase of leaf N (Wilson et al., 1988). Respiration rate and sex-ratio of *T. urticae* were increased by elevated leaf N (Wermelinger, 1989; Wermelinger and Delucchi, 1990). The few studies on the N effect on spider-mite life-table parameters as overall indices of mite population performance unanimously found a stimulating effect of N fertilization and leaf N concentration on the net reproductive rate, R_0 (Suski and Badowska, 1975) and on the intrinsic rate of increase, r_m (Jesiotr et al., 1979) of *T. urticae*. Also, Yaninek et al. (1989) attributed enhanced r_m values of *Mononychellus tanajoa* (Bondar) on young cassava leaves to higher leaf N concentration. In general, a positive effect of N fertilization and/or N content of the plant can be postulated for life-history parameters of spider mites.

Phosphorus. The effects of P on spider mites are less uniform, and fewer studies have been made concerning this element. Suski and Badowska (1975) found high P supply to enhance the survival of *P. ulmi*. Higher values of car-

bohydrates and insoluble N compounds in apple plants, induced by a P-deficient treatment, were positively correlated with higher population growth of *T. urticae* (Fritzsche et al., 1980). The P content of leaves of various cucurbit varieties, on the other hand, could not be related to the population size of *T. neocaledonicus* Andre (Sharma and Pande, 1986). Phosphorus fertilization of sorghum and corn showed only a slight influence on *O. pratensis* (Archer et al., 1988).

Potassium. Deficiency of K caused higher levels of amino acids in vegetables and ornamental plants, and an elevated fecundity of *T. urticae* (Tulisalo, 1971). Similarly, more eriophyids (*Eriophyes sheldoni* Ewing) developed on plants in K-free nutrient solutions than in standard solutions (Sternlicht et al., 1975). In addition, Jesiotr et al. (1979) reported that good K supply induced higher immature mortality of the two-spotted spider mite. Corresponding to these findings, the rate of population increase (r_m) of *T. urticae* was found to be negatively correlated with the K content of bean plants (Suski and Badowska, 1975). This may be due to higher values of carbohydrates and insoluble N compounds at K-deficiency which result in higher multiplication rates (Fritzsche et al., 1980). On the other hand, the K content of leaves of various cucurbit varieties was reported to positively influence populations of *T. neocaledonicus* Andre (Sharma and Pande, 1986).

Effects of 'good' and 'poor' leaves on *T. cinnabarinus* (Boisduval), as described by Wrensch and Young (1978), resulted from crowding and previous feeding rather than from plant nutrition. The sex-ratio of *T. urticae* was higher on leaves of 'poor' than of 'good' quality (Kondo and Takafuji, 1982).

Other nutritional components

Only a small number of articles concerned trace elements and secondary plant metabolites. Oil plant seedlings receiving little boron experienced a more intense attack of *T. piercei* McGregor than did well-supplied seedlings (Rajaratnam and Law Ing Hock, 1975). Manganese application together with ammonium reduced *T. arabicus* Attiah populations, but the same application without ammonium gave contrary results (Abou-Awad, 1981).

Primitive races of cotton that were almost immune to *T. urticae* had concentrations of tannins (phenols) of up to 20% higher (Lane and Schuster, 1981). *Oligonychus pratensis* was found to be insensitive to tannins (Perring et al., 1982), but the phenol content of peppermint leaves exerted a significant impact on *T. urticae* (Larson and Berry, 1984). On young leaves with high phenol levels, they produced the lowest number of eggs, the developmental time of the immatures increased and their dispersal was enhanced. A similar linear relationship between phenol content and fecundity was reported by Wermelinger et al. (1985).

