Experimental & Applied Acarology, 14 (1992) 185–199
Elsevier Science Publishers B.V., Amsterdam

A demonstration of asynchronous local cycles in an acarine predator–prey system

Gerrit van de Klashorst[a,c], J. Les Readshaw[b], Maurice W. Sabelis[c] and Robert Lingeman[c]

[a]*Australian National University, Zoology Department, Canberra, A.C.T., Australia*
[b]*CSIRO, Division of Entomology, Canberra, A.C.T., Australia*
[c]*University of Amsterdam, Department of Pure and Applied Ecology, Amsterdam, Netherlands*

ABSTRACT

van de Klashorst, G., Readshaw, J.L., Sabelis, M.W. and Lingeman, R., 1992. A demonstration of asynchronous local cycles in an acarine predator–prey system. *Exp. Appl. Acarol.*, 14: 185–199.

Population fluctuations in a continuous predator–prey system consisting of the spider mite, *Tetranychus urticae* Koch and its predator, *Typhlodromus occidentalis* Nesbitt, were assessed for almost 2 years (ca. 50 prey generations), on six mini-orchards of young apple trees in a climatically controlled glasshouse. During the first half of the experiment the plants were either 'connected' to each other with dowel rods or 'unconnected' and separate. In the second half, the plants were all 'connected'. Population densities of both prey and predator on the unconnected mini-orchards were always higher than on the connected ones. Within the mini-orchards (=local scale), prey and predator populations go through a pattern of large amplitude cycles which continued throughout the experimental period. At the regional scale (mean over all mini-orchards) two types of fluctuations were observed. Large amplitude fluctuations associated with synchrony of the local cycles and small amplitude fluctuations associated with periods when local population cycles are proceeding out of phase. Transition from synchronous to asynchronous cycles took place very fast (within a few weeks), suggesting a mechanism generating asynchrony and possibly also partial refuges, which in turn trigger stabilising mechanisms at a regional scale. Causes of the synchrony are unclear. They may relate to the application of a pesticide (pirimicarb) used to control aphids, but there may just as well be an indirect form of causation, e.g. whereby the factors that promote aphid outbreaks also promote spider-mite population growth and temporary escape from control by the predators. Despite the synchronising factors the predator–prey system persisted, without external inputs, at a fairly small spatial scale, the size of a small glasshouse. Assessing the spatial scale and heterogeneity whereby decoupling of local cycles is sufficient for the cycles to proceed out of phase, remains an important area of experimental research. The experiment reported here provides some first clues and may form a standard for forthcoming experiments to assess the mechanisms promoting asynchrony, persistence and possibly also stability.

Correspondence to: Dr Gerrit van de Klashorst, University of Amsterdam, Department of Pure and Applied Ecology, Section Population Biology, Kruislaan 302, 1098 SM Amsterdam, Netherlands.

0168-8162/92/$05.00 © 1992 Elsevier Science Publishers B.V. All rights reserved.

INTRODUCTION

Several predator–prey systems are known to persist under natural conditions, while they are demonstrably unstable at a local spatial scale (see Andrewartha and Birch, 1954; Murdoch et al., 1985). In view of this phenomenon, many theoretical workers have constructed mathematical models describing population events to address the question of why persistence depends on spatial scale (Maynard Smith, 1974; Hilborn, 1975; Gurney and Nisbet, 1978; Fujita, 1983; Takafuji et al. 1983; Nachman, 1987a,b). What their models show is not so much that persistence arises when local predator–prey cycles proceed out of phase. That would be no more than a truism. The important message of the models is that there are processes that keep local cycles out of phase. Such processes should contribute to the decoupling of local predator–prey populations. The answer to the question: "Why persistence?", should therefore be obtained by considering the dispersal processes. Dispersal success depends on the innate properties of the organism and on the spatial structure of its physical environment, but also on the distribution of its food source. Clearly, dispersal success should be neither too low, as this may lead to regional extinction, nor too high, as this leads to strong coupling of local cycles and therefore increased risk of regional extinction. So far it has been difficult to find the spatial scale at which such intermediate levels of dispersal success are realised. Current theoretical models, through their lack of a realistic spatial structure cannot make predictions of the relevant spatial scale and heterogeneity required. Therefore, experimental workers are bound to use a trial-and-error approach.

We contend that the population experiments published to date (A.D. Taylor, 1988) do not provide convincing evidence for long-term persistence in predator–prey systems, let alone for the roles of dispersal and asynchronous cycles in effectuating persistence. The reasons for this lack of evidence are manifold. Firstly, most experiments (e.g. Huffaker, 1958; Huffaker et al., 1963; McMurtry and van de Vrie, 1973; Burnett, 1979; Takafuji et al., 1983) were carried out over rather short periods; had the experiments been continued one may wonder what would happen to population persistence. Secondly, most, if not all experiments, show large cycles in the overall population, suggesting coupling of local cycles, rather than decoupling. In these cases, persistence might critically depend on survival probabilities during population troughs, rather than depend on asynchrony. For example, we suspect that much of the cycles demonstrated by Huffaker (1958) and Huffaker et al. (1963) may be due to the lucky few females that survived during the population troughs. Burnett's (1979) and Nachman's (1981) experiments in glasshouses also showed overall population cycles, making it difficult to distinguish between the role of asynchrony and that of survival in very small populations. Finally, all these experiments suffer from the fact that arbitrary initial

numbers of predators and prey were introduced. Hence, it should come as no surprise that populations initially oscillate. Many models of strongly regulated populations would show fluctuations starting from arbitrary initial numbers, but these fluctuations do not bear any relation to the ultimate dynamic phenomena after a longer period. This is a serious objection as it makes it even more difficult to assess cause and effect.

