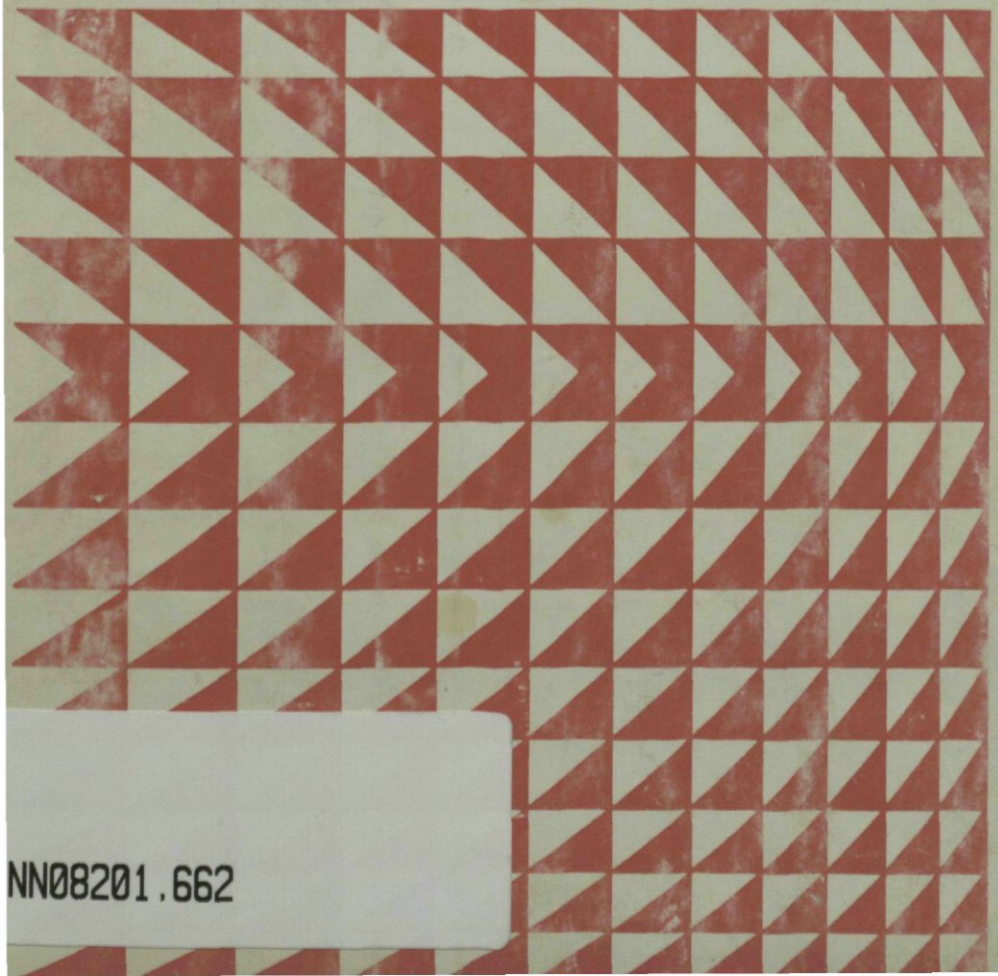
Biological control of fruit-tree red spider mite

R. Rabbinge



Dit proefschrift met stellingen van Roelof Rabbinge, landbouwkundig ingenieur, geboren te Kampen op 8 november 1946, is goedgekeurd door de promotoren, dr.ir. C.T. de Wit, buitengewoon hoogleraar in de theoretische teeltkunde, en dr. J. de Wilde, hoogleraar in het dierkundig deel van de plantenziektekunde.

Wageningen, 6 mei 1976

De rector magnificus
van de Landbouwhogeschool,
J.P.H. van der Want

Biological control of fruit-tree red spider mite

R. Rabbinge

Proefschrift
ter verkrijging van de graad van
doctor in de landbouwwetenschappen,
op gezag van de rector magnificus
prof.dr.ir. J.P.H. van der Want, hoogleraar in de virologie,
in het openbaar te verdedigen
op vrijdag 22 oktober 1976 des namiddags te vier uur
in de aula van de Landbouwhogeschool te Wageningen

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Stellingen

I

Roofmijten zijn te gebruiken voor de beheersing van de populatiedichtheid van de fruitspintmijt Panonychus ulmi Koch op een voor de huidige fruitteeltpraktijk acceptabel niveau.

M. van de Vrie, Proc, FAO-conf. Ecology Rel. Plant Pest Contrl., Rome, Dec. 1972 D. J. Kuenen, Meded. Tuinb. Voorl. Dienst 44, 68 p.
(Dit proefschrift)

II

Het gebruik van processimulatie-modellen bij onderzoek en toepassing van geïntegreerde bestrijding van ziekten en plagen is zinvol en dient te worden bevorderd.

(Dit proefschrift)

III

Voor berekeningen van de populatiefluctuaties van bewegende bladbewoners, zoals de fruitspintmijt Panonychus ulmi Koch, kan volstaan worden met de weergegevens van de Stevenson-hut.

(Dit proefschrift)

IV

Het biosystematisch onderzoek over roofmijten (Phytoseiidae) met nadruk op ecologische aspecten dient te worden bevorderd.

D. A. Chant, Nat. Acad. Sci. Publ. 1402, Washington D.C.
E. Collyer, Cr. Ier Congrès d'Acarologie, Fort Collins, Colo. (1963): 409–414.

V

Het in de dierecologie gangbare begrip 'area of discovery' om de parasiterings- of predatie-efficiëntie van een parasiet respectievelijk predator uit te drukken is verwarrend. Beter kunnen de begrippen relatieve parasiteringsnelheid respectievelijk relatieve predatiesnelheid voor dit doel worden gebruikt.

A. J. Nicholson & V. A. Bailey, Proc. Zool. Soc. London, 1935, 551–598.
(Dit proefschrift)

VI

Voor het analyseren van de relatieve invloed van verschillende factoren op populatiedynamische verschijnselen is toepassing van gevoeligheidsanalyse met processimulatiemodellen te verkiezen boven toepassing van de key factor analyse volgens Morris, Varley and Gradwell.

G. C. Varley & G. R. Gradwell, J. Anim. Ecol. 29, 399–401, 1960.

R. F. Morris, Ecology 40(4): 580–588, 1959. J. van den Bos & R. Rabbinge, Simulation of the fluctuations of the grey larch bud moth, 1976. Pudoc Simulation Monographs, 91 p.

VII

Het streven naar grotere opbrengsten per eenheid van oppervlak in de landbouw is in rijke landen zowel sociaal, maatschappelijk als uit oogpunt van natuurbehoud wenselijk, en voor arme landen zelfs noodzakelijk.

VIII

Voor het bereiken van het optimale effect van het onderzoek naar geïntegreerde bestrijdingsmethoden van ziekten en plagen in land- en tuinbouwgewassen is aanpassing van het voorlichtings- en ontwikkelingsapparaat dringend gewenst. Onderzoek naar geïntegreerde bestrijding kan alleen gedijen als directe relaties met de praktijk zijn gewaarborgd.

IX

De verwerping van het ideaalbeeld van de wetenschap zoals dit door Popper is gepropageerd heeft enerzijds relativering van het neopositivisme mogelijk gemaakt, anderzijds krijgen andere, verguisde wetenschapsopvattingen misschien de hun toekomende kans.

K. R. Popper: Conjectures and Refutations, 428 p., Routledge and Kegan Paul, London.

X

Kosten voor sociale voorzieningen als AOW en WW dienen niet alleen te worden toegerekend aan de factor arbeid, maar dienen ook op de factoren energie en grondstoffen te worden verhaald. De nu bestaande spiraalbeweging die steeds verder van de overheersende maatschappelijke doelen afleidt kan daarmee worden doorbroken.

XI

Het streven naar gelijke kansen op onderwijs en opleiding is meer gediend met de invoering van een onderwijsknipkaart en een vergroten van de mogelijkheden op tweede kans onderwijs dan met een verdere verlenging van de leerplicht. De afbouw van avondopleidingen moet daarom worden afgeremd.

Proefschrift van R. Rabbinge
Biological control of the fruit-tree red spider mite.

