Energy flow in an apple plant-aphid (*Aphis pomi* De Geer) (Homoptera: Aphididae) ecosystem, with respect to nitrogen fertilization

I. Life table analyses

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Abstract

The effect of nitrogen fertilization on the life table parameters of green apple aphids, feeding on apple saplings of different nutritional quality, was investigated. The experiments were carried out with cloned apple plants (cv. Golden Delicious), all originating from one seed, growing in a climate chamber under constant conditions. The apple saplings were irrigated with nutrient solutions containing different nitrogen levels (0.2, 0.5, 1, and 3 N), and infested with *Aphis pomi* De Geer. The 1 N treatment corresponded to a 15 mM nitrogen concentration, containing NO_3^- and NH_4^+ in a 14:1 ratio. The levels of nitrogen fertilization studied here influenced the life table parameters of *A. pomi* in the following way: the mean generation time of *A. pomi*, growing on the 0.5 N treatment, was lower than the corresponding values found on the 0.2 and 1 N treatments. The highest net reproduction rate was produced on low (0.2 N) nitrogen nutrition. The intrinsic rate of natural increase was highest on the 0.5 N treatment.

Introduction

As phloem feeding insects, aphids are affected by the nutritional status of their host plants. Several authors have suggested that nitrogen could be the limiting growth nutrient for phloem feeding insects and, therefore, account for the excess sap intake necessary to acquire sufficient nitrogen (*e.g.*, Dixon, 1975; Lindemann, 1948; Mittler, 1958). This dependence can be studied via energy budgets.

Research on energy distribution within an insect population has been quite common. The qualitative aspects of food requirements by insects were reviewed by Waldbauer (1968), whereas Wiegert and Petersen (1983) included insect energy budgets and their use in population modelling. In order to quantify the impact that resulted from the feeding of *Oryzaephilus* *surinamensis* (L.) on rolled oats, White and Sinha (1981) determined an energy budget for this insect species. Llewellyn and Leckstein (1978) showed for *Aphis fabae* Scop. that the aphids reared on synthetic diets used energy less efficiently than those feeding on broad beans. Llewellyn and Hargreaves (1984) presented differences in the biology and energetics of *Macrosiphum euphorbiae* (Thomas) feeding on different sites of the host plant. An interspecific comparison by Llewellyn (1982) revealed a higher production efficiency for *Aphis fabae* Scop. than for leaf chewing insects. This increased efficiency was ascribed to the higher quality of the food consumed by fluid feeders. Randolph *et al.* (1975) found a high production efficiency for *Acyrthosiphon pisum* (Harris), which they attributed to the high nutritive quality of the host plant.

In an ongoing project, we are studying the effect of nitrogen fertilization on the energy flow in green apple aphid colonies (*Aphis pomi* De Geer). This paper presents the preliminary results with respect to energy budgets by collecting and analysing basic life table data.

Materials and methods

Plants

Apple plants (cv. Golden Delicious), all originating from one seed, were propagated by cell culture techniques under sterile conditions. The propagation and rooting media were composed according to Broome and Zimmerman (1984) and Wermelinger (1985). The rooting media were composed according to Wermelinger (1985). For adaptation, the plants were kept in aerated hydroculture consisting of 1 N nutrient solution diluted with demineralized water in a 1:7 ratio. The macronutrients of the 1 N nutrient solution were those of a Hoagland solution 2 (Hoagland and Arnon, 1938). Micronutrients were applied as suggested by Hewitt and Smith (1975). The plants were then potted in 15-cm diameter plastic pots with a 2-liter volume filled with quartz sand. The apple plants were irrigated twice daily with 50 mL of nutrient solution containing different nitrogen levels (0.2 N = 3 mM; 0.5 N = 7.5 mM; 1 N = 15 mM; and 3 N = 45 mM nitrogen). These solutions were diluted with demineralized water in a 1:1 ratio before irrigation. Demineralized water was used for additional irrigations. The experiments were carried out during 60 days.