In this paper we present the results of an experiment, unique in that it was carried out over a relatively long period of nearly two years, which is equivalent to about 50 generations of the prey species *T. urticae*. Most importantly, the observations were started after populations of predator and prey had been established for almost a year. The results show that asynchrony and dispersal play crucial roles in producing erratic fluctuations of a small amplitude at the overall spatial scale, but of a larger amplitude at a local spatial scale.

MATERIALS AND METHODS

Cultural methods and spatial arrangement

The experiments were conducted in a glasshouse of 7.0 × 5.7 m at the CSIRO Division of Entomology, Canberra, Australia, in which temperature was kept at 25 °C with thermostatically controlled evaporative coolers and fan heaters (Fig. 1). In summer, peak temperatures of up to 28 °C occurred. During some winter nights the minimum fell to 19 °C. In winter, fluorescent tubes provided a daily photophase of 16 h.

For the experiments six blocks of 48 individually potted 'Granny Smith' apple seedlings were arranged on benches of 2.28 × 0.68 m. The distance be-

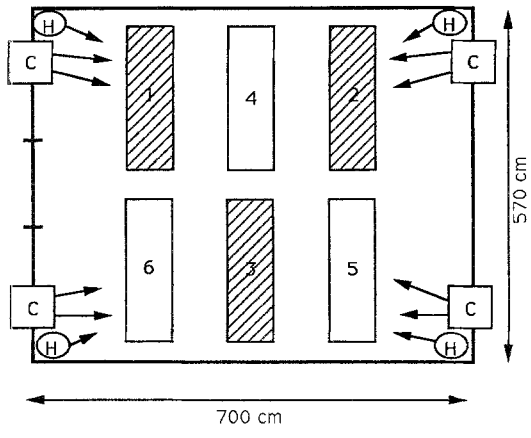

Fig. 1. Spatial arrangement of mini-orchards in the glasshouse; H, heating fans, C, cooling fans; arrows indicate air currents; plants on hatched benches were connected with wooden dowel rods during weeks 4–43; plants on all benches were connected after week 43.

tween plants was about 19 cm. These blocks of seedlings are referred to as 'mini-orchards'. The spatial arrangement of the mini-orchards is shown in Fig. 1.

Continuous foliage for the long-term population studies was maintained by a system of alternate pruning. Every alternate plant was pruned every 6–8 weeks. During the 96 weeks of the experiments there were 14 pruning cycles. After pruning, the pruned plants were about 15 cm in height and could not be used for sampling because they bore too few leaves; the alternate plants then had a height of about 50 cm and bore about 30–50 leaves. After a further 6–8 weeks the sample plants reached a height of 120–150 cm with about 100 leaves and were pruned again to keep the system manageable. Sampling then started from the alternate plants and this system of alternate pruning and sampling was continued until the end of the experiment.

To assess the effect of dispersal on predator–prey dynamics two levels of connectivity between plants were studied. After week 4, the plants within mini-orchards 1, 2 and 3 were connected to each other by a grid of dowel rods (6 mm diam.), at about 10 cm above soil level. After 43 weeks, plants within mini-orchards 4, 5 and 6 were also connected in the same way. These mini-orchards are referred to as 'connected' or 'unconnected'. Contact between adjacent plants within each mini-orchard was reduced by tying the plants to vertical wooden stakes.

Infestation and sampling

The mini-orchards had been infested with prey (*Tetranychus urticae* Koch) and predator (*Typhlodromus occidentalis* Nesbitt) originating from a commercial orchard near Canberra, nine months before the start of the observations considered here.

Preliminary sampling showed that *T. urticae* and *T. occidentalis* were unevenly distributed on upper and lower leaves. However, all stages of both species were well represented on leaves from the middle section of the plants. Therefore a relative estimate of population size both in time and space was obtained by weekly removing one leaf from the middle section of each plant. Thus, 24 leaves were taken from each mini-orchard, i.e. about 1–5% of the total leaf area. All stages of prey and predator mites were counted on both sides of each leaf, using a dissecting microscope ($\times 12$ or $\times 25$) and the results for each leaf were recorded separately. When spider mite densities were higher than 20 per leaf, only the mites on a 0.5-cm wide strip, at a right angle to the midrib, were counted. The number on this strip was then extrapolated to the whole leaf area to give an estimate of the mite density on the leaf (Readshaw, 1975). Predator mites, being fewer in number, were always counted on the whole leaf. Samples were taken each week except for weeks 17, 32, 45, 62, 77 and 79. Other potential prey, such as the false spider mite, *Brevipalpus obovatus* Donnadieu, were also recorded.

To assess whether aerial migration of mites occurred between mini-orchards, four cylindrical sticky traps, each with a surface area of 60 cm^2, were suspended from the frame of the glasshouse during weeks 86 and 87.

Pesticide and fertilizer treatments

The mini-orchards were sprayed every 2–3 weeks with bupirimate 0.01% a.i. for control of powdery mildew, and with azinphos-methyl 0.05% a.i. and captan 0.1% a.i. to simulate the pesticide regime in commercial orchards. The three chemicals were applied as a mixture. Aphids that entered the glasshouse occasionally (*Aphis citricola* Van Der Goot, *Aphis gossypii* Glover and *Aphis craccivora* Koch) were controlled with pirimicarb 0.034% a.i. The first chemical application was by spraying (PS in Fig. 2), but later by root drenches at 100 ml solution per plant (PD1 in Fig. 2). The last two root drench applications had a reduced concentration of 0.025% a.i. (PD2 in Fig. 2). The mini-orchard studies were terminated by two acaricide sprays (cyhexatin 0.01% a.i.) in weeks 95 and 96.