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Voorwoord

8814 uren van continu waarnemen, meer dan 1 are aan bos om computerpapier van te maken, 49.600 appelbladeren die met het binoculair werden bekeken, ontelbare computervellen om later als kladpapier te gebruiken en vele experimenten met miljoenen mijten waren ondermeer nodig om dit proefschrift tot stand te brengen.
Zeer velen zijn daarbij betrokken geweest en voor hun hulp en inzet wil ik ze allen hartelijk bedanken.
De aanvraag die prof.dr. J. de Wilde in 1971 tot het College van Bestuur richtte voor het toekennen van een promotieassistentschap voor onderzoek aan een ecofysiologisch onderwerp werd aanvankelijk afgewezen, maar in 1972 dank zij zijn vasthoudendheid toch gehonoreerd. Daardoor kon medio 1972 met het project worden begonnen.
In de loop van het onderzoek werd bij het werk steeds meer gebruik gemaakt van simulatietechnieken en het was prof.dr.ir. C.T. de Wit die mij leerde biologische processen met vaak eenvoudige formules te beschrijven. Zijn enthousiasme, zijn kritische zin en didactische gaven maakten het op schrift stellen en beëindigen van dit project mogelijk. Zijn politiek inzicht zorgde voor een uitbreiding van mijn promotieperiode.
Al voor de aanvang van het project voerde M. van de Vrie mij binnen in de kleine wereld van de acarologie. Zijn grote kennis van zaken, zijn enorme ervaring en zijn stimulerende invloed gedurende het werk maakten de verbinding met de praktijk mogelijk en behoedden de modellenbouwer voor droogzwemmen.
Veel studenten waren bij dit onderzoek ingeschakeld, sommigen waren zelfs langer dan een jaar bij het project betrokken. Hun inzet, de uitgebreide discussies met hen en de vele waarnemingsuren die zij bij nacht en ontij aan dit onderzoek hebben willen besteden, vormen het leeuwendeel van dit werk. Mous Sabelis, Peter Mols, Kees Booij, Cox Merkelijn, Rob de Reede, Cock Scheeuwe, Frank Wiedijk en Tony Wijnen hebben ieder op hun eigen wijze een waardevolle bijdrage geleverd.
De enorme hulp die ik heb genoten van Jan Goudriaan bij het programmeren en het formuleren van de probleemstelling wil ik met nadruk noemen; deze waardering geldt ook voor Gonnie van Laar die tal van uren besteedde aan de gevoeligheidsanalyse van het model. Bij

de redactie van de computerprogramma's en het verwijderen van fouten was ir. C. de Jonge behulpzaam; ook zijn bereidwillige medewerking strekte zich uit tot de nachtelijke uren. George Fransz leverde met zijn analyse van het prooi-predatorproces een belangrijk aandeel aan het leggen van de basis voor de populatiemodellen.
Veel experimenten werden uitgevoerd bij het Instituut voor Plantenziektenkundig Onderzoek en bij het Proefstation voor de Fruitteelt te Wilhelminadorp. De medewerking die ik daar kreeg van de leiding, het kas- en tuinpersoneel wil ik graag noemen. De meteorologische metingen werden in teamverband verricht met dr.ir. P.A.M. Hopmans en H.A. Schouwink van de vakgroep Tuinbouwplantenteelt, en W.N. Lablans en prof.dr. P. Groen van het KNMI. De laatsten namen ook kritisch het hoofdstuk over micrometeorologische modellen door. Een groot deel van de meetapparatuur kon worden geleend van de vakgroep Natuur- en Weerkunde dank zij de bereidwillige medewerking van Kees Stigter.
Metingen werden verricht bij het CABO en op de Schuylenburg te Lienden, ook daar ontving ik de medewerking van velen.
Werkers aan het Binnenhavencomplex, in kas, werkplaats en bibliotheek zorgden voor hetzij levend, hetzij dood materiaal. Otto van Geffen zorgde voor vernuftige windmeters, Herman Dijkman voor proefdieren en vele tellingen, Ria Cuperus, Ans Klunder en Lien van Gulijk voor het vele typewerk en Frits von Planta en W.C.Th. Middelplaats voor de talrijke figuren en tekeningen.
In de laatste fase van het werk speelde het Pudoc een belangrijke rol, met name Erica Brouns.
Vooral prof.dr. J. de Wilde was in de laatste periode van mijn studie, waarin hij zo'n belangrijke rol speelde, een uitstekend leermeester.

Curriculum vitae

Rudy Rabbinge werd geboren op 8 november 1946 te Kampen en bezocht in die plaats het Gemeentelijk Lyceum (HBS-B). In 1964 begon hij zijn studie aan de Landbouwhogeschool te Wageningen (studierichting Planteziektenkunde), waar hem in januari 1972 het ingenieursdiploma werd uitgereikt. Van januari 1970 tot juli 1972 was hij leraar Scheikunde en Biologie aan middelbare scholen te Ede en Amsterdam en in juli 1972 werd hij aangesteld als promotie-assistent bij de vakgroepen Entomologie en Theoretische Teeltkunde. Vanaf 1 september 1975 is hij als wetenschappelijk medewerker werkzaam bij de vakgroep Theoretische Teeltkunde.

Samenvatting

Gedurende de laatste 10 jaar zijn er geïntegreerde insektenbestrijdingssystemen ontwikkeld voor verschillende gewassen. Eén van de belangrijkste onderzoeksgebieden was de ontwikkeling van geïntegreerde bestrijding in boomgaarden. De ervaring met gewijzigde bestrijdingsprogramma's in appelboomgaarden, de toenemende resistentie van spintmijten tegen acariciden, en de uitgebreide biologische gegevens van vele plaagverwekkers bevorderden deze ontwikkeling van geïntegreerde bestrijdingssystemen.
Proeven met losgelaten roofmijten in appelboomgaarden toonden aan dat deze natuurlijke vijanden van het fruitspint in staat zijn de populatiedichtheid van het fruitspint te reguleren bij zeer lage dichtheden en op het ogenblik worden roofmijten al gebruikt in verscheidene praktijkbedrijven. Toch is er nog weinig bekend over de wijze waarop dit regulatiemechanisme werkt en een verklaring die niet gebaseerd is op goede kwantitatieve gegevens en goede verificaties is betrekkelijk zinloos.
De verwezenlijking van een voor de teler gegarandeerd bestrijdingssysteem vergt gedetailleerde kennis van de interacties van mijt- en roofmijtpopulaties, van hun relaties met de voedselplant en van de effecten van de abiotische factoren (temperatuur, relatieve luchtvochtigheid, wind en regen) en teeltmaatregelen (bemesting en bestrijding van insekten en schimmels) op mijt en roofmijt.

In deze studie worden basismodellen voor fruitspint *Panonychus ulmi* Koch en de inheemse roofmijt *Amblyseius potentillae* beschreven. Deze modellen zijn geconstrueerd volgens de toestandsvariabele benadering, die wordt beschreven in hoofdstuk 3.
De modellen overbruggen de kloof tussen de toepassing van roofmijten op veldschaal en de analytische methoden van de natuurwetenschappen en kunnen daardoor dienstbaar zijn bij de introductie en begeleiding van biologische bestrijding van het fruitspint.
De simulatiemodellen zijn gebaseerd op diepgaande kennis van het effect van temperatuur, vocht, waardplant en daglengte op zowel prooi als predator (hoofdstuk 4). De relaties van ontwikkelings-, sterfte-, predatie- en ovipositie-snelheden met temperatuur en andere fysische factoren werden vastgesteld met behulp van literatuurgegevens,