Concluding remarks

Discrepancies between the results of the reviewed studies are partly due to different ranges of fertilization. These are difficult to compare because of different methodologies (field, greenhouse, soil nutrient solutions) and plant species. Often, spider-mite development is related to the variation of one nutrient in the plant, assuming that the other components remain unchanged. However, herbivore performance is more likely the response to the overall physiological state of the plant. Very few studies related life-table analyses of *T. urticae* to the N, P, K composition of the plant, and none related life-tables to secondary plant metabolites or made life-table statistics. The present work should help to fill these gaps in our knowledge.

MATERIAL AND METHODS

Experiments

All plant material originated from one seed of the apple variety 'Glockenapfel' which was shoot-propagated and rooted by means of tissue cultures (Wermelinger, 1985). The plantlets were transferred when 5 cm high to low-concentration nutrient solutions under non-sterile conditions. At a height of 10 cm they were transplanted to the nutrient solutions of the respective treatments, composition of which was based on a Hoagland solution (Epstein, 1972), the standards (1 N, 1 P and 1 K) containing 210 ppm N, 31 ppm P and 235 ppm K at pH 6.0. Based on the standards, concentrations of each of N, P and K were varied by factors of 5, 1/5, and 1/25, thereby keeping the other two macronutrients and the micronutrients constant. Hence, the four treatments for N, for example, are referred to as 5 N, 1 N, 0.2 N and 0.04 N. For each nutrient N, P and K, a separate experiment was carried out. Each treatment consisted of eight plants in two containers holding 30 l of nutrient solution which was aerated and mixed by compressed air. The solutions were renewed monthly. At the end of the experiment the apple trees were about 1.5 m high.

Six weeks after commencing the experiments, leaf disks (\varnothing 4 cm) were punched out of young leaves, on which females of the two-spotted spider mite *T. urticae* were allowed to oviposit for one day. The disks were placed on moist support tissue in plastic trays covered by lids with aerating holes to prevent condensation. The resulting progeny completed its immature development on these leaf disks. Four disks (\varnothing 2 cm) of young leaves from each apple tree were settled with one newly emerged female each. These 32 mites per treatment were checked daily for egg production and survival. Eggs were removed daily and leaf disks replaced weekly. In the growth chambers the conditions for plant growth and spider-mite reproduction were 27°C/19°C

(28°C/19°C for the K experiment) with a photoperiod of 16 L:8 D h and 70% RH. For the determination of the developmental time, approximately 20 eggs per treatment of an age difference of not greater than 4 h were monitored every 4 h until emergence to adulthood. About ten young females of each of these resulting cohorts were killed with CO₂ and weighed individually on a microbalance (Sartorius, d=0.1 µg). The development studies were conducted in growth cabinets at a constant temperature of 24°C and a photoperiod of 16 L:8 D.

Analyses

Chemical analyses were carried out on young leaves, dried for 1 h at 105°C and subsequently for two days at 60°C. They were analyzed for N, P, K, phenolic compounds, and the four main sugars sorbitol, sucrose, glucose and fructose (summarized in the Results as carbohydrates). Nitrogen was determined by a volumetric N autoanalyzer (Heraeus), P photometrically (Hitachi) as phospho-molybdate, and K in an atomic absorption spectrometer (Perkin-Elmer). The sugars were analyzed enzymatically with UV test kits (Boehringer Mannheim) and subsequent photometry (Kontron), whereas the phenolic compounds were measured as tannin equivalents with the Folin-Ciocalteus reagent (Allen et al., 1974).

For the data analysis, only females suffering a natural death were considered. From the data on development and reproduction, life-tables were constructed assuming a general immature mortality of 20% (Herbert, 1981) regardless of possible N effects (Suski and Badowska, 1975). For the N experiments, a leaf-N-dependent sex-ratio between 0.73 and 0.77 (Wermelinger and Delucchi, 1990) was used. For the other experiments, this ratio was assumed to average 0.75 (Carey and Bradley, 1982). The life-tables were analyzed according to Southwood (1978), calculating net reproductive rate (R_0) and intrinsic rate of natural increase (r_m). This was calculated iteratively by a computer program from the equation

