

Effect of sex-ratio on multiplication of the two-spotted spider mite as affected by leaf nitrogen

B. Wermelinger and V. Delucchi

*Institute of Plant Science, Division of Phytomedicine, ETH Zürich, Clausiusstr. 21,
8092 Zürich, Switzerland*

(Accepted 6 April 1989)

ABSTRACT

Wermelinger, B. and Delucchi, V., 1990. Effect of sex-ratio on multiplication of the two-spotted spider mite as affected by leaf nitrogen. *Exp. Appl. Acarol.*, 9: 11–18.

Spider mites (*Tetranychus urticae*) were reared individually on leaf discs of apple trees fertilized with three different N levels. Leaf nitrogen, female fecundity and mortality as well as offspring sex-ratio were determined. The sex-ratio and fecundity in the three treatments showed a slight increase at high leaf N. The correlation between sex-ratio and respective leaf N contents proved significant. In a range of 1.8–3.0% N, sex-ratio increased from 0.64 to 0.76. A relationship between increasing fecundity and higher sex-ratio was found. Mortality was not affected. Assessing these results from a population-dynamics point of view, the intrinsic rate of natural increase r_m was raised at high leaf N by 29%.

INTRODUCTION

World-wide, spider mites are of great economic importance; the two-spotted spider mite *Tetranychus urticae* Koch (Tetranychidae) is one of the most investigated, because of its widespread occurrence, feeding preferences and its simplicity to rear. While much work has been focused on its biology regulated by abiotic extrinsic factors, and on the effects (damage) on crops (for summary see Helle and Sabelis, 1985), less has been done on the effect of the physiological status of the host plants on the development of their associated pest. Spider mites reproduce arrhenotokously. Males are derived from unfertilized haploid eggs, while females arise from fertilized diploid eggs. Thus, unmated females deposit only male eggs and a mixture of both sexes is produced by mated females. The sex-ratio is a crucial factor for population growth among other physiological, behavioral, predation and abiotic parameters, because it affects the number of female offspring and hence the potential growth and spread of a population. In addition, females cause greater damage than the smaller males. There exists no 'normal' sex-ratio (Boudreaux, 1963). This depends on factors such as strain (Young et al., 1986), mating period and

male vitality (amount of spermatozoa transferred; Boudreaux, 1963), density (Wrensch and Young, 1978), maternal age (Shih, 1979; Wrensch, 1979) and host quality (Wrensch, 1979; Kondo and Takafuji, 1982; Jackson and Hunter, 1983; Youngman et al., 1988).

MATERIAL AND METHODS

Apple plants. Thirty-six seedlings of the variety Golden Delicious in the 5-leaf stage were planted in 0.9-l pots. They were divided into three equal groups, one of which was supplied with plain water (treatment 'low N'), the second with 16 mM nitrogen solution (treatment 'medium N') and the third with 32 mM N (treatment 'high N'). In order to ensure good growth the plants received a single fertilization of a nutrient solution of 1 mM P and 6 mM K after two months. Three months after planting, the small trees had reached a height of 40 cm and possessed sufficient leaves for the experiments. During rearing and experiments all plants were kept at 20°C at a photophase of 16 h in a growth chamber.

Spider mites. Young females of a *T. urticae* culture were kept for oviposition on two leaf discs (2.5 cm diameter) of each of the above described plants for 1.5 days and then removed. The resulting eggs developed into adults on these discs. From this generation, one newly emerged female and one male per disc were placed on leaf discs of the same trees and age; they were subsequently transferred to new discs 4, 7, 12, 17, 22, and 27 days after emergence. Thus, for every treatment and every female age-class, offspring were subdivided in 24 cohorts (2 discs per tree, 12 plants) unless the mother had died. During the first week, dead females were replaced by new ones of the same age and origin and males of the respective treatments were present at all times to allow mating. The resulting female-age-dependent offspring on these leaf discs were reared to adulthood to determine the sex. Tertiary sex-ratio (ratio at adulthood) was calculated as number of females/total offspring. The discs were kept in plastic trays on moist support tissue. The lids had small aerating holes to prevent condensation. The temperature inside the trays was $24.5 \pm 0.5^\circ\text{C}$; the photophase in the growth chamber was 16 h at a relative humidity of approximately 70%.