schattingen en een groot aantal laboratoriumexperimenten (hoofdstuk 5). Veel van de temperatuur-responsies van snelheden bleken lineair te zijn en momentaan op temperatuur fluctuaties te reageren. De predator-prooi interacties in de modellen zijn gebaseerd op een gedetailleerde analyse van het predatieproces. Deze prooi-predator interactie is zeer ingewikkeld. Vijf ontwikkelingsstadia van de prooi (larve, protonymf, deutonymf, adulte man en vrouw) en vier ontwikkelingsstadia van de predator (protonymf, deutonymf, adulte man en vrouw) zijn er bij betrokken. De attractiviteit van de verschillende stadia van de prooi is variabel en hangt sterk van het verzadigingsniveau van de predator af.
Het volwassen vrouwtje van de predator heeft een sterke voorkeur voor de jongere stadia; maar wanneer de mate van verzadiging erg gering is worden ook andere prooistadia gegeten. De voedselopnamesnelheid en de benutting van een gedode prooi worden eveneens sterk door het verzadigingsniveau bepaald. Door een gedetailleerde analyse van het predatieproces en met behulp van verklarende computersimulatiemodellen toonde Fransz (1974) aan dat een eenvoudig systeem (één gestandaardiseerde predator en een constant aantal prooien) in korte tijd een evenwicht bereikt. Het verzadigingsniveau van de predator schommelt rond een bepaald niveau met geringe amplitudes, de hoogte van dit niveau hangt af van de prooi- en de predator dichtheid en van de temperatuur van het systeem.
Deze eigenschap maakt introductie van het ingewikkelde predatieproces in een model voor een populatie mogelijk door de relatieve predatiesnelheid en prooibenutting uit te drukken als een functie van temperatuur en verzadigingsniveau van de predator. Kwantificering van het verzadigingsniveau van de predator is hier gemakkelijk omdat goed gevoede predatoren rood en slecht gevoede predatoren wit gekleurd zijn. Een kleurschaal wordt beschreven die het gedrag van de rover uitgedrukt in de succesratio (het aantal succesvolle ontmoetingen gedeeld door het totaal aantal ontmoetingen) verbindt met de hoeveelheid plantaardige en dierlijke pigmenten in de predator die de kleur bepalen (sectie 6.2).
Experimenten werden uitgevoerd om de afnamesnelheid van de kleur van de predator te bepalen en om de relatie tussen predatiesnelheid en kleur van de predator vast te leggen bij verschillende temperaturen.
De voor de modellen benodigde relaties tussen relatieve predatiesnelheid en kleur van de predator kunnen gemakkelijk van deze relaties worden afgeleid. De numerieke respons van de predator (een verlaagde ovipositiesnelheid en een vertraagde ontwikkeling van ei tot adult als voedsel beperkt is) hangt eveneens van het verzadigingsniveau en van

de temperatuur af. Deze relaties werden eveneens experimenteel gekwantificeerd (sectie 6.3).

Het vereiste detail in kennis van de sturende variabelen van het systeem; de kwaliteit van de waardplant en de temperatuur, werden vastgesteld met behulp van experiment en simulatie. Het effect van de voedselkwaliteit van de waardplant is vastgesteld in waterculture experimenten en gerelateerd aan het stikstofpercentage van bladeren van bomen in praktijkboomgaarden. Er wordt aangetoond (sectie 7.2) dat binnen de variatie in voedselkwaliteit van de bomen onder praktijkomstandigheden een effect op ontwikkelingssnelheid en ovipositiesnelheid van fruitspint afwezig is. Om de vereiste mate van gedetailleerdheid van het microweer na te gaan is een aan boomgaard-omstandigheden aangepaste microweersimulator verbonden met het populatiemodel. De geringe verschillen in resultaten bij simulatie met de bladtemperaturen als sturende variabelen en luchttemperatuur als sturende variabele rechtvaardigt het gebruik van de luchttemperatuur als sturende variabele bij de verdere berekeningen (sectie 7.3).
De aannamen in het model die ten grondslag liggen aan de behandeling van het predatieproces werden geverifieerd door de resultaten van een onafhankelijk experiment over predatie in een vervangingsreeks van verschillende prooistadia te vergelijken met simulatieresultaten (sectie 9.1). Er wordt tevens aangetoond dat de berekeningsprocedure voor opbrengsten van plantesoorten in mengcultuur uit zaaidichtheids-experimenten in monocultuur kan worden toegepast om de predatie-snelheden van een soort in mengcultuur te berekenen uit z'n functionele responscurve in monocultuur (sectie 9.2).

De modellen voor het uitkomen van wintereieren, voor populatieontwikkeling van prooi en predator gedurende het seizoen en voor de inductie van diapauze zijn geverifieerd op verschillende integratieniveaus door onafhankelijke populatie-experimenten. De eenvoudigste verificatie is de bepaling van populatiegroei in kleine ecosystemen onder gecontroleerde omstandigheden in situaties met en zonder predatoren en deze te vergelijken met de resultaten van simulatie.

Verificatie in het veld is gedaan door de simulatieresultaten te vergelijken met populatiemetingen in verscheidene boomgaarden. De overeenkomst in het algemene beeld van populatiefluctuaties van prooi en predator en de goede overeenkomst tussen gesimuleerde en gemeten kleurniveaus van de predator maakt het model bruikbaar voor gevoeligheidsanalyse.

Deze gevoeligheidsanalyse, hoofdstuk 10, toont aan dat er geen bijzondere sleutelfactoren in het systeem zijn en dat de initiële prooi-roververhoudingen behoorlijk mogen variëren. De predatie-activiteit van de ontwikkelingsstadia en van de mannetjes van de rover blijken relatief onbelangrijk te zijn en het adulte wijfje is de belangrijke regulator als gevolg van haar grote roofactiviteit, haar lange levensduur en de toename in ovipositiesnelheid wanneer de rover goed gevoed is. Het systeem is betrekkelijk gevoelig voor de lengte van de jeugdperiode van de prooi, de predatiesnelheid, de eilegsnelheid van de volwassen vrouwelijke predator en de vertraging in ontwikkeling van de predator als gevolg van onvoldoende voedsel.

Contents

1 Introduction

1.1 Biological control of mites

Biological control was described by Thompson (1930) as a method of pest control that relies on natural enemies — parasites, predators and pathogens — to reduce pest populations to tolerable levels. Biological control is only a part of integrated control, which also incorporates other methods of pest control including, host plant resistance, cultivation methods, genetic manipulation of pests and moreover selective use of chemicals such as pheromones, hormones and also pesticides (FAO, 1973). In the Netherlands, the Working Group for Integrated Control of Insect Pests, TNO, was established in 1958. This group chose the apple orchard for the application of integrated control mainly because of the permanence of this crop that enables a stable ecosystem to be established. Further reasons were as follows.

- the frequent application of pesticides (20–30 times per year)
- the development of resistance to acaricides in the fruit-tree red spider mite (van de Vrie, 1956)
- the availability of fundamental studies on the population dynamics of this spider mite (Kuenen, 1949, 1946)
- the knowledge of bionomics of many pest species occurring in orchards (Evenhuis, 1958; De Fluiter, 1957)
- the results already obtained by workers abroad (Lord, 1949; Pickett, 1949)

The fruit-tree red spider mite was almost unknown as a pest before World War II. It became a serious pest when tar oil was introduced as a dormant spray against overwintering insects and Bordeaux mixture and lime sulphur became increasingly applied against scab and powdery mildew.

Probably predators regulated the numbers of the mite before that time but were killed by foliar applications of pesticides against other pests leaving the spider mites unharmed. The evidence for this hypothesis was critically reviewed by Huffaker et al., (1970). The development of resistance in spider mite populations is unpredictable; speculations based on laboratory experiments are unsatisfactory but sooner or later many, if not all, acaricides may become ineffective. The wide variety in response of mite populations to many potent acarides may indicate

these future developments (Helle & van de Vrie, 1974). To obtain a long-lasting effect, predators should be employed to regulate the populations of fruit-tree red spider mites. Then there would be less need to apply acaricides so frequently and the possibilities for regulating other pest species on fruit trees by biological means would be improved.

1.2 Application of simulation

Biological control has long been based on the idea that pests exist because there are insufficient essential predators or parasites. Such natural enemies were therefore introduced from appropriate regions until the pest was brought under control. Many examples of biological control are based on this time-consuming procedure which merely depends on the experience of the biologist or agriculturist. Speculative explanations are often given afterwards without sound experimental verification.

Laboratory experiments and observations in field situations on the fruit-tree red spider mite led to the hypothesis that this mite is most successfully controlled by predacious mites (Kuenen, 1946; Collyer, 1964; Kropczynska & van de Vrie, 1967; van de Vrie & Boersma, 1970). Attempts were made to introduce predatory mites or to improve their effectiveness; these experiments clearly demonstrated the capacity of these natural enemies to reduce and maintain spider mite populations, below the economic threshold level. At present predacious mites are widely used to control spider mites in apple orchards.