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

where l_x is probability of survival to age class x , and m_x is age-specific fertility. From r_m the mean generation time ($G = \ln R_0 / r_m$) and doubling time ($DT = \ln 2 / r_m$) of the populations were obtained. The Jackknife technique was used to estimate the variance of these parameters. This computer-intensive method, based on the recombination of the original data, is described in more detail by Efron (1982). Examples of this technique are provided by Sokal and Rohlf (1981), Meyer et al. (1986) and Krebs (1989). The computer program calculates the life-table parameters first from the original sample. From this data set with n observations, each observation is left out in turn and the

parameters are calculated on the remaining $n - 1$ observations. From the life-table parameters thus obtained, the pseudovalues ϕ_i for recombination i can be computed as

$$\phi_i = nP_T - (n - 1)P_i$$

Where P_T is the parameter (R_0 , r_m , G or DT) of the total sample, and P_i the parameters of recombination i omitting observation i . From the total of n pseudovalues for each parameter, the mean and its standard error can be calculated in the usual way.

Where appropriate, Duncan's multiple-range test was used to separate the means.

RESULTS

In all experiments, the concentrations of the elements N, P and K in the leaves varied according to the nutrient solutions supplied to the plants. The variation of a specific element in the nutrient solution affected the leaf concentrations, not only of this nutrient, but partly of the other macroelements as well. Therefore, nutritional effects on the spider mites cannot be attributed exclusively to a specific element. All data are summarized in Table 1, while the experiments are discussed individually below.

Nitrogen

The marked decrease in leaf N concentration was correlated ($P < 0.01$) with a clear reduction of carbohydrates and an equally significant augmentation of the phenolic compounds. Only the control and the two deficiency treatments differed significantly, while within the deficiency treatments and between the control and excess treatment (5 N) only minor differences were found. The concentration of the single sugars ranged from 5 to 8% for sorbitol and 1.5 to 4.5% for glucose in all experiments (for details see Wermelinger, 1985). Potassium tended to be elevated at N excess supply. The immature developmental time and the preoviposition period of the spider mites were prolonged in the N-deficiency treatments. Developmental rate, i.e., the portion of development completed each day, was positively correlated with leaf N (Fig. 1). At the lowest N level, total fecundity broke down to one-tenth that of the control, the rate of egg production being linearly correlated to leaf N in a range between 1.5% and 3.5% N (Fig. 2). Fecundity was positively correlated with total carbohydrates and negatively with phenolic compounds (cf. Wermelinger et al., 1985). The temporal pattern of oviposition is depicted in Fig. 3A. While the control and the 5-N treatment peaked on day 4, the deficiency treatments remained at a more constant, lower level. The drop on day 5 was due to the replacement of the leaf disks the day before, and the new accommodation and webbing of the spider mites. According to fecundity, female

TABLE 1

Chemical composition of apple tree leaves (CH, carbohydrates; PC, phenolic compounds) and resulting developmental time, preoviposition period, fecundity and female weight of *Tetranychus urticae* at four different levels of N, P and K supply