The plants were supplied weekly with a water-soluble complete fertilizer (1 g Aquasol® /l water) and once every 3 to 4 weeks with iron chelate (13.2 mg Sequestrene® /l water). Thus, depletion of N, P and K is unlikely to have occurred during the experiment.

RESULTS

Regional population trends

The average weekly population densities of *T. urticae* and of *T. occidentalis* for the whole glasshouse system, i.e. the mean values for all six mini-orchards, are illustrated in Fig. 2 together with the details of the pirimicarb treatments. Population trends for each of the six mini-orchards are shown separately in Figs. 3 and 4. In Fig. 2 one can see a clear distinction between the first and the second part of the experiment, which are therefore designated Period I (week 1–52) and Period II (week 53–96). This distinction into two periods was supported by time series analysis of our data discussed by Lingeman and van de Klashorst (1992).

There were nine predator–prey fluctuations in the populations of both species during the 96 weeks of the experiments (Fig. 2). During the first half of the experiment (Period I), when three of the mini-orchards were unconnected, there were four distinct fluctuations with *T. urticae* peaks of 367, 13, 143 and 476 mites/leaf (all stages) and *T. occidentalis* peaks of 1.1, 0.7, 5.2 and 4.8 mites/ leaf, reflecting the abundance of the prey population in each of the cycles. The first, third and fourth population fluctuations caused severe leaf damage (bronzing) on many plants, irrespective of whether they were connected or not (shading in Fig. 3). During the second half of the experi-

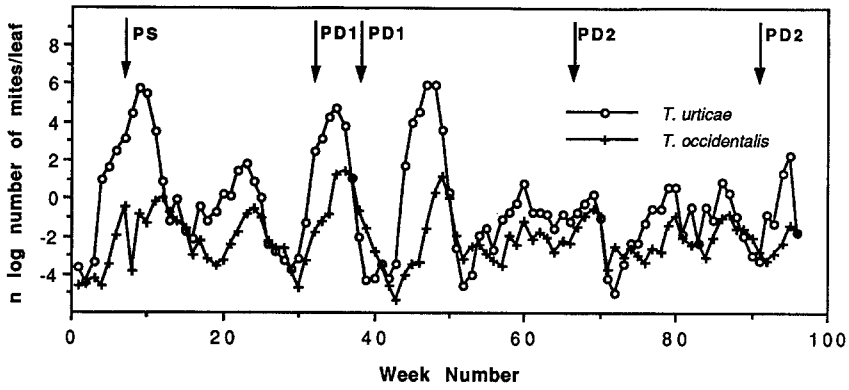

Fig. 2. Regional population trends (mean of six mini-orchards) for *T. urticae* and *T. occidentalis*. Applications of pirimicarb: PS, spray at 0.034% active ingredient (a.i.); PD1, root drench at 0.034% a.i.; PD2, root drench at 0.025% a.i.

ment (Period II) when the mini-orchards were all connected, the average population peaks were much lower and indeed the cycles were hard to distinguish. The mean peak densities were 3.9, 11.3, 6.0, 10.7 and 39.6 per leaf for *T. urticae* and 0.5, 1.5, 0.8, 1.2 and 0.6 per leaf for *T. occidentalis*. There was no leaf damage during this period.

The estimates of the means for all weekly sample abundances for each of the mini-orchards and the overall mean are presented in the upper part of fig. 2 in Lingeman and van de Klashorst (1992) and estimates of the associated variances are given in the lower part of the same figure. During Period I the means of both *T. urticae* and *T. occidentalis* in mini-orchard 1–3 are considerably lower than those in mini-orchard 4–6. This difference is as expected because connectivity between plants provides the predatory mites with better opportunities to track the colonisation of spider mites within the mini-orchards, causing lower population densities and lower amplitudes of the cycles. During Period II there is no difference of connectivity between plants in any mini-orchard. During Period II both means and variances of *T. urticae* are much smaller compared to Period I. For *T. occidentalis* the differences of the means are less evident. Only mini-orchard 6 shows a different behaviour with very large differences of the means but practically equal variances between Period I and Period II.

Finally note that the variance in *T. occidentalis* abundance is consistently smaller than the variance for *T. urticae* abundance.

Local population trends

Figures 3 and 4 illustrate the population trends on each of the mini-orchards for prey and predator mites respectively. In both sets of graphs it is clear that the four population fluctuations during Period I were closely syn-