However the changes in the system have still not been quantitatively assessed, and explanations of how the system operates are mere speculation if not supported by knowledge of the underlying ecological processes. To develop a stable pest control system, it is necessary to know how spider mite and predacious mite populations interact with each other and with the host plant, and how the system is influenced by abiotic factors (temperature, relative humidity, wind and rain) and by cultivation methods (including the use of fertilizers as well as insecticides and fungicides).

The aim of the simulation approach in this book is to bridge the gap between biological control with predacious mites in the field and the analytical methods of natural sciences, thus assisting in the introduction and management of biological agents in the control of the fruit-tree red spider mite. The system studied, comprises the fruit tree, the fruit-tree red spider mite and the predatory mites. The population growth of the fruit-tree red spider mite and its predatory mites was simulated in relation to the changing biotic and abiotic environment.

All simulations refer to commercial fruit orchards, with spindle culture and the cultivar Golden Delicious on rootstock M 9, most frequently used in the Netherlands. These orchards are tended as those of the integrated control system; the number of sprayings are minimal and pruning and other treatments do not differ from those in chemically treated orchards. In the system the tree is considered to be an unlimited food source. High density effects in populations of the fruit-tree red spider mite such as reduced fecundity, delayed development and accelerated diapause do not occur when the densities are below the economic damage level. This is fixed at 2–3 females per leaf according to standards set by the OILB (Organisation Internationale pour la Lutte Biologique). This economic threshold is not merely defined by biological parameters, but also by socio-economic factors. Well kept, well fertilized orchards have more tolerance to the fruit-tree red spider mite, but because population growth is much faster in these orchards (Post, 1962; van de Vrie & Boersma, 1970), it is here especially that the fruit-tree red spider mite is a severe problem. Since all calculations are done for commercial fruit orchards only nitrogen levels within the range found in practice are considered. It is assumed that the effects of other natural enemies of the prey are absent since their predatory role is relatively unimportant at the considered population densities of the fruit-tree red spider mite. Whenever the population increases above the economic threshold their role may become of importance. The simulated system may give erroneous results when densities are very high, above 10 females per leaf, but sprayings rather than biological control methods are necessary in those situations.

The calculations with the model are based on the surface for 100 July leaves, this being the sample unit for the determination of the population densities in the integrated control system (van de Vrie, 1966). Within the orchard considerable differences in microweather may occur and these have to be taken into consideration. An adapted microweather simulation model, according to the microweather simulator for closed crops designed by Goudriaan (in prep.) is used for this purpose. It is assumed that the occurrence of the spider mite, 0.3–0.7 mm in size, is limited to the laminar layer around the leaf.

2 Biological elements

2.1 Fruit-tree red spider mite

Panonychus ulmi Koch belongs to the family Tetranychidae, a subgroup of the class Acarina. The members of the vast family Tetranychidae are nearly all phytophagous and mites are found all over the world from the Arctic to the Tropics.
Since *Panonychus ulmi* Koch causes considerable damage in deciduous fruit orchards, many publications on its biology and ecology have appeared (e.g. Gilliatt, 1935; Geijskes, 1938; Cagle, 1946; Andersen, 1947; Wybou, 1949, 1951; Blair & Groves, 1952; Fjelddalen, 1952; Kuenen, 1946; Hueck, 1953; Mori, 1967; Parent & Beaulieu, 1957; Günthart, 1945; Ehara, 1964; Rota, 1961 – 1962; Cutright, 1963; Bondarenko, 1964; Collyer, 1974; Livisic, 1964; Saba, 1964; Musa & Dosse, 1966; Huffaker et al., 1969; van de Vrie et al., 1972).
From these literature sources it is clear that the fruit-tree red spider mite occurs in almost all commercial fruit-growing regions. Especially in well kept orchards the fruit-tree red spider mite is continuously a potential pest and needs much attention by the fruit grower.

Hibernation takes place in the winter-egg stage on branches and twigs. The eggs are mostly found on the lower side of these branches, around the buds, on the leaf scars and the joints between the first and second year twigs. At very high densities of eggs a reddish shade shows their presence. In the Netherlands the diapause eggs hatch in spring and give rise to 4 – 6 generations of mites. The start of the hatching period varies according to the climate zone. In Canada hatching starts in the middle of May (Gilliatt, 1935; Parent & Beaulieu, 1957), in Virginia in the last week of April (Cagle, 1946), in the Netherlands usually in the second or third week of April.
Hueck (1951) found that winter eggs hatch less successfully in continuous darkness than in daylight. He reported that winter eggs of *P. ulmi* hatch during daytime and suggested that the absorption of short wavelengths of light were related in some way to the red pigment of the winter eggs and that they influenced the embryonic development. This hypothesis of Hueck is not in agreement with the results of Becker (1952). A necessary prerequisite for hatching is that winter eggs must be

exposed for at least 100 days to a temperature below 10° C.
Once hatching starts there is an instantaneous temperature reaction (Mori, 1961). At 20° C, 50% of the vital eggs have hatched after 6 days and within the 50–100% range, relative humidity does not affect vitality and rate of hatching (Mori, 1957).
The 0.1–0.3 mm diapause egg, described by Beament (1951) has a common basic shell structure, consisting of an outer thick wax layer and a cement 'shell' layer enclosing the living material. The egg is attached to the bark by an adhesive substance. The winter mortality of the eggs may be between 10 and 90%. (Sømme, 1966; Lienk & Chapman, 1958; Bengston, 1965). After hatching six developmental juvenile stages are distinguished: larva, protochrysalis, protonymph, deutochrysalis, deutonymph, teleiochrysalis.
The developmental rate of each stage depends on temperature, relative humidity and food supply. The optimum temperature is 24° C and the relative humidity 90% (Becker, 1952). These conditions are also optimum for the hatching of summer eggs. Mortality as related to temperature has not been studied in much detail. Total development from egg to female or male adult takes about 11 days at 20° C. After 2–3.5 days the female starts ovipositing.
The fruit-tree red spider mite has, as most Tetranychidae, an arrhenotokous reproduction, i.e. females develop from fertilized eggs and are diploid, whereas males develop from unfertilized eggs and are haploid. The developmental period of the male is 0.5–1 day shorter than that of the female. It waits until the female moults near her final quiescent stage, before it copulates with the young female. In field populations the sex ratios may vary (Putman, 1970; Herbert et al., 1975), but most common is a value of 0.67. Therefore this value is used in the models.
Summer eggs are deposited on the leaves. They are pale red and have a thinner scale than the winter eggs. Summer eggs hatch after a period of about 10 days at 20° C; natural mortality of these eggs is negligible. The females of the last summer generation deposit the winter eggs on the twigs and branches. The induction of 'winter' females i.e. the female that oviposits winter eggs, takes place in the deutonymph stage in response to a combination of temperature, daylength and food condition. Other stages, the teleiochrysalis and adult female are also receptive but less strongly. Lees' (1953) diapause data are presented in Table 1. He reported a partial reversibility from winter form to summer form when, after diapause-inducing conditions, a new period of warm weather starts. The winter eggs are then deposited on the leaves and are lost.
The damage caused by *P. ulmi* has been studied by several workers

Table 1 The influence of temperature and photoperiod on the incidence of diapause (% females laying winter eggs) in *Panonychus ulmi* (data from Lees, 1953).

Temperature (°C)	Proportion (%) of winter females diapausing with a photoperiod of					
	0h	4h	8h	12h	16h	24h
10	91	90	100	100	45	0
15	60	85	100	97	0	0
20	36	54	72	70	0	0
25	0	3	27	21	0	0

(Blair, 1951; Kuenen, 1946; Trägard, 1915; van de Vrie, 1956). With its stylets *P. ulmi* pierces through the epidermis into the mesophyll and sucks the content of the mesophyll cells. Both sides of the leaves are colonized, with a preference for the lower surface. The mesophyll cell fragments desiccate and their necrosis results in a bronzing of the leaves, when many cells are damaged.
Boulanger (1958) and Avery (1964) showed that until the leaves become visibly damaged the assimilation of carbon dioxide is only slightly reduced. The possible economic loss caused by the fruit-tree red spider mite has been estimated by different workers at more than 30% of the harvest (Chapman & al., 1952; van de Vrie, 1956). The growth of the fruit trees and the number of flower buds may be strongly reduced in the year after the attack. In hot dry years the damage caused by *P. ulmi* is more severe than in other years (Kuenen, 1946, 1949). Jary & Austin (1937), however, reported damage to be particularly severe in cool, wet weather.