Aphids

A group of parthenogenetically reproducing, viviparous *A. pomi* was raised on cloned apple plants (cv. Golden Delicious) growing in earth-filled pots.

The experiments were carried out in a controlled environment at 20°C/16°C (sinuous day/night temperature curve with a minimum at 6 a.m. and a maximum at 4 p.m.), a L:D = 16:8 regime, and 70% RH.

Life tables and analyses

The plants were irrigated with the four respective treatments for 11 days. Thereafter at each nitrogen fertilization level 15 plants were infested with *A. pomi*. The life table data, *i.e.* individual nymphal development time, individual number of nymphs born per virginopara, and individual mortality of two aphids per plant, were collected. The plants were inspected every two to four days for live adults and newly born nymphs. Between the sampling dates the survivorship was interpolated, and the number of nymphs born per virginopara was assigned equally to the days of the interval. At each sampling date the newly born nymphs were removed. This procedure was continued until the virginoparae died. Between the beginning of the experiments and the first sampling date some aphids were lost, and some others were damaged by manipulations. These aphids were not considered in the further evaluations.

The survivorship and the cumulative number of nymphs born per virginopara were plotted against aphid age in days.

In the first analysis, an interactive program, originally developed by A.P. Gutierrez and co-workers (University of California, Berkeley), was used to evaluate the mean generation time (T), the net reproduction rate (R_0), and the intrinsic rate of natural increase (r_m) of the *A. pomi* colonies.

In our study, the mean generation time is given in days from the birth of a virginopara until 50% of her nymphs were born. The cumulation of the products of survivorship and number of nymphs born per virginopara to each day equals R_0. The division of $\log_{10} R_0$ by T gives an approximate value of r_m. The algorithm used for calculating the life table parameters iteratively approached the exact value of r_m. For a detailed description of these parameters and their use in ecological studies, see Birch (1948), Messenger (1964a), and Southwood (1978).

In the second analysis, the variability within the life table data was considered in the computations of T, R_0, and r_m, as suggested by Chi (1988). The theoretical bases of that method were described by Chi and Liu (1985). In those studies the life table parameters are calculated
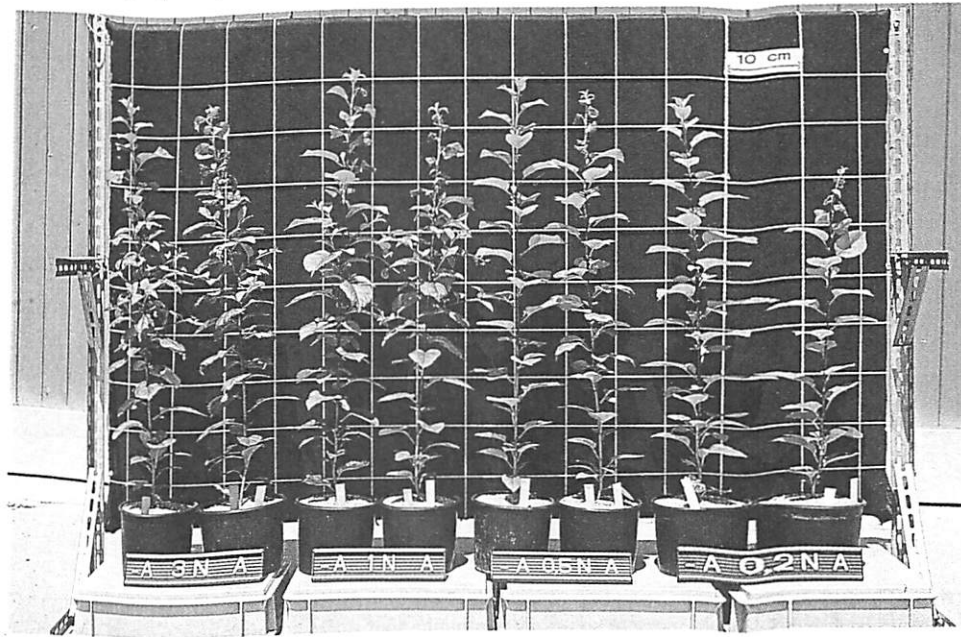
with respect to both sexes, incorporating variable developmental rates among individuals. In the present study, only virginoparae and no males were considered.