Chemical analysis. Leaves of the same age as used in the experiment were dried for 1 h at 105°C, and subsequently for two days at 60°C. They were analyzed for total N by a Carlo Erba autoanalyzer on a chromatographic basis with thermal conductivity detection.

Data analysis. The means were separated by the chi-square test (for sex-ratio), and analysis of variance followed by the Duncan multiple-range test (for

leaf N and oviposition). Correlations were calculated including 95% confidence intervals. Data were subjected to a 'lowess smoother' (Cleveland, 1985) to illustrate the fecundity/sex-ratio relationship. The effect of leaf N on population growth was assessed by life-table analysis (intrinsic rate of natural increase r_m , net reproductive rate R_o , generation time t_g ; Krebs, 1972).

RESULTS

A summary of the treatment means is given in Table 1. The varying N supply to the plants resulted in significantly different N contents of the leaf discs the mites fed upon. All sex-ratios varied around 0.75, and there was a tendency of nitrogen favoring the proportion of females. Since the variations of individual sex-ratio ranged from 0 to 1 in each treatment (cf. Overmeer and Harrison, 1969) the differences were not significant. These values represent the average sex-ratio of the total progeny produced by a female. If sex-ratio is considered in relation to the female age (Fig. 1A), however, there is evidence for differences in sex-ratio of early offspring (day 3 and 6, representing oviposition periods of days 0–4 and 5–7). The sex-ratio curves of the two high-N treatments showed a peak after approximately 1 week, roughly corresponding to the oviposition rate (Fig. 1B), but the low-N treatment steadily increased, approaching a sex-ratio level of 0.8. In the first 7 days mites of the high-N treatment exhibited a 23% higher sex-ratio than those on N-poor leaves. Generally, sex-ratio increased at the beginning, and the further course of these curves showed a levelling-off and an approximation of the treatments towards the end of the oviposition period, except for the last two dates. However, these last values are based on only a few eggs.

The three N treatments induced different oviposition rates (Table 1), which are also visible in Fig. 1B. Oviposition period and, at the same time, longevity lasted about 4 weeks regardless of the treatment, maximum oviposition rate occurring at the age of approximately 5 days. The peak on day 20 in the high-N treatment is provoked by only one female, whereas in the other treatments

TABLE 1

Nitrogen content of apple leaves (leaf N; %), sex-ratio (SR), oviposition rate (OR); eggs $\text{♀}^{-1} \text{day}^{-1}$, intrinsic rate of natural increase (r_m), net reproductive rate (R_o) and generation time (t_g ; days) of *Tetranychus urticae* at three N supply levels (treatments)¹

| Treatment | Leaf N | SR | OR | r_m | R_o | t_g |
|-----------|--------------------------|--------------------------|--------------------------|-------|-------|-------|
| Low N | 2.07 ^a ± 0.22 | 0.73 ^a ± 0.68 | 1.48 ^a ± 0.71 | 0.136 | 13.4 | 20.3 |
| Medium N | 2.50 ^b ± 0.18 | 0.74 ^a ± 0.73 | 1.68 ^a ± 0.70 | 0.157 | 15.0 | 18.4 |
| High N | 2.73 ^c ± 0.12 | 0.77 ^a ± 0.75 | 2.19 ^b ± 1.00 | 0.176 | 18.8 | 17.7 |

¹Values are means ± standard deviations; means of each column followed by different letters differ significantly ($P < 0.05$).