2.2 Predators

In a world review on the fruit-tree red spider mite, Groves (1951) reported 65 species of predators. After three years of study in Germany Berker (1958) reported 59 species of predators of *P. ulmi*. The most important species are discussed briefly, to show why only the phytoseiidae are considered in this study.

Coleoptera. The two important predatory groups in this insect order, Coccinellidae and Staphylinidae, have some acarophagous representa-

tives. *Stethorus punctillum* Weise and *Stethorus bifidus* (Coccinellidae) are known as *P. ulmi* predators. They are relatively small and remarkably well-adapted to live and search for prey in the micro-environments where the tetranychid mite occurs (McMurtry et al., 1970). Development proceeds from the egg through four larval instars and a pupal stage to the adult in 19.3 days at 25° C (Geyskes, 1938; Günthart, 1945).

The sex ratio is 1 and the oviposition period is relatively long and the daily oviposition rate higher when food is abundant.

The food requirements for survival of these small ladybirds is low and thus they could be effective at low prey densities. However at higher densities, the daily rate of prey consumption of ovipositing females may exceed 40 adult or large immature spider mites, and that of fourth instar larvae may be even higher, with the total consumption during larval development usually in excess of 200 mites per day.

Stethorus spp. are specialized predators of spider mites, commonly associated with high prey densities. However they probably do not suppress the population before the economic threshold is reached, because high densities of prey are generally required before the predators begin to increase in numbers (McMurtry et al., 1970). Thus only low prey densities are required for survival but high numbers should be present before oviposition can begin. *Oligota flavicornis* and *Oligota oviformis* (Staphylinidae) are described as predators for phytophagous mites. These predators survive only at high mite densities.

Hemiptera. Anthocorus musculus and *Anthocorus nemorum* are reported to feed on *P. ulmi* in apple orchards in many parts of Europe (Massee & Steer, 1929; Geijskes, 1938; Listo & al., 1939).

Anthocorus is polyphagous and preys on aphids and scale insects as well as spider mites. Young instars of this species readily feed on *P. ulmi* (van de Vrie, 1972) and the later instars seem to prefer larger prey species. Another well studied predatory bug is *Blepharidopterus angulatus* (Fall) (Miridae). In England, Collyer (1964) studied in detail its effects on *P. ulmi* populations in commercial orchards. The duration of development under field conditions was 35 to 39 days, with only one generation per year. During their life-span female bugs consumed as many as 4000 adult mites, up to 50 per day during the adult stage. However Collyer (1964) stated: 'the mirid requires a fairly high level of food supply and being univoltine requires more than one season to build up again after it has been reduced to low numbers by inadequate food supply...' Therefore it was considered that predacious mites are more useful predators of the phytophagous mites.

The predatory mites. Several predatory mites occur in neglected fruit orchards, but in well kept orchards very few species appear: *Typhlodromus pyri, Amblyseius finlandicus* and *Amblyseius potentillae* are most common. Therefore these species are considered in this study. All three belong to the family Phytoseiidae, Acarina, which occur from the Arctic to the Tropics.

They have 4 developmental stages, the egg: the six-legged larva, the protonymph and the deutonymph. The quiescent period between two stages is short and the total duration of development in phytoseiids is generally shorter than that of the Tetranychidae under comparable conditions. The size of the predatory mite is about that of its prey 0.7–0.9 mm. They only oviposit after fertilization and the sex ratio seems to be about 1. Their rate of oviposition is maximally about 2 eggs per day, with a total maximum fecundity of approximately 30. The fecundity, and especially the development rate, are influenced by the availability of prey (van de Vrie, 1972). Their main food is the phytophagous mite *Panonychus ulmi,* with a clear preference for the younger stages. *Eriophyidae*, pollen, honey and honeydew are also accepted as food (Chant, 1959; McMurtry & Scriven, 1966). *Amblyseius finlandicus* also feeds on apple mildew *(Podosphaera leucotricha)* and even reproduces on this food, but shows a shorter lifetime (Kropczynska, 1970). The life cycle is synchronized with that of *P. ulmi.* Diapause starts in August in the adult fertilized female. The sensitive stage for daylength and temperature is the deutonymph (van de Vrie, pers. commun.). The winter females shelter in crevices in basic bud scales and scars of the trunk and branches. The mortality in winter is normally low (van de Vrie, 1964).

Some workers reported winter mortality in predatory mites on fruit trees (Dosse, 1956; Chant, 1959).

Their estimations may be incorrect because they may have included non-diapausing and diapausing females, as well as males during the autumn count while in fact, only fertilized winter females overwinter. Predation potentials differ widely and contrasting data are given (Dosse, 1956; Collyer, 1964; van de Vrie, 1972) possibly because of different methods of evaluation.

Although the bionomics of the three species mentioned seem to be similar, there are some regional differences in their relative abundance. *A. potentillae* is quite common in the South West of the Netherlands, *A. finlandicus* is more numerous in the central part, while *T. pyri* seems to be equally distributed throughout almost all neglected orchards in the Netherlands.

2.3 The orchard

In the Netherlands commercial apple growing mainly takes place in spindle bush orchards. These are orchards with a plant density of 1000–3000 trees per ha, in rows so that many operations can be mechanized. In some a system of integrated pest control is being introduced; this study was undertaken on behalf of these orchards.
Normally 15–20 sprayings per year are applied against apple scab, powdery mildew and some insect pests; and 80–200 kg nitrogen per ha is given annually.
In the Netherlands the production cultivars grafted on weak rootstocks are: Golden Delicious, Cox Orange Pippin, Boskoop Beauty, James Grieve, Winston, Melrose, Jonathan and Karmine. These cultivars are often mixed row by row. The cultivar used in this study is Golden Delicious, economically the most important variety in the Netherlands. The results are easily transferred to other cultivars.

3 The simulation technique

3.1 Development and growth

A system is a limited part of reality with related elements. The set of relations is called the structure of the system. Examples of a system are a cell, a plant or a field. The boundary between system and environment is preferentially chosen in such a way that the behaviour of the system does not depend on its environment. The system is dynamic when it changes with time.
A simplified representation of a dynamic system is a dynamic model. If the model is the same as the original, there is no need to construct it. The model only has to agree with the original on relevant points. The differences between model and original can make the model more simple, easier to handle and more lucid than reality.
A fairly wide definition of simulation is the building of a model and studying its behaviour. Simulation is useful if it increases the insight in reality by extrapolation and analogy, if it is the basis for the design of new experiments and if the model accounts for the most relevant phenomena and contains no assumptions that are proven to be false. Simulation with the help of computers is only useful if the system studied is too complex and an analytical-mathematical approach becomes too difficult. The biological processes that underlie an ecological system can be represented in a simulation model with the help of computer languages that are especially designed for this purpose.
The simulations in this monograph were carried out according to the state variable approach. This approach is based on the use of digital computers. A digital computer, where all executions are discrete and take place in a sequential order, seems to be a most unsuitable instrument for simulating ecological systems, as the changes in this kind of system are parallel and continuous. The main feature of simulation languages is to overcome these limitations. These languages are based on the axiom that changes of the conditions in a system are not mutually dependent, but can be derived separately from the state of the system. All rates of change between time t and time $(t + \Delta t)$ are calculated from the condition at time t and if necessary data from the past. Only after the calculation of all the rates at the moment of