Using the jackknife technique (Efron, 1982; Meyer *et al.*, 1986), the standard deviations of each life table parameter were estimated. The differences between the life table parameters among different nitrogen treatments were tested for significance by using Duncan's new multiple range test (Duncan, 1955).

Results and discussion

Growth of apple plants

A qualitative evaluation of the apple plants' performance revealed that the 0.2 N fertilized apple plants had a reduced growth rate and showed slightly chlorotic leaves. The apex growth of the 0.5, 1, and 3 N fertilized plants was nearly identical. The 1 N and 3 N fertilized plants tended to produce lateral shoots. The upper leaves of aphid infested plants were typically curled (see photograph 1).

Life tables

The losses of *A. pomi* between the beginning of the experiments and the first sampling date were 4 and 10% on the 0.5 and 3 N treatments, respectively, and zero on the 0.2 and 1 N treatments. Accidental losses due to manipulations varied between 11 and 27% on the four treatments. As stated above, these losses were not considered in the further evaluations.

The survivorship and the cumulative number of nymphs born per virginopara to each day are shown in Figure 1. Between the first sampling date and the beginning of the reproductive period, preadult mortality was observed on the lowest (0.2 N) and the highest (3 N) nitrogen fertilization level (4 and 9%, respectively). No preadult mortality was found on the intermediate treatments (0.5 and 1 N). The survivorship of *A. pomi* at adult stage was highest on low (0.2 N) nitrogen nutrition. The aphids growing on the 0.2, 0.5, and 1 N treatments tended to have a higher number of nymphs born per virginopara than those growing on the 3 N treatment.

In contrast to the results reported by Graf *et al.* (1985), survivorship started to decrease before the reproductive period of *A. pomi* was
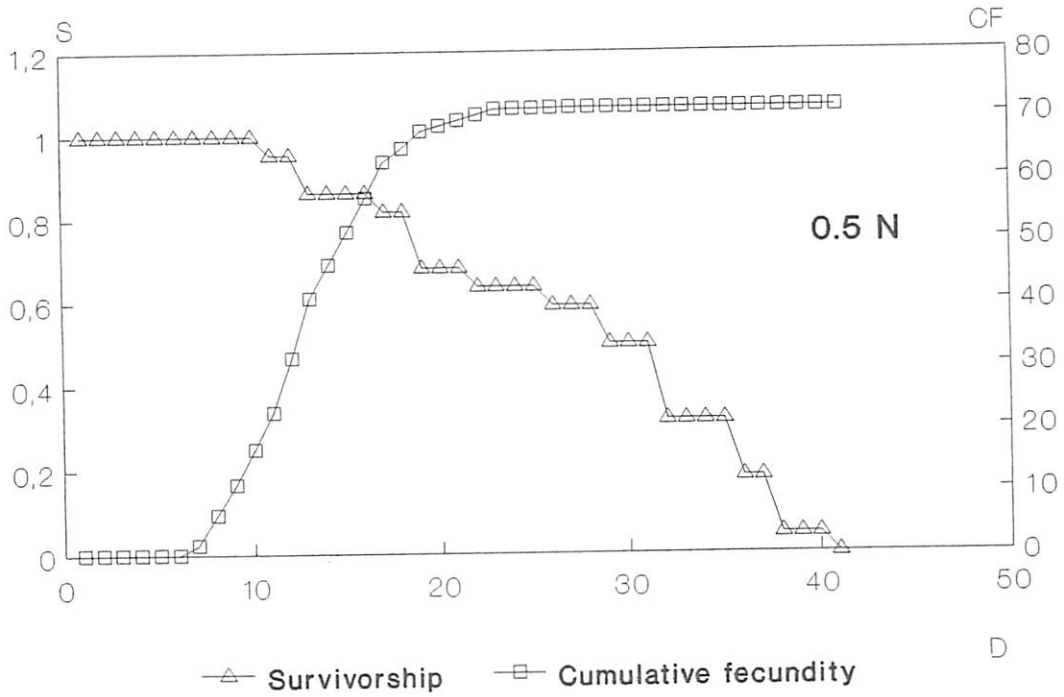