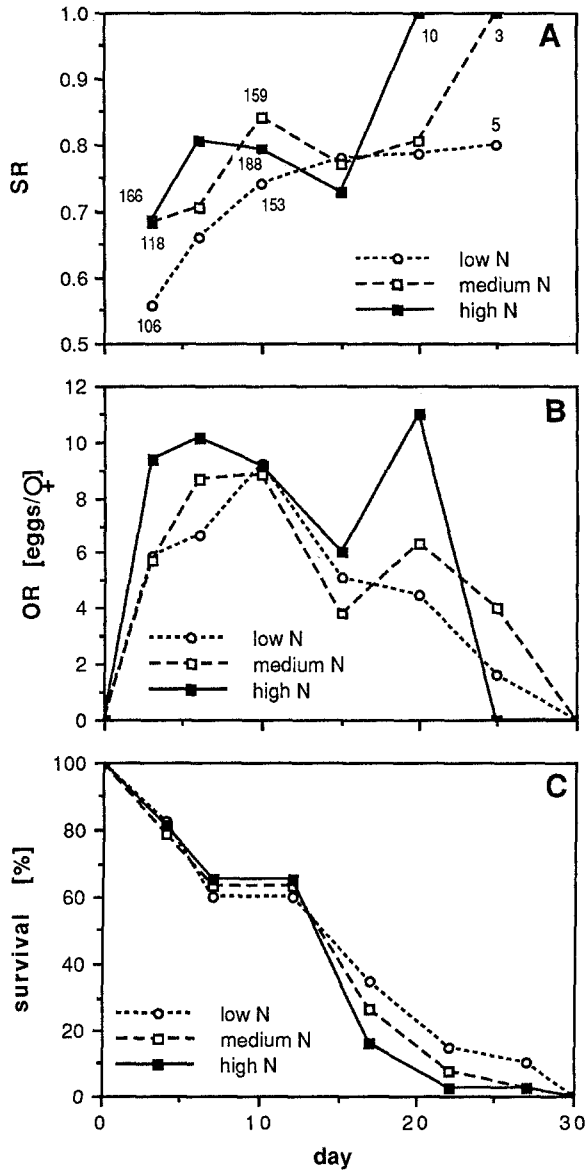


Fig. 1. Dynamics of sex-ratio SR (A), oviposition rate OR (B), and mortality (C) of *Tetranychus urticae* on apple leaves at different leaf-N levels. Values in (A) indicate number of eggs yielding sex-ratio.

more females contributed to the lower averages. The temporal distribution of the mortality was independent of the leaf N content (Fig. 1C).

Figure 2 depicts the relationship of sex-ratio and leaf N. Relating the progeny of each female to the N content of the respective tree yielded a significant

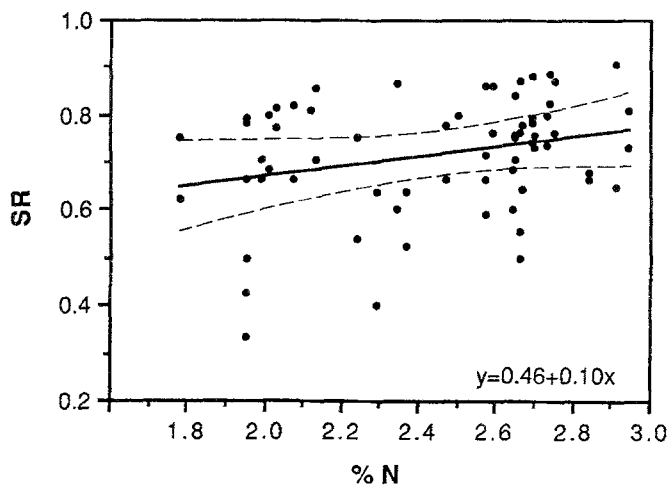


Fig. 2. Relation between apple-leaf N content and sex-ratio (SR) of *Tetranychus urticae* (correlation $P < 0.05$, confidence intervals 95%).

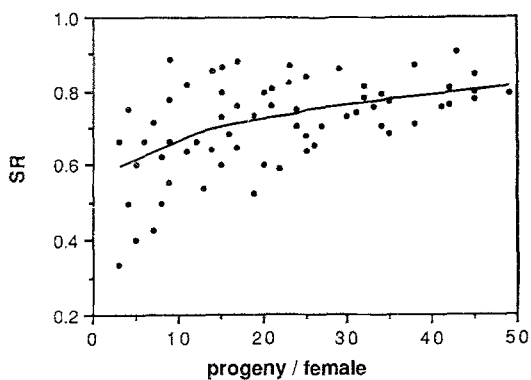


Fig. 3. Relation between female progeny and sex-ratio (SR) of *Tetranychus urticae* on apple leaves at different N supply. Line fitted by a 'lowess' smooth (see text).

correlation; however, it should be noted that variations of sex-ratio between females are large. Due to this variation, average sex-ratios of the treatments (Table 1) do not differ significantly. Nevertheless, sex-ratio was raised from 0.64 to 0.76 within the range of 1.8–3.0% leaf N, which means an increase by 19%.