simulation, can the changes be executed by semi-parallel integration over a small time interval.
For practical reasons the time interval for integration cannot be infinitely small. It must be at least so short that the rates can be assumed to be constant during this interval. The simplest integration method available is the Eulerian or rectilinear one, in which the new value of an integral equals the old value plus the product of the time interval and the rate of change. The time interval is kept at a fixed value during simulation when this method is used.
In process simulation models, five different kinds of variables can be distinguished: state variables, driving or forcing variables, auxiliary variables, rate variables and output variables. The state variables characterize and quantify all observed properties of the system, such as number of larvae, number of parasites, amount of food and so on. At the onset of the simulation the values of all state variables have to be known. In mathematical terms they are quantified by the contents of integrals. In relational diagrams they are represented by squares.
Driving or forcing variables are those that are not affected by processes within the system but characterize the influence from outside. These may be for instance the temperature or the temperature sum. Depending on the boundary of the system to be simulated, the same variables may be classified either as state or as driving variables. In relational diagrams driving variables are represented between brackets.
The rates of change of the state variables are quantified by rate variables. Knowledge of the underlying biological and physical processes makes the formulation of rules possible, according to which the values of the rate variables are determined. In relational diagrams rate variables are represented by valves.
For complicated processes the use of properly chosen intermediate auxiliary variables makes the calculation process more lucid. In relational diagrams these variables are represented by circles. Output variables are the quantities that the model produces for the user. They may be state, rate or auxiliary variables.
Parameters, that have a constant value, are underlined in relational diagrams. Flow of material is represented by solid lines, while flow of information is represented by broken lines.
The application of the state variable approach in ecosystem modelling and the simulation language used here, Continuous System Modelling Program CSMP, is explained in detail in another volume of the Simulation Monograph Series (De Wit & Goudriaan, 1974).

The relational diagram in Fig. 1 shows one simple way to simulate

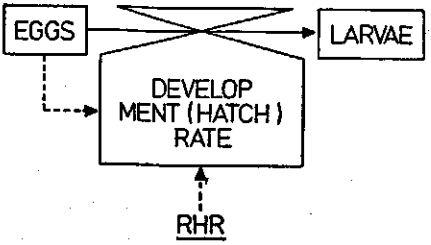


Fig. 1 | Simplest relational diagram for the hatching process of eggs.

hatching, i.e. the emergence of young larvae from eggs. The amount of eggs, and the amount of young larvae, two state variables, are given within rectangles. They are connected by a solid arrow that designates the flow of individuals from one state to the other. This flow is regulated by the hatching rate, HR, a variable presented within the valve symbol, dependent on a constant the relative hatching rate, RHR, which is underlined and on the amount of eggs; both dependences being presented by broken lines.

In CSMP, the two state variables are presented by integrals.

```
EGGS = INTGRL (100., - HR)
LARV = INTGRL (0., HR)
```

The first number in the argument is the initial value, which is here, of course, zero for the number of larvae and arbitrarily assumed to be 100 for the number of eggs. The second variable in the argument is the rate of change of the number of larvae. This hatching rate may be equal to HR = RHR*EGGS in which the relative hatching rate is defined as a parameter at, for instance, 0.1 day^{-1} with

```
PARAMETER RHR = 0.1
```

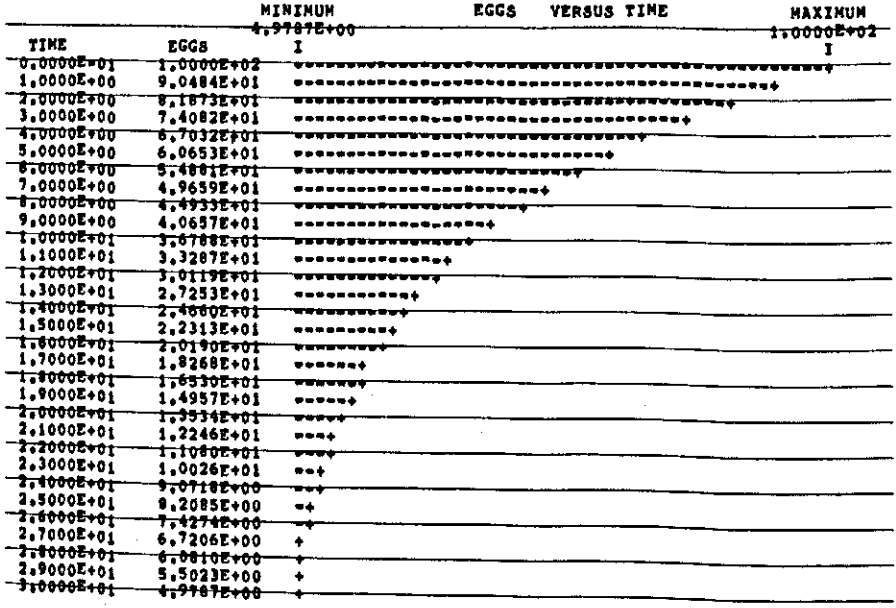
The actual simulation program is completed with a statement that specifies the time period over which the system is simulated and the interval at which output is wanted:

```
TIMER FINTIM = 30., OUTDEL = 1.
```

a statement that specifies the output:

```
PRTPLT EGGS, LARV
```

The output is given in Fig. 2.



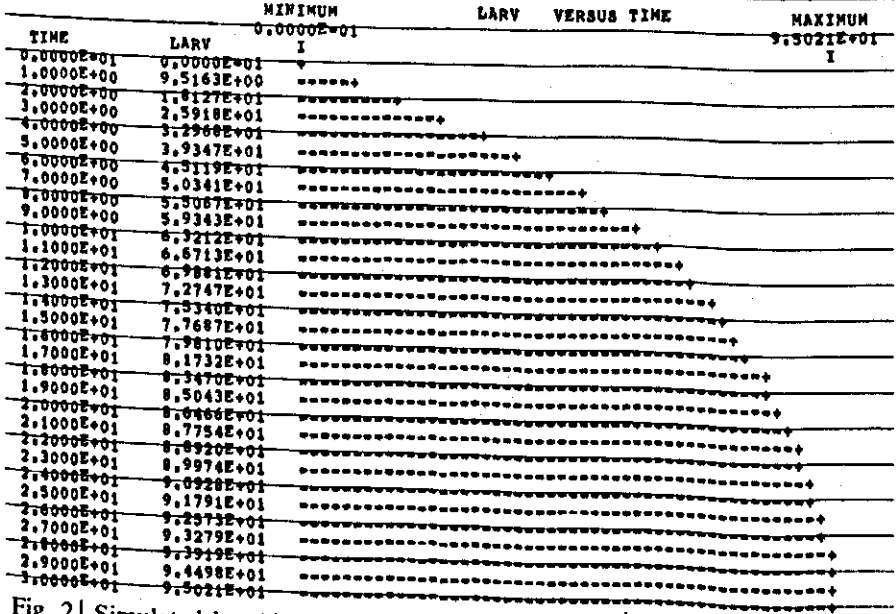


Fig. 2| Simulated hatching curve of eggs and corresponding emergence of larvae, when only one integral is used (Poisson process).

Obviously there is an exponential decrease in the number of eggs and a corresponding increase in the number of larvae.
The hatching rate may also be a function of temperature. If a birth rate, BR, and a death rate of eggs, DR, is added the first integral becomes

```
EGGS = INTGRL (100.,BR - DR - HR)
```

and the hatching rate becomes

```
HR = EGGS * AFGEN (RHRT, TEMP)
```

The AFGEN function (Arbitrary Function GENerator) makes linear interpolation possible between given values for RHR.
The other rates: birth rate and death rate should, of course, also be quantified.
It is well known that the average residence time in the egg stage is the inverse of the relative hatching rate, i.e. 10 days for Fig. 2. Hence the duration of the process is controlled by the relative hatching rate.
The form of the resulting curve, however, is still unrealistic. Actual experiments show that for some days after the onset of hatching small numbers of larvae appear. Then the hatching rate increases and decreases again. The complexity of the hatching process and the many subprocesses concerned, obviously causes a bell-shaped hatching curve. Without analysing these underlying processes in detail, they may be mimiced by constructing a number of development classes according to the relational diagram of Fig. 3.

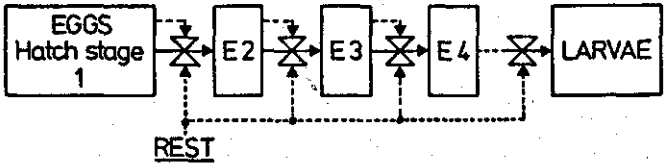


Fig. 3 | Relational diagram of the hatching process of eggs, application of the boxcar train or age classes approach.