Photograph 1. Cloned apple plants (cv. Golden Delicious), all originating from one seed, after 23 days of irrigation with nutrient solutions containing four different nitrogen levels (0.2, 0.5, 1, and 3 N). The plants marked "A" had been infested with *A. pomi* for 10 days, whereas the plants marked "−A" were uninfested.
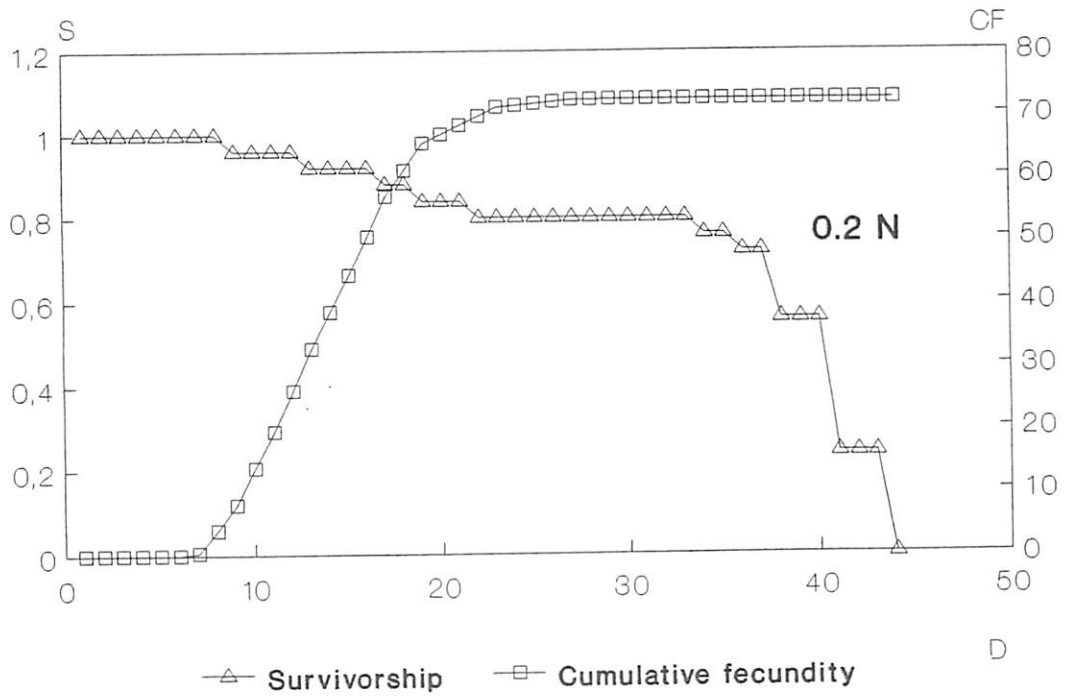
Fig. 1. Survivorship (S) and cumulative number of nymphs born per virginopara (cumulative fecundity) (CF) of *A. pomi,* growing on apple plants fertilized with nutrient solutions containing four different nitrogen levels (0.2, 0.5, 1, and 3 *N*), against aphid age (D) in days. (D = days at 20°C/16°C with a sinuous day/night temperature curve).