Treatment	Leaf composition					Mite life-history parameters				
	N (%)	P (%)	K (%)	CH (%)	PC (%)	Devel. (days)	Preovip. (days)	Fecundity (eggs/♀)	Longevity (days)	Weight (µg)
Nitrogen										
5	3.16 ^a	1.04 ^a	1.85 ^a	10.6 ^a	8.4 ^a	9.2 ^a	1.6 ^a	73.9 ^a	14.9 ^a	17.0 ^a
1	3.03 ^a	0.84 ^b	1.77 ^{ab}	10.8 ^a	9.1 ^a	9.6 ^b	1.8 ^a	76.5 ^a	14.3 ^a	15.9 ^a
0.2	1.93 ^b	0.77 ^b	1.63 ^b	8.6 ^b	12.6 ^b	10.6 ^c	2.6 ^b	30.1 ^b	16.4 ^a	12.1 ^b
0.04	1.54 ^c	1.04 ^a	1.62 ^b	7.5 ^b	13.9 ^b	11.8 ^d	5.8 ^c	7.0 ^c	14.1 ^a	8.5 ^c
Phosphorus										
5	3.75 ^a	1.52 ^a	1.90 ^a	10.6 ^{ab}	8.8 ^a	9.2 ^a	1.0 ^a	70.7 ^a	13.6 ^a	16.0 ^a
1	3.43 ^b	1.50 ^{ab}	1.79 ^a	10.4 ^a	9.8 ^b	9.2 ^a	1.0 ^a	68.1 ^a	13.7 ^a	15.3 ^a
0.2	3.92 ^a	0.95 ^c	1.78 ^a	11.4 ^b	7.6 ^c	9.7 ^b	1.0 ^a	79.3 ^b	15.1 ^a	13.2 ^b
0.04	3.43 ^b	0.49 ^d	1.46 ^a	12.5 ^c	11.0 ^d	10.9 ^c	1.9 ^b	30.6 ^c	15.5 ^a	9.9 ^c
Potassium										
5	3.42 ^a	1.24 ^a	2.65 ^a	10.4 ^a	10.5 ^a	10.7 ^a	1.1 ^a	65.4 ^a	15.3 ^a	18.1 ^a
1	3.50 ^a	1.61 ^b	1.97 ^b	10.6 ^a	10.6 ^a	10.6 ^a	1.1 ^a	68.0 ^{ab}	14.9 ^a	19.1 ^{ab}
0.2	3.53 ^a	1.60 ^b	1.78 ^{cd}	9.7 ^a	10.2 ^a	10.7 ^a	1.0 ^a	73.9 ^b	14.1 ^a	19.8 ^b
0.04	3.50 ^a	1.56 ^b	1.62 ^d	10.0 ^a	10.6 ^a	10.9 ^a	1.0 ^a	65.6 ^a	14.4 ^a	18.9 ^{ab}

a,b,c,d Within the same nutrient experiment, different letters indicate significant difference ($P < 0.01$).

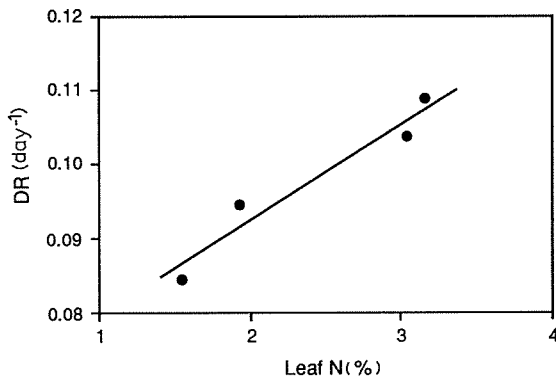


Fig. 1. Correlation between developmental rate (DR) of *T. urticae* and N content of apple leaves ($y = 0.067 + 0.013x$ $r^2 = 0.94$).

weight decreased with increasing N deficiency. With excess N supply, developmental time was further reduced, but fecundity stayed at the level of the 1-N standard. Longevity was unaffected.

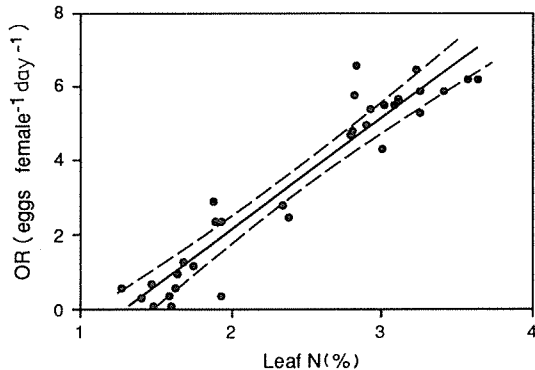


Fig. 2. Correlation between oviposition rate (OR) of *T. urticae* and N content of apple leaves ($y = -3.87 + 3.01x$ $r^2 = 0.91$, 95% confidence interval).