Figure 3 shows the relation between the fecundity of females and the sex-ratio of their progenies. A high fecundity coincided with an elevated sex-ratio. This relationship was more evident at low fecundities. Again, the figure illustrates the variation in fecundity as well as in sex-ratio.

DISCUSSION

The sex-ratio curves were age-dependent rather than independent (Young et al., 1986). The curve shapes of the two high-N treatments were similar to those for spider-mite oviposition rate, and corresponding in magnitude to those described in the literature (Wrensch, 1979; Sabelis and van der Meer, 1986). At low N, sex-ratio increased from a low starting point until the end of oviposition. In contrast to reports by Shih (1979) and Hamilton et al. (1986), females outnumbered males at any maternal age, sex-ratio averaging ca. 0.75. Ageing *T. urticae* females did not run out of sperm after 2 weeks, as hypothesized by some authors (Shih, 1979; Wrensch, 1979). Sex-ratio was even highest at the end of the oviposition period. The relation between fecundity and sex-ratio indicates either that sex-ratio female bias is N-promoted or it increases with increasing fitness of the female, sperm not being a limiting factor (Overmeer and Harrison, 1969) and considering mating as non-recurring. Despite the non-significant differences between the treatments, the positive correlation evidences that the N content of leaves affects the sex-ratio of the two-spotted spider mite, even though the changes of sex-ratio are relatively small. From a population-dynamics point of view, however, this may prove important. The maxima as well as the differences in oviposition were smaller than in earlier experiments with wider ranges of leaf N (Wermelinger et al., 1985). Mortality was not affected. The N effect on the spider-mite parameters sex-ratio, oviposition and mortality (Fig. 1) compound to a stimulation of the population growth in the following way: sex-ratio is increased by high leaf N, most pronounced at the beginning of the oviposition period. At the same time, egg production reaches its maximum and is additionally elevated by N, and most females are still alive. Conversely, when N-induced sex-ratio differences decrease at the end of the oviposition period, the females are more likely to die, produce less eggs and therefore have a lesser effect on population growth. In other words, sex-ratio is most influenced by leaf N when its effect on population growth is strongest. For assessing the effect of sex-ratio in particular and N in general, some population parameters were calculated. Keeping fecundity and mortality uniform for all treatments, and varying only age-specific sex-ratio, the innate capacity for increase r_m was raised by 8% in the highest N treatment compared to the zero treatment. Including treatment-specific fecundity and mortality, r_m increased by 29% (Table 1). The net reproductive rate R_0 (multiplication rate per generation) increased at high leaf N by 41%, while generation time t_g was shortened by 13%. The stimulating effect of N on both fecundity and sex-ratio contributes to faster population growth and dispersal by females. However, a high r_m does not necessarily mean that a population is successful. Too high multiplication of a population may exhaust its food resources.

The increase of sex-ratio at high leaf N is in contrast to the findings of

Wrench and Young (1978) on *T. cinnabarinus* Boisd., and of Kondo and Takafuji (1982) and Young et al. (1986), who found fewer females on 'good' leaves). These authors, however, used the terms 'poor' and 'good' leaves to mean leaves with and without previous mite feeding, and no leaf analyses were performed. These results imply a leaf reaction to a previous mite population (saliva injection!) rather than a mere response to host-plant nutritional status. Our results are consistent with those of Jackson and Hunter (1983) for *Eotetranychus hicoriae* McGregor on plants with varying N supply. The higher tertiary sex-ratio (at adulthood) at high N supply found in our study may be the result of better survival of the female eggs and immature stages during development relative to the males (Kondo and Takafuji, 1982) or caused by lower quantity/quality of sperm supply by males at N deficiency.