S
1,2
1
0,8
0,6
0,4
0,2
0

CF
80
70
60
50
40
30
20
10
0

0   10   20   30   40   50

1 N

—△— Survivorship   —□— Cumulative fecundity

D

S
1,2
1
0,8
0,6
0,4
0,2
0

CF
80
70
60
50
40
30
20
10
0

0   10   20   30   40   50

3 N

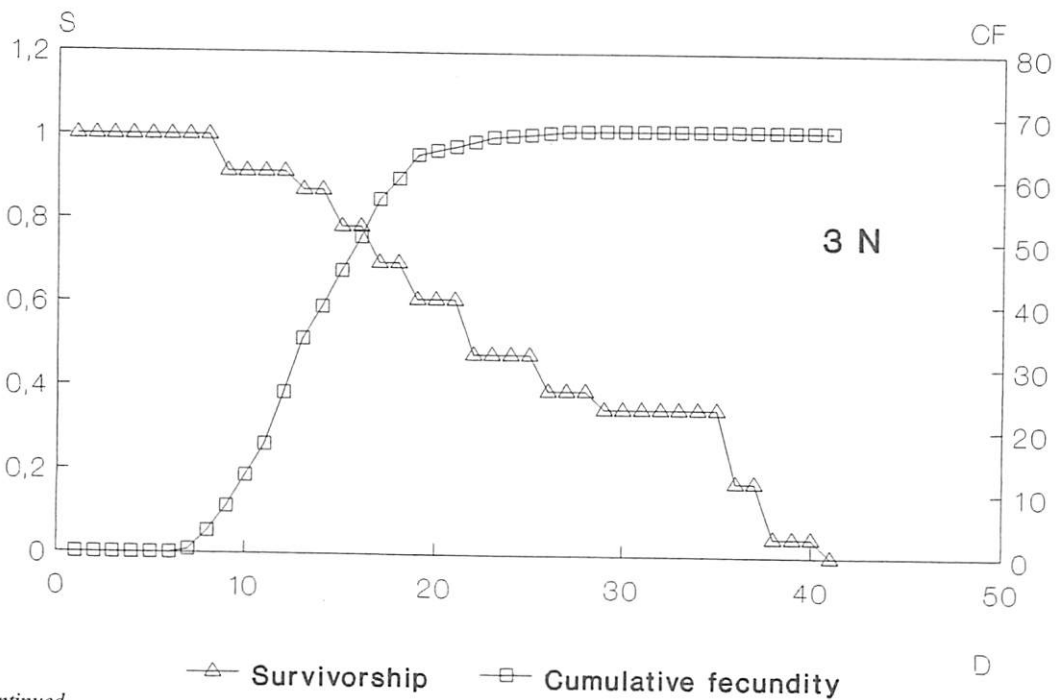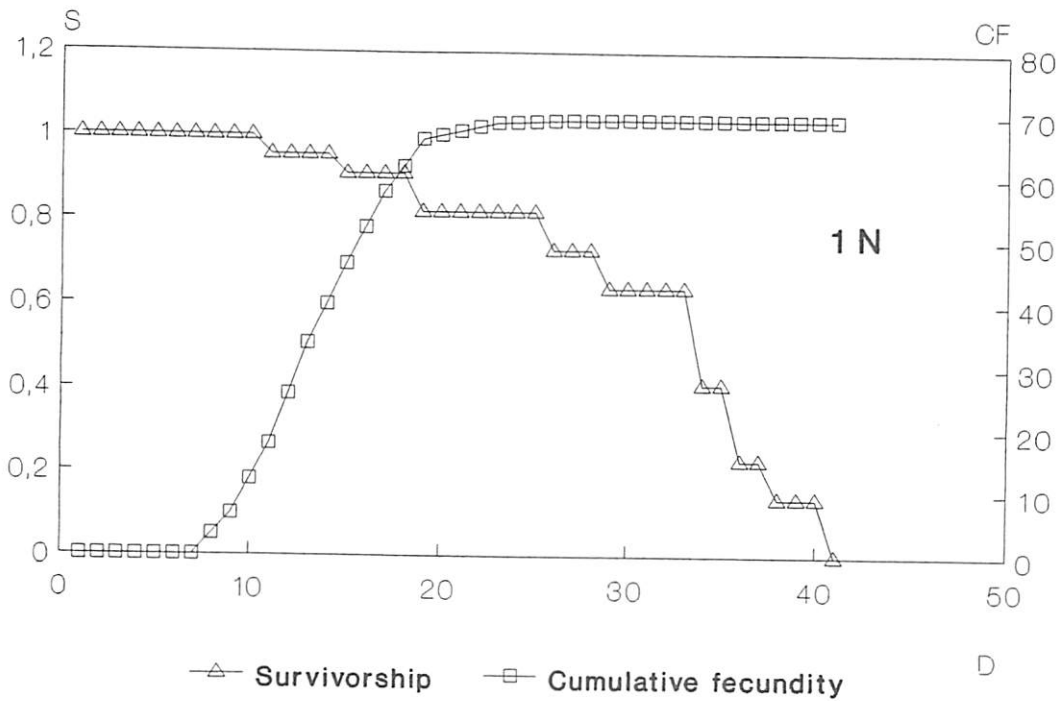—△— Survivorship   —□— Cumulative fecundity