Phosphorus

While P concentration in the plant corresponded to the treatments, N content showed an irregular pattern and peaked at mild-deficiency 0.2 P. Phenolic compounds and, in contrast to the N experiment, carbohydrates increased under P deficiency stress, whereas K did not vary significantly. The development and preoviposition period of the two-spotted spider mite were slightly prolonged with P deficiency, but fecundity peaked at moderate P shortage where the N concentration was also highest. Correlations of fecundity were found with carbohydrates and phenolic compounds as well as with P content. The pattern of egg production was similar in the three higher P treatments (Fig. 3B), but at 0.04 P, oviposition stayed at a low level. Longevity tended to be increased by deficiency, and female weight was negatively affected. Considering all parameters among the four treatments, strong P deficiency differed most clearly from the others.

Potassium

This experiment showed the least variations between treatments in terms of both plant compounds and mite parameters. At 0.2 K, tendencies to low carbohydrates and phenolic compounds were observed. Corresponding to the fairly homogeneous results of plant contents, spider-mite parameters did not differ strongly either. Only egg production and female weight were significantly higher in the moderate K-deficiency treatment, both being positively correlated with the N content of the leaves. The oviposition pattern (Fig. 3C) illustrates the similar reaction to the treatments.

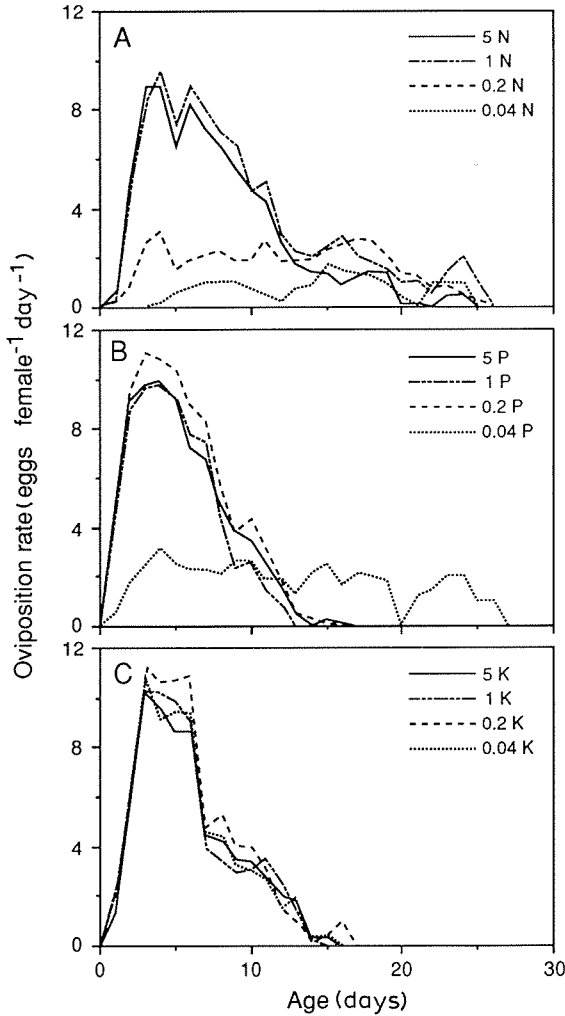


Fig. 3. Oviposition dynamics of *T. urticae* at four different levels of nitrogen (A), phosphorus (B) and potassium (C) supply to the host plants.

Life-table analysis

The analysis of the life-tables of the above life-history data on *T. urticae* is presented in Table 2. Increasing N deficiency was clearly related to a decline of the intrinsic rate of natural increase (r_m). Under unlimited conditions in terms of space and food availability, a population would grow four times faster in treatment 5 N than in treatment 0.04 N, due to faster development and higher egg production. The net reproductive rate (R_0), i.e., the number of multiplications in one generation, even differed by a factor of more than 11.