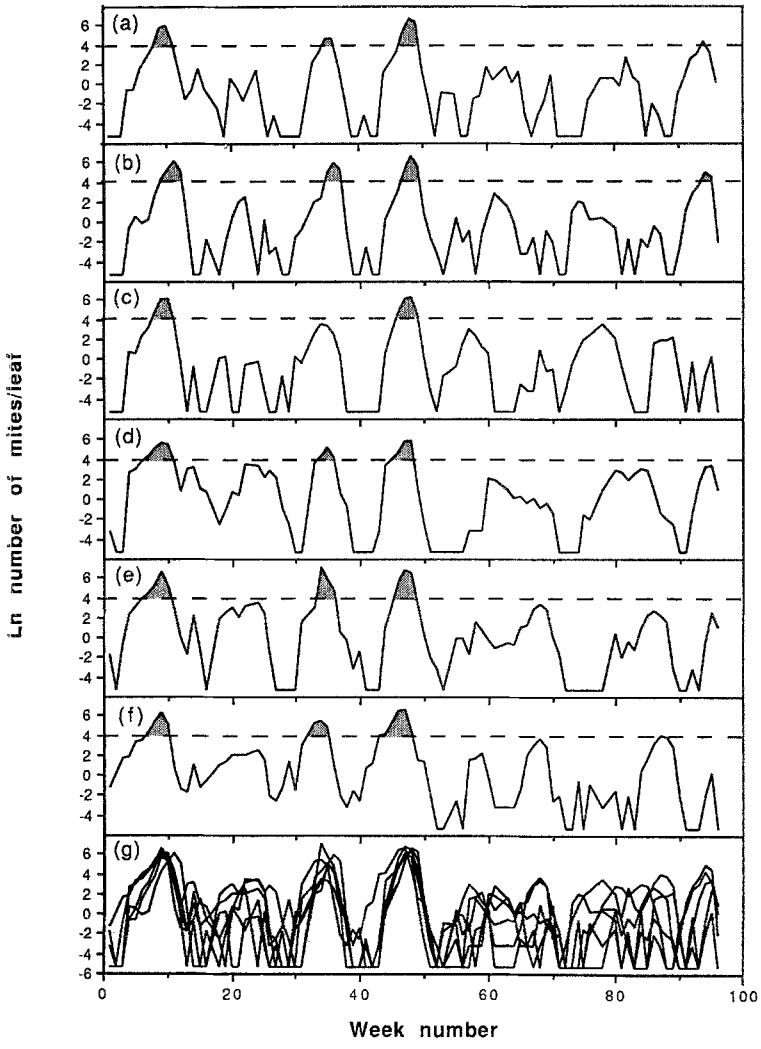

Fig. 3. Population trends in mini-orchards 1–6 (a–f) and combined (g) for *T. urticae*.

chronized irrespective of whether the mini-orchards were connected or unconnected. The second population fluctuation was lower in amplitude than the other three. During the other three population fluctuations, severe leaf damage was caused (shading in Fig. 3). During the second half of the experiment (Period II), after all the plants had been connected, the cycles became asynchronous and the mite peaks were lower, resulting in a generally lower amplitude (0–30 versus 0–500 mites per leaf) and a slightly shorter period (8–9 versus 12–14 weeks). The asynchrony in Period II also caused mean population fluctuations to level off.

That the fluctuations in Period I differ from those in Period II becomes

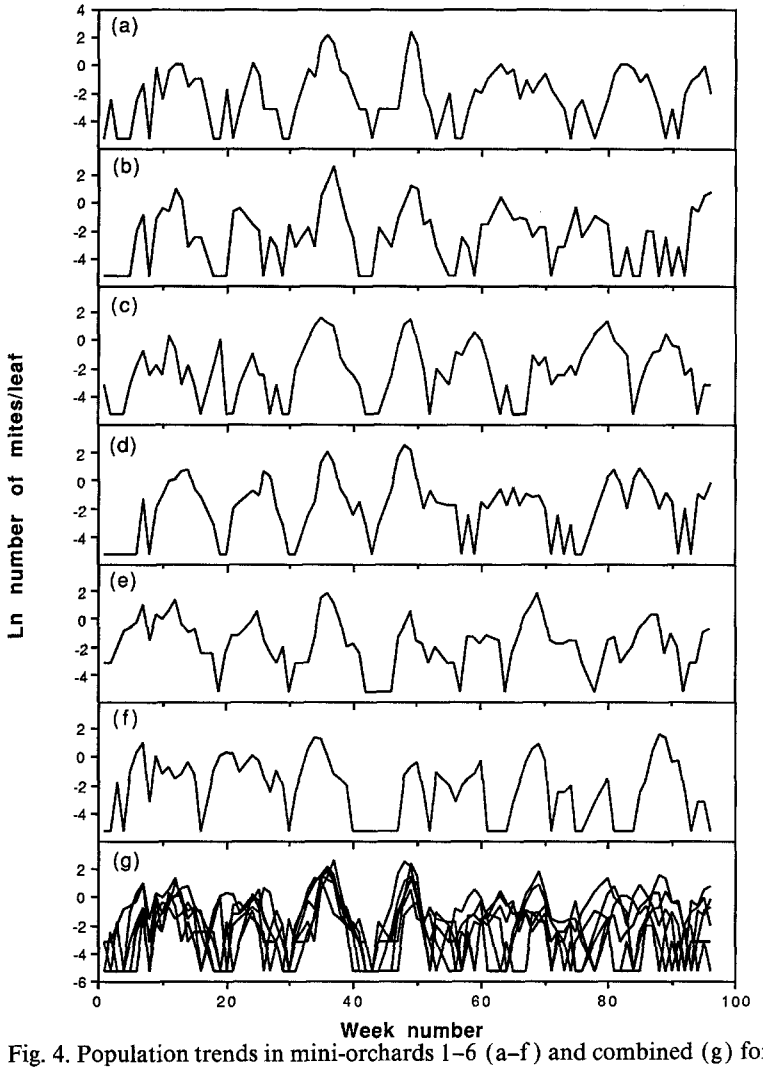

Fig. 4. Population trends in mini-orchards 1–6 (a–f) and combined (g) for *T. occidentalis*.

even more obvious at closer inspection of the within-mini-orchard dispersion patterns as presented in Figs. 5 and 6. In Period I, the predator–prey fluctuations in all mini-orchards are rather synchronous, whereas in Period II this is not so. In addition (leaving problems of representativeness of samples aside), in Period II there appears to be asynchrony at a smaller spatial scale than mini-orchard level. Within each mini-orchard different local populations can be distinguished that behave more or less independent.