D

Fig. 1. continued

terminated (see Fig. 1). However, in the experiments reported by Graf *et al.* (1985), the plants were replaced weekly in order to maintain a constant food quality, and the influence of differ-

ent constant temperatures was investigated. In our study, the aphids remained on the same plants throughout the experiments, and they were exposed to rhythmically fluctuating tem-

peratures. The purpose of this work was to analyse the effect of the host plants' nutritional status on aphid life table parameters.

An additional difference in the aphids' behaviour may be due to the original properties of the *A. pomi* colonies: In the experiments described by Graf *et al.* (1985), the virginoparae were taken from an orchard, whereas the aphids used in our experiments were reared on cloned apple saplings (cv. Golden Delicious) for several generations.

The calculated values of mean generation time, net reproduction rate, and intrinsic rate of natural increase are summarized in Table 1. The mean generation time of *A. pomi*, growing on the 0.5 N treatment, was lower than the corresponding values found on the 0.2 and 1 N treatments. The highest net reproduction rate was produced on low (0.2 N) nitrogen nutrition. The intrinsic rate of natural increase of *A. pomi* was highest on the 0.5 N treatment. In field experiments with *Drepanosiphum platanoides* (Schr.), Dixon (1963; 1966) found a positive correlation between the nutritive status of the host plant, expressed as soluble nitrogen content in the leaves, and the net reproduction rate of the aphids. Based on his results, we expected to find

a positive correlation between the life table parameters and the levels of nitrogen supply.

We did not find such a result. The differences between our work and the experiments described by Dixon (1963; 1966) were as follows: In his study, the variability in soluble nitrogen contents was due to redistribution processes during senescence, whereas we used young plants, and we controlled the amount of available nitrogen by different nitrogen fertilization levels. Moreover, in Dixon's experiments, senescence may have affected the aphid population in other ways than through soluble nitrogen content.

If age was expressed in physiological units of day-degrees above a developmental threshold of 5.9°C rather than in days, then a comparison with the values reported by Graf *et al.* (1985) could also be made. From a rough evaluation of the life table parameters of *A. pomi*, we expect that the intrinsic rates of natural increase, as presented in Table 1, will be considerably higher than the corresponding values reported by Graf *et al.* (1985). As stated above, the aphids reared by Graf *et al.* (1985) were kept at constant temperatures, whereas those used in our experiments were subjected to rhythmically fluctuating temperatures of 24-hour periodicity. Messenger (1964a; 1964b) found for *Therioaphis maculata* (Buckton) that the life table data monitored at fluctuating temperatures revealed higher values of T, R_0, and r_m. A crude comparison of our results with those presented by Graf *et al.* appears to support this finding also for *A. pomi*.