TABLE 2

Life-table analysis¹ for *Tetranychus urticae* on apple leaves at different levels of N, P and K supply

Treatment	r_m (day ⁻¹)		R_0		G (days)		DT (days)	
Nitrogen								
5	0.255 ^a	±0.006	45.2 ^a	±5.0	14.9 ^a	±0.3	2.7 ^a	±0.06
1	0.249 ^a	±0.005	46.7 ^a	±4.9	15.4 ^a	±0.4	2.8 ^a	±0.05
0.2	0.154 ^b	±0.016	18.0 ^b	±6.1	18.9 ^b	±1.1	4.5 ^b	±0.46
0.04	0.064 ^c	±0.014	4.1 ^c	±1.4	22.1 ^c	±1.6	10.9 ^c	±2.48
Phosphorus								
5	0.276 ^a	±0.007	41.9 ^a	±3.4	13.5 ^{ab}	±0.3	2.5 ^a	±0.04
1	0.275 ^a	±0.004	40.8 ^a	±2.8	13.5 ^a	±0.2	2.5 ^a	±0.04
0.2	0.271 ^a	±0.004	47.0 ^b	±3.0	14.2 ^b	±0.2	2.6 ^a	±0.04
0.04	0.163 ^b	±0.009	17.9 ^c	±3.4	17.8 ^c	±0.9	4.3 ^b	±0.22
Potassium								
5	0.236 ^{ab}	±0.005	39.0 ^a	±2.5	15.5 ^{ab}	±0.3	2.9 ^{ab}	±0.06
1	0.242 ^a	±0.004	39.7 ^a	±2.8	15.2 ^a	±0.2	2.9 ^a	±0.05
0.2	0.243 ^a	±0.006	42.4 ^a	±3.6	15.4 ^{ab}	±0.3	2.8 ^a	±0.07
0.04	0.232 ^b	±0.009	38.6 ^a	±4.2	15.8 ^b	±0.5	3.0 ^{ab}	±0.11

¹ r_m , R_0 and G , see text; DT, doubling time; means and 95% confidence limits.^{a,b,c}Within the same nutrient experiment, different letters indicate significant difference ($P < 0.05$).

Generation time (G) and doubling time of the population were significantly prolonged with N deficiency. The mite population in the 0.04-N treatment needed four times longer to double than that in the 5-N treatment.

The P experiments revealed a more heterogeneous pattern. With strong P deficiency, r_m and R_0 were markedly lower, and generation time and doubling time were longer than in the other treatments. Moderate deficiency caused, on the one hand, the highest reproductive rate R_0 (multiplications per generation), and on the other hand generation time (strongly influenced by developmental time) was longer than the control, thus yielding a slightly lower r_m than the two higher P treatments. Only the 0.04-P treatment differed in r_m from the other treatments.

Different K supplies resulted in lower r_m in the excess and strong-deficiency treatments, and in a longer generation time at 0.04 K. However, G and DT differed only slightly in all treatments, and R_0 tended to be elevated with a moderate shortage of K.

The best index of a population's performance, i.e. r_m was most strongly related to leaf N and carbohydrates in the N and P experiments. The most distinct correlation was found between r_m and the content of phenolic compounds in the leaves with all the treatments pooled (Fig. 4). Above a concentration of 10% of these secondary metabolites, spider-mite population growth