Effect of connectedness

Apart from the factors described above, at first sight the effects of connectedness during the first half of the experiment are not at all clear. There appear

to be no obvious differences between the first four population fluctuations whether the mini-orchards were connected or not connected (Figs. 3 and 4). However, when the average mite and predator densities for connected and unconnected plants are compared (Fig. 7), it can be seen that mite increase on the unconnected plants preceded that on the connected plants by about 1–2 weeks. In addition, a comparison of mean mite densities between the connected and unconnected mini-orchards shows that the population densities of *T. urticae* and *T. occidentalis* in the unconnected mini-orchards were almost always higher than those in the connected mini-orchards (Fig. 7).

Dispersion statistics

Aggregation is shown to be an important factor in stabilising simple predator–prey models (e.g. Hassell and May, 1974; Chesson and Murdoch, 1986). Hence, it may be questioned to what extent aggregation manifests itself in the course of the experiment. We used Morisita's (1962) index, I_δ, as a dispersion statistic and made calculations for mini-orchards 1 and 4, merely to illustrate the point that aggregation on a plant-to-plant basis within a mini-orchard prevails and that it fluctuates considerably. The indices $I\delta$ for both *T. urticae* and *T. occidentalis* are presented in Fig. 8a and b.

Taylor's power law (L.R. Taylor, 1961, 1965) another method to quantify aggregation, gave much the same picture. The *b* parameter of Taylor's model always exceeded unity. For *T. urticae* and *T. occidentalis* respectively the values were 1.64 and 1.43, indicating that both species are highly aggregated.

Effect of pesticides

The pesticides azinphos-methyl, bupirimate and captan, were applied every 2–3 weeks. They are known to affect neither *T. urticae* nor *T. occidentalis.* (Hoyt, 1969; Johnson et al., 1979; note that we used an organophosphate-resistant strain of *T. occidentalis*). However, the other pesticide used, namely pirimicarb, a selective aphicide, may have had an impact on the predatory mites, as indicated by the decrease in numbers of *T. occidentalis* immediately after the pirimicarb spray (week 7). This detrimental effect on the predator was confirmed in laboratory tests. Hence it was decided to reduce this effect by changing firstly the mode of application (from spraying to root drenching) and secondly the dose (from 0.034% to 0.025% a.i.).

Presence of other mite species

Towards the end of the experiment *Brevipalpus obovatus*, another phytophagous mite, was noted on the leaves. Its population slowly increased and did not follow any of the fluctuations in populations of *T. occidentalis.* Nearing week 90 their numbers became high, making a chemical treatment necessary. However, one of the few chemicals effective against *Brevipalpus obovatus* is cyhexatin, a general acaricide, which also affects *T. urticae* and *T. occidentalis.* Hence, it was decided to stop the experiment.

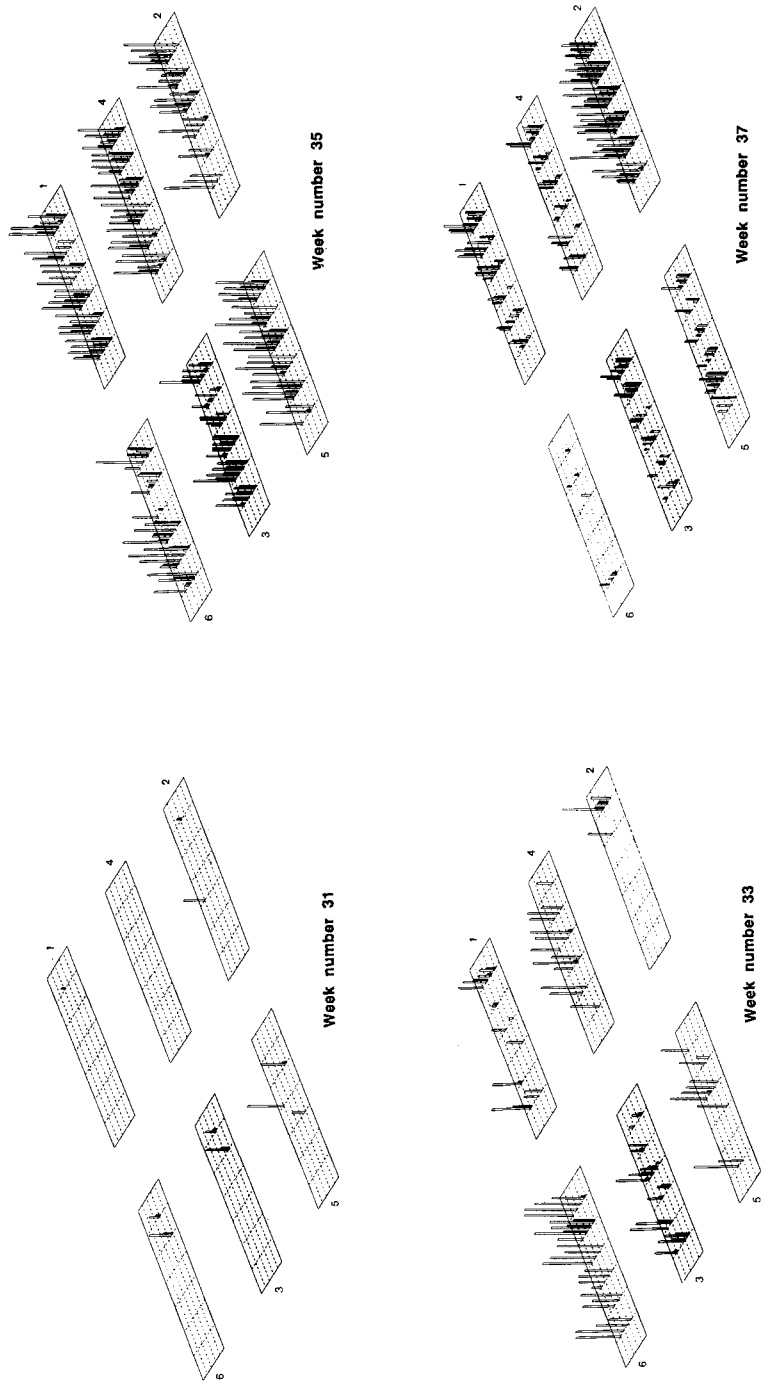

Fig. 5. Mite dispersal in mini-orchards 1–6 during weeks 31–37 of Period I. Histogram bars indicate relative densities of *T. urticae* (white) and *T. occidentalis* (black). The intersections of the dashed lines indicate locations of sample plants. Scale in Fig. 6.