Incorporation of variability among individuals produced different values of T, R_0, and r_m for *Phthorimaea operculella* (Zeller), as reported by Chi (1988). The results from our experiments tend to support this finding also for *A. pomi*. Incorporation of variability among individuals increased the mean generation time of *A. pomi* by 5% and left the net reproduction rate unchanged. The intrinsic rate of natural increase of *A. pomi* was decreased by 5% after the incorporation of variability among individuals.

A statistical analysis of the values of T and r_m revealed the following significant differences: The mean generation time of *A. pomi*, growing on the 0.5 N treatment, was significantly lower ($P < 0.05$) than the corresponding values found on the 0.2 and 1 N treatments (see Table 1). The

Table 1. Mean generation time (T) in days, net reproduction rate (R_0), and intrinsic rate of natural increase (r_m) per day of *A. pomi*, growing on apple plants fertilized with nutrient solutions containing four different nitrogen levels (0.2, 0.5, 1, and 3N, with 25, 22, 22, and 23 as number of replicates, respectively). (S.D. = standard deviation). Means followed by the same letter are not significantly different from each other at 5% level

Excluding variability

N	T	R_0	r_m
0.2	11.49	66.16	0.3650
0.5	10.65	63.27	0.3895
1	11.57	64.68	0.3603
3	11.26	55.17	0.3561

Including variability

N	T ± S.D.	R_0 ± S.D.	r_m ± S.D.
0.2	12.06 ± 1.04a	66.16 ± 17.94	0.3476 ± 0.0294a
0.5	11.24 ± 0.83b	63.77 ± 16.50	0.3698 ± 0.0307b
1	12.14 ± 0.84a	64.68 ± 13.33	0.3437 ± 0.0230a
3	11.72 ± 1.25ab	55.17 ± 22.99	0.3424 ± 0.0496a

intrinsic rate of natural increase was highest ($P < 0.05$) on the 0.5 N treatment. The differences between the other values of T and r_m were not significant at 5% level.

In conclusion, the life table analyses of *A. pomi*, growing on apple plants fertilized with nutrient solutions containing different nitrogen levels, produced different values of T, R_0, and r_m. The mean generation time of *A. pomi*, growing on the 0.5 N treatment, was lower than the corresponding values found on the 0.2 and 1 N treatments. The highest net reproduction rate was produced on low (0.2 N) nitrogen nutrition. Within the range of nitrogen fertilization levels investigated here, the intrinsic rate of natural increase reached a maximum on the 0.5 N treatment. Therefore we consider the range of nitrogen treatments evaluated here appropriate for further experimentation.

Life table analyses alone cannot reveal the causes underlying the differences between the values of T, R_0, and r_m. A more complete investigation of the energy flow in the apple plant-aphid ecosystem, as affected by nitrogen fertilization, is necessary.