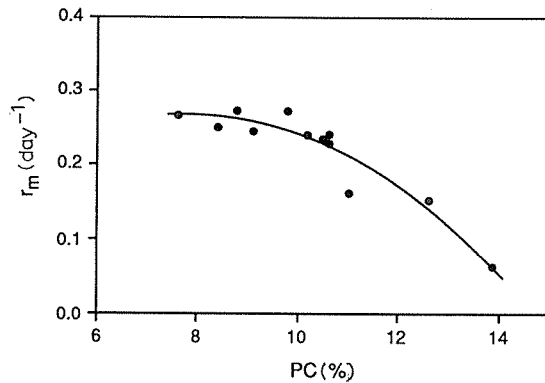


Fig. 4. Relationship between intrinsic rate of natural increase (r_m) of *T. urticae* and content of phenolic compounds (PC) in apple leaves ($y = -0.075 + 0.088x - 0.056x^2$ $8 < x < 14$, $r^2 = 0.91$).

was severely depressed. A tentative, biologically reasonable regression line was calculated.

DISCUSSION

The response of mite life-history parameters to the nutritional stress corresponds to the pattern generally reported and documented in the literature reviewed. The life-table analysis, a summarizing assessment of population performance, showed that r_m values decreased concomitantly with nutrient supply in the N and P experiments but not in the K treatments. The relatively novel Jackknife technique used for the statistical treatment of the life-tables revealed, as far as the N treatments are concerned, significant differences of all calculated life-table parameters between the standard and the two deficiency treatments. The negative effect of N deficiency on the intrinsic population growth rate (r_m) was the result of retarded development (preimaginal development and preoviposition period), diminished egg production and a slightly male-biased sex-ratio at lower N supply. Nitrogen was clearly the most important nutrient affecting plant composition and hence spider-mite population growth. Net reproductive rate (R_0) declined 11-fold in the severe N-deficiency treatment, and the time required for a population to double was four times longer. In most treatments, development and oviposition of the two-spotted spider mite were positively related not only to leaf N but also to the carbohydrate level (primarily sorbitol) and negatively to the phenolic content.

To our knowledge, there are only two studies to compare our life-table analysis to, and both investigate *T. urticae* on bean plants. Watson (1964), having two treatments of each of N, P and K, found much smaller differences in r_m values between standard and deficiency treatments for both N and P than in

our case. Potassium deficiency did not induce an altered r_m , in contrast to our findings. Watson's values for the standard treatments as determined on beans were consistently lower than ours on apple. The second study was conducted by Suski and Badowska (1975) with three fertilization levels of each N, P, K macronutrient. The N experiments showed only a modest increase of r_m with a higher N supply. In contrast to our results, excess P supply caused the highest increase rates, whereas K showed the least effects. In both studies, no plant analyses were carried out.

Some secondary plant metabolites such as phenolic compounds are known to adversely affect pathogens and insect/mite populations (Ishaaya, 1986; Dale, 1988). In the present study, total phenolics were strongly negatively related to spider-mite development, oviposition (cf. Larson and Berry, 1984) and population development, as indicated by r_m . On the other hand, negative correlations were found between phenols and nitrogen or sugar content. Therefore, it is not possible from this study to pinpoint a single factor as the true cause controlling the development of spider-mite populations. In fact, the balance between the adverse effects of phenolic compounds and the beneficial effects of amino acids and carbohydrates is suggested as the determining factor in the performance of a population. This may be illustrated by the P experiment: leaves with slight P deficiency have a somewhat lower concentration of phenolic compounds and more N and carbohydrates than in the standard treatment. This coincides with the fecundity peak. With severe deficiency, where fecundity suddenly drops, phenolic compounds are markedly higher and N is lower, thus overriding the favorable effect of still elevated carbohydrates. Similar balances were found between temperature and food quality under water stress (Wermelinger et al., 1990b).

A noteworthy aspect of all our experiments was the increase of variation with stress (cf. Table 2). This phenomenon is best evidenced by the parameters affected by development (r_m , G , DT) in the N experiment, where stress was apparently most severe. Although the mean values of e.g., r_m , in the N deficiency treatments were considerably smaller than with a sufficient N supply, their variation was much higher. Under unfavorable conditions, the genetic heterogeneity of a population, in terms of individual fitness of the females, seems to become more evident than in an optimal environment.

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