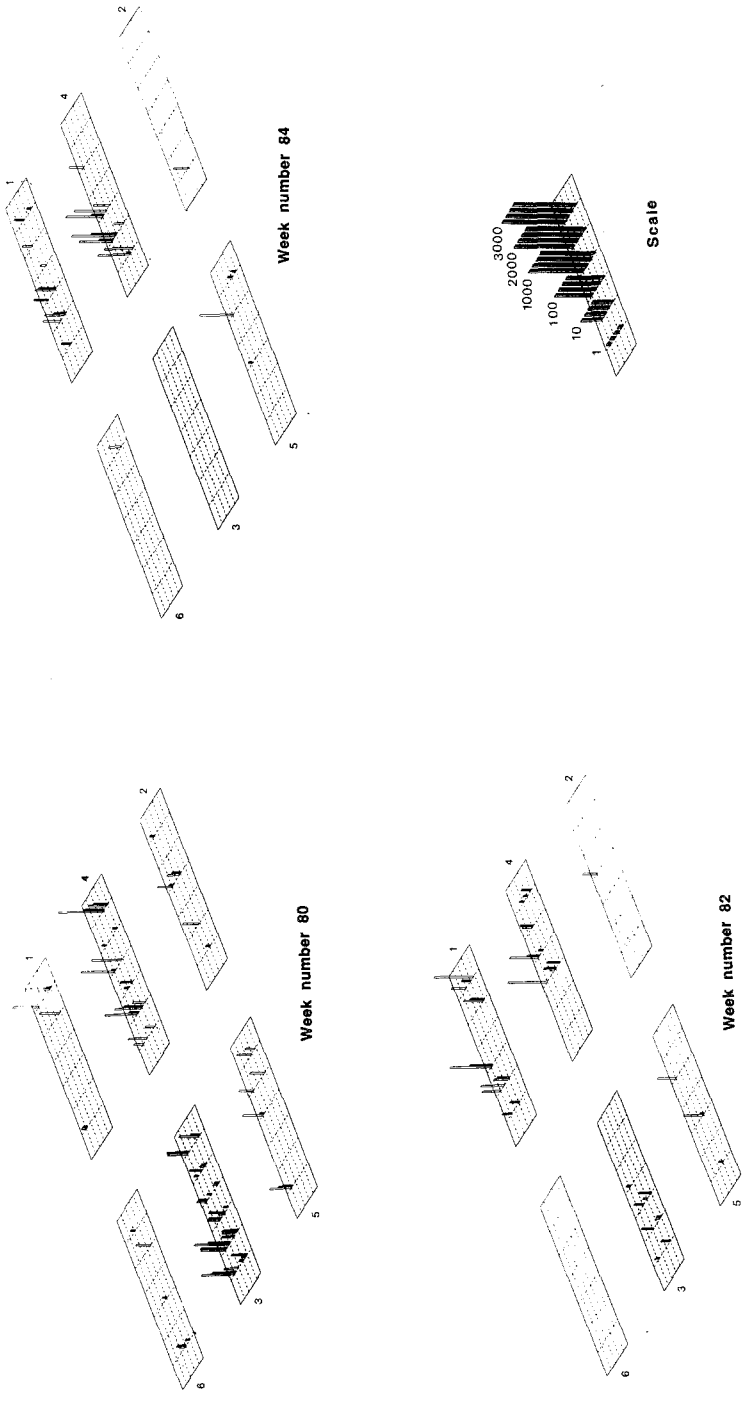

Fig. 6. Mite dispersal and scale in mini-orchards 1–6 during weeks 80–84 of Period II. Histogram bars indicate relative densities of mites on sample plants as in Fig. 8; Scale gives natural log number of mites per leaf.

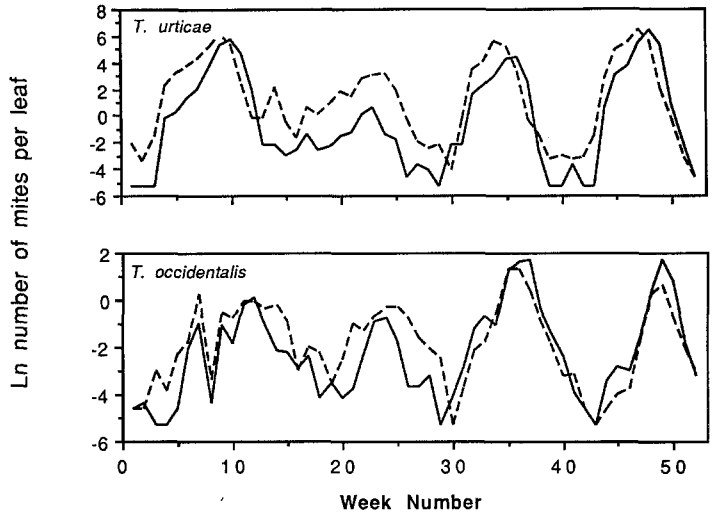

Fig. 7. Mean population density for *T. urticae* and *T. occidentalis* on 'connected' (solid lines) and 'unconnected' (dashed lines) mini-orchards from week 1–52.