References

Birch L C 1948 The intrinsic rate of natural increase of an insect population. J. Anim. Ecol. 17, 15–26.
Broome O C and Zimmerman R H 1984 Culture of shoot meristems: Fruit plants. In Cell Culture and Somatic Cell Genetics in Plants, Vol. 1. Ed. I K Vasil. pp 118–119. Academic Press, London.
Chi H 1988 Life-table analysis incorporating both sexes and variable development rates among individuals. Environ. Entomol. 17, 26–34.
Chi H and Liu H 1985 Two new methods for the study of insect population ecology. Acad. Sin., Bull. Inst. Zool. 24, 225–240.
Dixon A F G 1963 Reproductive activity of the sycamore aphid, Drepanosiphum platanoides (Schr.) (Hemiptera, Aphididae). J. Anim. Ecol. 32, 33–48.
Dixon A F G 1966 The effect of population density and nutritive status of the host on the summer reproductive activity of the sycamore aphid, Drepanosiphum platanoides (Schr.). J. Anim. Ecol. 35, 105–112.
Dixon A F G 1975 Aphids and translocation. In Encyclopedia of Plant Physiology, Vol. 1. Eds. M H Zimmermann and J A Milburn. pp 154–170. Springer-Verlag, Berlin.
Duncan D B 1955 Multiple range and multiple F tests. Biometrics 11, 1–42.
Efron B 1982 The Jackknife, the Bootstrap and Other Resampling Plans. CBMS-NSF Regional Conference Series in Applied Mathematics. Society for Industrial and Applied Mathematics, Philadelphia, PA.
Graf B, Baumgärtner J and Delucchi V 1985 Life table statistics of three apple aphids, Dysaphis plantaginea, Rhopalosiphum insertum, and Aphis pomi (Homoptera, Aphididae), at constant temperatures. Z. ang. Ent. 99, 285–294.
Hewitt E J and Smith T A 1975 Plant Mineral Nutrition. The English Universities Press, London, 298 p.
Hoagland D R and Arnon D I 1938 The water-culture method for growing plants without soil. Agric. Exp. Sta. Calif. Circ. 347.
Lindemann C 1948 Beitrag zur Ernährungsphysiologie der Blattläuse. Z. Vergl. Physiol. 31, 112–133.
Llewellyn M 1982 The energy economy of fluid-feeding herbivorous insects. In Proc. 5th Int. Symp. Insect-Plant Relationships, Wageningen, 1982. Eds. J H Visser and A K Minks. pp 243–251. Pudoc, Wageningen.
Llewellyn M and Hargreaves C E M 1984 The biology and energetics of the potato aphid Macrosiphum euphorbiae, living in galls of the apple aphids Dysaphis devecta and Aphis pomi. Entomol. Exp. Appl. 35, 147–158.
Llewellyn M and Leckstein P M 1978 A comparison of energy budgets and growth efficiency for Aphis fabae Scop. reared on synthetic diets with aphids reared on broad beans. Entomol. Exp. Appl. 23, 66–71.
Messenger P S 1964a Use of life tables in a bioclimatic study of an experimental aphid-braconid wasp host-parasite system. Ecology 45, 119–131.
Messenger P S 1964b The influence of rhythmically fluctuating temperatures on the development and reproduction of the spotted alfalfa aphid, Therioaphis maculata. J. Econ. Entomol. 57, 71–76.
Meyer J S, Ingersoll C G, McDonald L L and Boyce M S 1986 Estimating uncertainty in population growth rates: Jackknife vs. bootstrap techniques. Ecology 67, 1156–1166.
Mittler T E 1958 Studies on the feeding and nutrition of Tuberolachnus salignus (Gmelin) (Homoptera, Aphididae). III. The nitrogen economy. J. Exp. Biol. 35, 626–638.
Randolph P A, Randolph J C and Barlow C A 1975 Age-specific energetics of the pea aphid, Acyrthosiphon pisum. Ecology 56, 359–369.
Southwood T R E 1987 Ecological Methods. Chapman and Hall, London, 548 p.
Waldbauer G P 1968 The consumption and utilization of food by insects. Adv. Insect Physiol. 5, 229–288.
Wermelinger B 1985 Einfluss des Ernährungszustandes der Wirtspflanze auf den Befall durch die Gemeine Spinnmilbe (Tetranychus urticae Koch). Diss. ETH Nr. 7821, Zürich, 99 p.
White N D G and Sinha R N 1981 Energy budget for Oryzaephilus surinamensis (Coleoptera: Cucujidae) feeding on rolled oats. Environ. Entomol. 10, 320–326.
Wiegert R G and Petersen C E 1983 Energy transfer in insects. Annu. Rev. Entomol. 28, 455–486.