The relation of sex-ratio to fecundity (Fig. 3) can be explained by their common correlation base nitrogen. Therefore the N dependence of SR may be triggered directly by high leaf N or may be another feature of increased fitness of the females, sex-ratio and fecundity depending on one another. It illustrates in a different way the two-fold effect of N raising sex-ratio and fecundity. A relation between sex-ratio and the oviposition rate was also reported for phytoseiid mites (Sabelis and Nagelkerke, 1987).

REFERENCES

- Boudreaux, H.B., 1963. Biological aspects of some phytophagous mites. *Annu. Rev. Entomol.*, 8: 137-154.
- Cleveland, W.S. (Editor), 1985. *The Elements of Graphing Data*. Woodsworth Advanced Books and Software, Monterey, California, 323 pp.
- Hamilton, A., Botsford, L.W. and Carey, J.R., 1986. Demographic examination of sex ratio in the two-spotted spider mite, *Tetranychus urticae*. *Entomol. Exp. Appl.*, 41: 147-151.
- Helle, W. and Sabelis, M.W. (Editors), 1985. *Spider Mites: Their Biology, Natural Enemies and Control*. Vol 1A. Elsevier, Amsterdam, 405 pp.
- Jackson, P.R. and Hunter, P.E., 1983. Effects of nitrogen fertilizer level on development and populations of the pecan leaf scorch mite (Acari: Tetranychidae). *J. Econ. Entomol.*, 76: 432-435.
- Kondo, A. and Takafuji, A., 1982. Effect of host quality on sex ratio in the two-spotted spider mite, *Tetranychus urticae* Koch (Acarina: Tetranychidae). *Jpn. J. Appl. Entomol. Zool.*, 26: 200-202.
- Krebs, C.J., 1972. *The Experimental Analysis of Distribution and Abundance*. Harper & Row, New York, 694 pp.
- Overmeer, W.P.J. and Harrison, R.A., 1969. Notes on the control of the sex ratio in populations of the two-spotted spider mite, *Tetranychus urticae* Koch (Acarina, Tetranychidae). *N.Z. J. Sci.*, 12: 920-928.
- Sabelis, M.W. and Nagelkerke, C.J., 1987. Sex allocation strategies of pseudo-arrhenotokous phytoseiid mites. *Neth. J. Zool.*, 37: 117-136.
- Sabelis, M.W. and van der Meer, J., 1986. Local dynamics of the interaction between predatory

- mites and two-spotted spider mites. In: J.A.J. Metz and O. Diekmann (Editors), *Dynamics of Physiologically Structured Populations*. Springer, Berlin, pp. 322–345.
- Shih, C.T., 1979. The influence of age of female *Tetranychus kanzawai* on sex ratio and life cycle of its progeny. In: J.G. Rodriguez (Editor), *Recent Advances in Acarology*, Vol. I. Academic Press, London, pp. 511–517.
- Wermelinger, B., Oertli, J.J. and Delucchi, V., 1985. Effect of host plant nitrogen fertilization on the biology of the two-spotted spider mite, *Tetranychus urticae*. *Entomol. Exp. Appl.*, 38: 23–28.
- Wrensch, D.L., 1979. Components of reproductive success in spider mites. In: J.G. Rodriguez (Editor), *Recent Advances in Acarology*, Vol. I. Academic Press, London, pp. 155–164.
- Wrensch, D.L. and Young, S.S.Y., 1978. Effects of density and host quality on rate of development, survivorship, and sex ratio in the carmine spider mite. *Environ. Entomol.*, 7: 499–501.
- Young, S.S.Y., Wrensch, D.L. and Kongchuensin, M., 1986. Control of sex ratio by female spider mites. *Entomol. Exp. Appl.*, 40: 53–60.
- Youngman, R.R., Sanderson, J.P. and Barnes, M.M., 1988. Life history parameters of *Tetranychus pacificus* McGregor (Acari: Tetranychidae) on almonds under differential water stress. *Environ. Entomol.*, 17: 488–495.