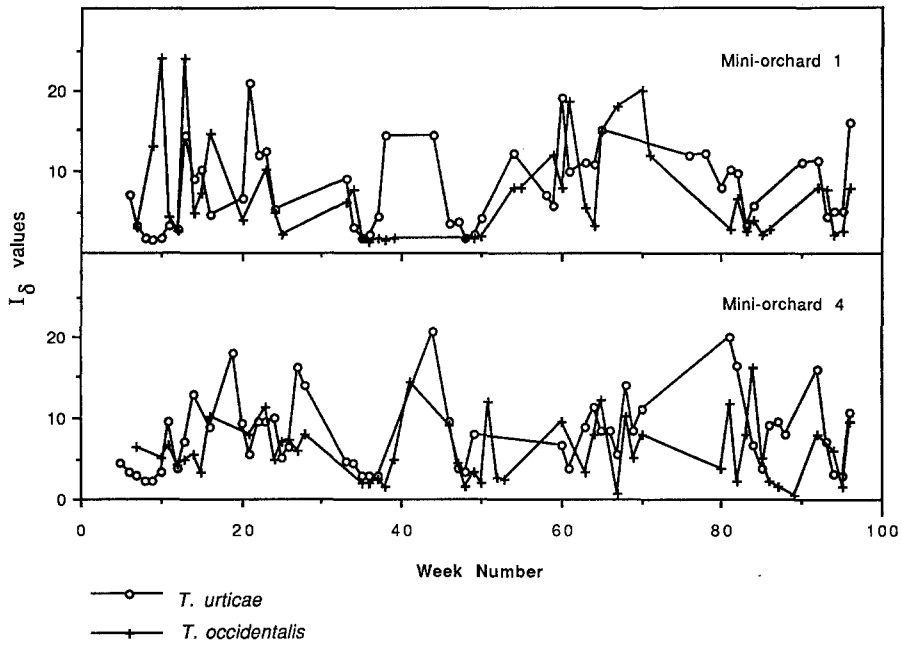

Fig. 8. Fluctuations of Morisita's index (I_δ) in mini-orchards 1 and 4 for *T. urticae* and *T. occidentalis*; I_δ values of equal or greater than 2 indicate an aggregated distribution.

Aerial dispersal

Observations on sticky traps confirmed that the mites dispersed aerially, probably aided by air movement caused by the cooling and heating fans situ-

ated in each corner of the glasshouse (Fig. 1). In week 86 and 87, the traps caught a total of five *T. urticae* and one *T. occidentalis* at a time when the populations in the leaf samples were on average quite low (about 7–10 prey mites and 0.5 predators per leaf). Nevertheless, it is clear that migration between mini-orchards is possible, the more so because ambulatory dispersal on the dowel rods was repeatedly observed during the experiment.

DISCUSSION

While our population experiment has revealed a spatial scale at which asynchrony of local cycles occurs (i.e. in Period II), it still remains to be elucidated why Period I is characterised by strong synchrony. In fact, what the experiment shows, is that periods of synchrony and asynchrony alternate. This may be explained in two essentially different ways. Firstly, assuming absence of causal factors that change with time, one may think of both synchrony and asynchrony being generated by one mechanism, as shown to be the case in the simulations presented in fig. 2c of Nachman (1987b; see Lingeman and van de Klashorst (1992) for discussion) or in fig. 5 presented in Woolhouse and Harmsen (1987). Secondly, there may be time-related changes in factors that have a decisive influence on the (a) synchrony of the local predator–prey fluctuations. One may think of cultural methods such as (1) connectivity and (2) pesticide use.

Connectivity may be involved in causing the alternation of synchronous and asynchronous population fluctuations, albeit in a rather complicated way. For one thing, one should note that in Period I only half of the mini-orchards were provided with connections between plants and that on the 'connected' mini-orchards this led to lower mean densities and lower fluctuation amplitudes (Fig. 8); whereas all mini-orchards had connections between plants in Period II. For another, one may suppose that unconnectedness of the plants is bound to lead to a higher probability of prey avoiding discovery and therefore to overexploitation of the host plants. This, in turn will lead to increased prey dispersal which results in synchrony of the spider mite population build-up in the various mini-orchards. Much the same reasons can be applied to the predators. Thus, unconnectedness of part of the mini-orchards in Period I may have led to synchrony, while its absence in Period II may have provided suitable conditions for asynchrony to arise.

It is interesting to note that synchrony in local cycles reveals itself roundabout the first pirimicarb spray and the next three high dose root drenches (PS and PD1, Fig. 2), whereas the subsequent low dose root drenches (PD2, Fig. 2) do not have such a synchronising effect. Because synchrony has arisen

before the actual pesticide application, the pesticides cannot be the only cause of synchrony. Thus, it seems more likely that the coincidence of synchrony and pesticide application is an association rather than a cause-and-effect relationship, for instance through a mechanism whereby the factors that promote aphid outbreaks also promote spider-mite population growth and temporary escape from control by the predators. After the last high dose pirimicarb root drench (PD1, week 38, Fig. 2), there appears to be a strong tendency towards asynchrony in local cycles. This return to asynchrony is very fast, comprising just a few weeks which suggests a mechanism generating asynchrony, resulting in lower amplitude fluctuations at the regional scale.

More analytically planned experiments and testable hypotheses will be required to elucidate the operation of stabilising mechanisms. One class of mechanisms relates to density dependence in the prey population. Especially, during population peaks in mini-orchards, local food supply to the spider mite would have reduced population growth, thereby keeping prey density within limits and also promoting dispersal.

In addition to density dependence in the prey population, there is a class of mechanisms that relates to the predators. Sabelis and Diekmann (1988) and Sabelis et al. (1991) reviewed possible mechanisms stabilising predator–prey–plant interactions in a patchy environment. One of these mechanisms relates to predators' differential attack on prey patches of different sizes. Since aggregation may be the result of differential attack, it is of interest to note that populations at the mini-orchard level show large amplitude cycles, despite the fact that mites have an aggregated distribution over the plant leaves. Evidently, aggregation is not sufficient to stabilize the predator–prey interactions on leaves at the mini-orchard level. whether differential aggregation between mini-orchards is important in conferring stability at the regional level, remains an important question for future research.

ACKNOWLEDGEMENTS

Technical advice and help from the staffs of the CSIRO Division of Entomology and the A.N.U. Zoology Department is gratefully acknowledged. Minus van Baalen, Arne Janssen and Kees Nagelkerke are thanked for their comments on an earlier version of this manuscript.

REFERENCES

Andrewartha, H.G. and Birch, L.C., 1954. The Distribution and Abundance of Animals. University of Chicago Press, Chicago, 782 pp.

Burnett, T., 1979. An acarine predator–prey population infesting roses. Res. Popul. Ecol., 20: 227–234.

Chesson, P.L. and Murdoch, W.W., 1986. Aggregation of risk: relationships among host–parasitoid models. Am. Nat., 127: 696–715.

Fujita, K., 1983. Systems analysis of an acarine predator–prey system II. Interactions in discontinuous environment. Res. Popul. Ecol., 25: 387–399.

Gurney, W.S.C. and Nisbet, R.M., 1978. Single-species population fluctuations in patchy environments. Am. Nat., 112: 1075–1090.

Hassell, M.P. and May, R.M., 1974. Aggregation of predators and insect parasites and its effect on stability. J. Anim. Ecol., 43: 567–594.

Hilborn, R., 1975. The effect of spatial heterogeneity on the persistence of predator–prey interactions. Theor. Popul. Biol., 8: 346–355.

Hoyt, S.C., 1969. Integrated chemical control of insects and biological control of mites on apple in Washington. J. Econ. Entomol., 62: 74–86.

Huffaker, C.B., 1958. Experimental studies on predation: Dispersion factors and predator–prey oscillations. Hilgardia, 27: 343–383.

Huffaker, C.B., Shea, K.P. and Herman, S.G., 1963. Experimental studies on predation: Complex dispersion and levels of food in an acarine predator–prey interaction. Hilgardia, 34: 305–330.

Johnson, J.F., Penrose, L.J. and Thwaite, W.G., 1979. Deciduous Fruits Spray Calendar 19th Edition. New South Wales Department of Agriculture, Sydney, 108 pp.

Lingeman, R. and van de Klashorst, G., 1992. Local and global cycles in an acarine predator–prey system: a frequency domain analysis. Exp. Appl. Acarol., 14: 201–214.

Maynard Smith, J., 1974. Models in Ecology. Cambridge University Press, Cambridge, 146 pp.

McMurtry, J.A. and van de Vrie, M., 1973. Ecology of tetranychid mites and predation by *Amblyseius potentillae* (Garman) on *Panonychus ulmi* (Koch) in simple ecosystems (Acarina: Phytoseiidae, Tetranychidae). Hilgardia, 42: 17–34.

Morisita, M., 1962. I_δ-index, a measure of dispersion of individuals. Res. Popul. Ecol., 4: 1–7.

Murdoch, W.W., Chesson, J. and Chesson, P.L., 1985. Biological control in theory and practice. Am. Nat., 125: 344–366.

Nachman, G., 1981. Temporal and spatial dynamics of an acarine predator–prey system. J. Anim. Ecol., 50: 435–451.

Nachman, G., 1987a. Systems analysis of acarine predator–prey interactions. I. A stochastic simulation model of spatial processes. J. Anim. Ecol., 56: 247–265.

Nachman, G., 1987b. Systems analysis of acarine predator–prey interactions. II. The role of spatial processes in system stability. J. Anim. Ecol., 56: 267–281.

Readshaw, J.L., 1975. The ecology of tetranychid mites in Australian orchards. J. Appl. Ecol., 12: 473–495.

Sabelis, M.W. and Diekmann, O., 1988. Overall population stability despite local extinction: the stabilizing influence of prey dispersal from predator-invaded patches. Theor. Popul. Biol., 34: 169–176.

Sabelis, M.W., Diekmann, O. and Jansen, V.A.A., 1991. Metapopulation persistence despite local extinction: predator–prey patch models of the Lotka–Volterra type. Biol. J. Linnean Soc., 42: 267–283.

Takafuji, A., Tsuda, Y. and Miki, T., 1983. System behaviour in predator–prey interaction, with special reference to acarine predator–prey system. Res. Popul. Ecol., Suppl. 3: 75–92.

Taylor, A.D., 1988. Large-scale spatial structure and population dynamics in arthropod predator–prey systems. Ann. Zool. Fenn., 25: 63–74.

Taylor, L.R., 1961. Aggregation, variance and the mean. Nature, 189: 732–735.

Taylor, L.R., 1965. A natural law for the spatial disposition of insects. Proceedings XII International Congress of Entomology, London, pp. 396–397.

Woolhouse, M.E.J. and Harmsen, R., 1987. Prey–predator cycles and lags in space: Descriptive models from a laboratory experiment. Theor. Popul. Biol., 32: 366–382.