In each class the residence time, RT, is 1/N of the total residence time (hatching time) REST, N being the number of classes (N = 10). This is programmed as follows:

```
EGG 1 = INTGRL (100., - EGG 1/RT)
EGG '2,10'= INTGRL (0., (EGG '1,9' - EGG '2,10') /RT)
LARV = INTGRL (0., EGG 10/RT)
```

The second integral statement stands for the 9 integrals EGG2 – EGG10. For instance:

```
EGG5 = INTGRL (0., (EGG4 - EGG5) / RT)
```

The residence time in each class, being defined by:

```
RT = (1/N)*REST
REST = 1/RHR
PARAMETER RHR = .1, N = 10.
```

The resulting emergence curve of larvae is presented in Fig. 4. A Gaussian distribution function with its maximum at 10 days (1/RHR) is obtained.
Goudriaan (1973) showed that the variance of this Gaussian distribution function is defined as:

$$S^2 = N \times (RT)^2$$

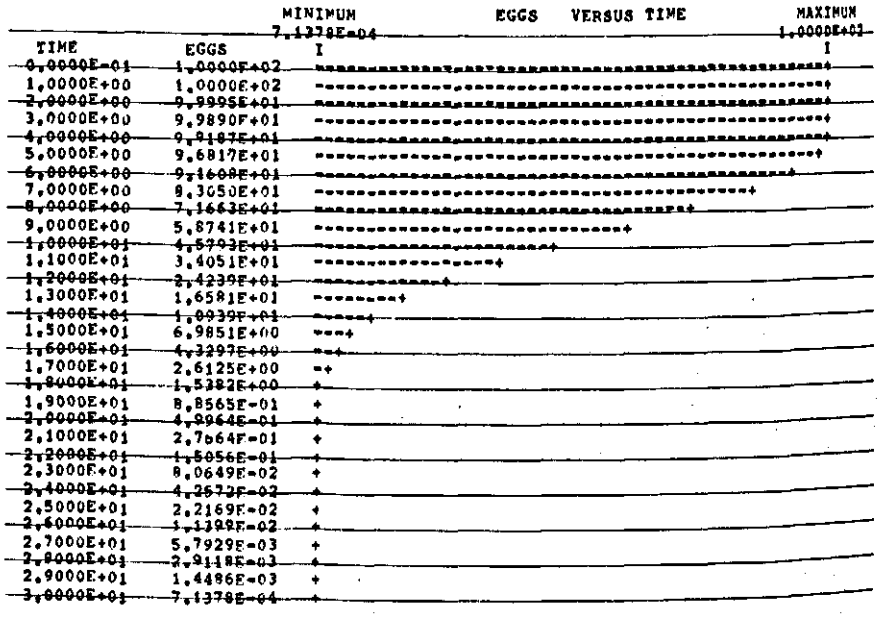
$N \times RT$ representing the average total residence time REST.
Hence the relative standard deviation is constant according to:

$$S/REST = S/(N \times RT) = (1/\sqrt{N})$$

and only dependent on the number of development classes.
So a relative standard deviation of 0.2 is realized when 25 classes are distinguished, and for a relative standard deviation of 0.1, 100 hatching (development) classes must be distinguished.
This large number of classes takes too much computing time and moreover, once the number of classes is chosen, the relative standard deviation is fixed.
It is possible that the relative standard deviation depends on the abiotic conditions for growth and development. A solution for this problem is found by a versatile combination of the presented method with a modelling system which moves the eggs through the development classes without dispersion, like the contents of the boxcars of a train moving along a track.
To achieve movement without dispersion the whole contents of the development classes are shifted at the moment at which one residence time is passed. This is done as follows:

```
EGG1 = INTGRL (100., -PUSH * EGG1)
EGG '2,10' = INTGRL (0., PUSH * (EGG '1,9' - EGG '2,10'))
LARV = INTGRL (0., PUSH * EGG10)
```

The variable PUSH is always zero, except at the moment when the residence time is passed. Then it has the value 1/DELT, in which



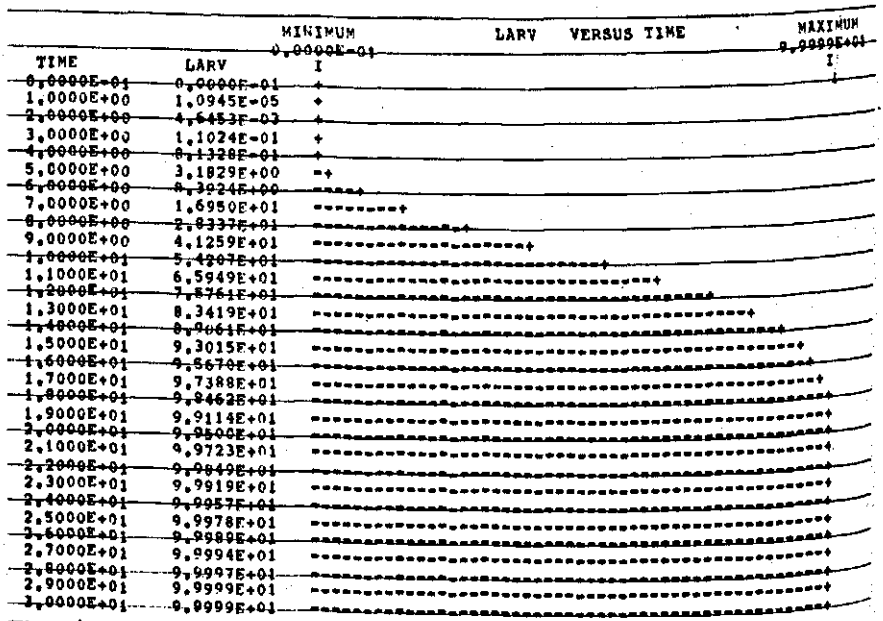


Fig. 4 | Simulated hatching curve and corresponding emergence with several development classes and the 'continuous' method of simulation of development.

DELT is the small time step of integration. At the moment the rate of change of, for instance, the integral EGG1 becomes EGG1/DELT, the content of the integral changes with numerical integration to:

$$EGG1_{t+DELT} = EGG1_t - (1/DELT) \times EGG1_t \times DELT = 0$$

In this way the first development class is completely emptied. Similar shifts occur in the other classes.
The control of the value of PUSH requires two additional statements

```
PUSH = INSW (HST - 1/N, 0.,1/DELT)
HST = INTGRL (0.,(RHR - PUSH/N))
```

The hatching stage, HST, is the integral of the relative hatching rate. HST accumulates until it exceeds 1/N. Then 1/N is subtracted. PUSH is set at zero by the INSWitch as long as HST is smaller than 1/N and equals 1/DELT when HST is larger. In Fig. 5 the result of this way of modelling is given, with N = 10 and a relative hatching rate of 0.1 day^{-1}. Hence there are now two programming systems available. One, the continuous one, which generates a constant relative standard deviation and the other, the discontinuous method, that generates no standard deviation at all. A combination of both methods for which the relative standard deviation is not constant can be mimiced by an intermediate method. A fraction F of the content of the development classes is shifted with a frequency which is 1/F time larger. F may depend on abiotic conditions or on other driving variables. This fraction is 1 when complete 'discontinuous' simulation is required and is DELT/RT when complete 'continuous' simulation suffices to mimic the dispersion.
This is shown in the following notations:
Continuous:

$$F = DELT/RT$$
$$HR = -EGG1 \times PUSH \times DELT/RT$$

As PUSH is 1/DELT:

$$HR = -EGG \times 1/RT$$

Discontinuous:

$$F = 1$$
$$HR = -EGG1 \times PUSH \times 1$$

In the intermediate cases the fraction F equals

$$1 - N \times (S/REST)^2$$

	MINIMUM 0,0000E-01	EGGS VERSUS TIME	MAXIMUM 1,0000E+02
TIME	EGGS	I	I
0,0000E-01	1,0000E+02	----------	+
1,0000E+00	1,0000E+02	----------	+
2,0000E+00	1,0000E+02	----------	+
3,0000E+00	1,0000E+02	----------	+
4,0000E+00	1,0000E+02	----------	+
5,0000E+00	1,0000E+02	----------	+
6,0000E+00	1,0000E+02	----------	+
7,0000E+00	1,0000E+02	----------	+
8,0000E+00	1,0000E+02	----------	+
9,0000E+00	1,0000E+02	----------	+
1,0000E+01	1,0000E+02	----------	+
1,1000E+01	0,0000E-01	+	
1,2000E+01	0,0000E-01	+	
1,3000E+01	0,0000E-01	+	
1,4000E+01	0,0000E-01	+	
1,5000E+01	0,0000E-01	+	
1,6000E+01	0,0000E-01	+	
1,7000E+01	0,0000E-01	+	
1,8000E+01	0,0000E-01	+	
1,9000E+01	0,0000E-01	+	
2,0000E+01	0,0000E-01	+	
2,1000E+01	0,0000E-01	+	
2,2000E+01	0,0000E-01	+	
2,3000E+01	0,0000E-01	+	
2,4000E+01	0,0000E-01	+	
2,5000E+01	0,0000E-01	+	
2,6000E+01	0,0000E-01	+	
2,7000E+01	0,0000E-01	+	
2,8000E+01	0,0000E-01	+	
2,9000E+01	0,0000E-01	+	
3,0000E+01	0,0000E-01	+	

	MINIMUM 0,0000E-01	LARV VERSUS TIME	MAXIMUM 1,0000E+02
TIME	LARV	I	I
0,0000E-01	0,0000E-01	+	
1,0000E+00	0,0000E-01	+	
2,0000E+00	0,0000E-01	+	
3,0000E+00	0,0000E-01	+	
4,0000E+00	0,0000E-01	+	
5,0000E+00	0,0000E-01	+	
6,0000E+00	0,0000E-01	+	
7,0000E+00	0,0000E-01	+	
8,0000E+00	0,0000E-01	+	
9,0000E+00	0,0000E-01	+	
1,0000E+01	0,0000E-01	+	
1,1000E+01	1,0000E+02	----------	+
1,2000E+01	1,0000E+02	----------	+
1,3000E+01	1,0000E+02	----------	+
1,4000E+01	1,0000E+02	----------	+
1,5000E+01	1,0000E+02	----------	+
1,6000E+01	1,0000E+02	----------	+
1,7000E+01	1,0000E+02	----------	+
1,8000E+01	1,0000E+02	----------	+
1,9000E+01	1,0000E+02	----------	+
2,0000E+01	1,0000E+02	----------	+
2,1000E+01	1,0000E+02	----------	+
2,2000E+01	1,0000E+02	----------	+
2,3000E+01	1,0000E+02	----------	+
2,4000E+01	1,0000E+02	----------	+
2,5000E+01	1,0000E+02	----------	+
2,6000E+01	1,0000E+02	----------	+
2,7000E+01	1,0000E+02	----------	+
2,8000E+01	1,0000E+02	----------	+
2,9000E+01	1,0000E+02	----------	+
3,0000E+01	1,0000E+02	----------	+

Fig. 5 | Simulated hatching curve with the 'discontinuous' method of simulation.

so the size of the fraction is determined by the deviation from the 'continuous' situation, i.e. $N = (REST/S)^2$. Thus the value of F can be adjusted to give different values of the relative standard deviation. When the standard deviation becomes relatively small, the size of the fraction increases until the extreme case of complete 'discontinuous' simulation without any dispersion occurs.
In CSMP this is written:

```
EGG1 = INTGRL (100., - PUSH * EGG1 * F)
EGG '2,10' = INTGRL (0., PUSH * (EGG '1,9' - EGG '2,10') * F)
LARV = INTGRL (0., PUSH * EGG10 * F)
PUSH = INSW (HST - 1.,0., 1./DELT)
HST = INTGRL (0., 1/RT - PUSH)
  F = AMAX1 (DELT/RT, 1. - N * ((S/REST) ** 2))
```

The expression AMAX1 (- -,- -) is a CSMP function that takes the largest of the two arguments between the brackets.
The resulting birth-rate curve is given in Fig. 6. It can be shown that the resulting variance is given by

$$S^2 = N \times RT^2 \times (1 - F)$$

In this way $(S)^2$ equals zero when $F = 1$, and whole contents of the classes are shifted. It approaches its maximum value when F approaches DELT/RT.
As has been said F and the relative hatching rate are often functions of biotic and abiotic conditions. This combined method of modelling is used in this monograph to simulate the development of the larval, pupal and adult stages of the larch bud moth. However the lumping of populations into development classes introduces errors of approximation. In the most extreme case when $F = 1$, the contents of the classes are shifted as a whole and when a limited number of classes is distinguished the approximation errors can be considerable. For instance, in a development model of eggs at a constant temperature of 15°C, age classes of 0–2, 2–4, 4–6, 6–8 days may be distinguished. Every two days the contents of the classes (as $F = 1$) are shifted one place, so that generally the residence time in each class is two days. This does not hold however for the first development class, as it has a continuous inflow, formed by the birth rate. Only individuals born just after a shift will stay here for two days. As time proceeds the residence time of individuals born later will become progressively shorter. On the average the residence time in the first class will be half of the interval of pushing. So the average age of the eggs pushed from the first age class to the second is not 2 days, but 1 day, and this means that the next age

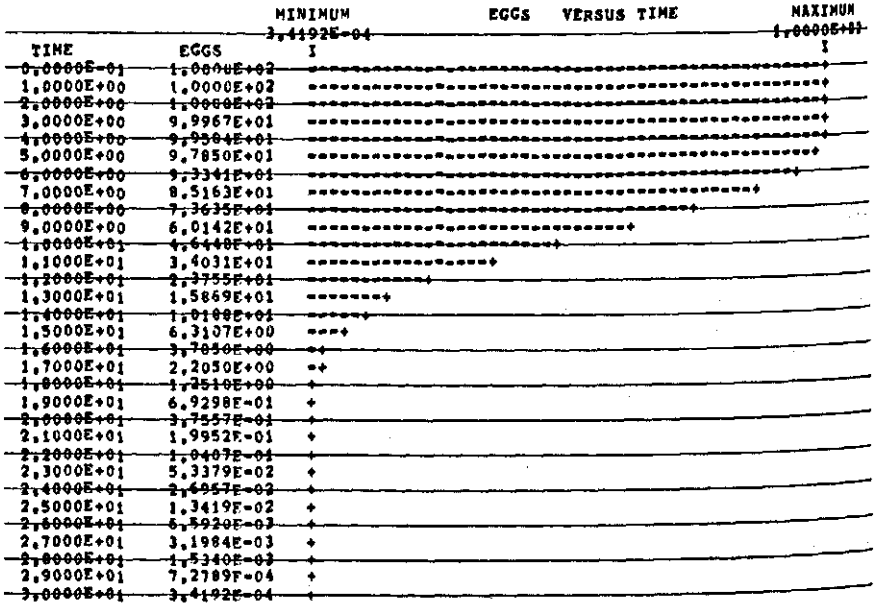


Fig. 6| Simulated hatching curve and corresponding appearance with the method of 'controlled' dispersion.

classes are 1–3, 3–5, 5–7 days, instead of 2–4, 4–6, 6–8 days, respectively.
A solution for this error is found by placing a preclass before the different development classes. This class is filled continuously by the birth rate and emptied continuously with a rate that is half the residence time of the considered age class multiplied by the content of this class, so:

EGG0 = INTGRL (0., BR – (1/(RT * .5)) * EGG0)

and as F = 1

EGG1 = INTGRL (0., (1/(RT * .5)) * EGG0 – PUSH * EGG1 * 1.)

In this way the first development class is filled with a continuous rate of eggs with an average age of one day. The average age of the eggs in the first age class at the moment of shifting is then two days instead of one day.
When F = 1, this error occurs and the given solution for this problem should be applied, but, when F = DELT/RT, there is no error of approximation. Therefore in the intermediate cases and when F = DELT/RT, an additional correction should be introduced. This is done by multiplying the rate of transfer from the preclass to the first development class by the reciprocal of the fraction F. Thus a preclass with an outflow of 2/RT when F = 1, and of (2/RT)×(1/F) in the intermediate cases, synchronizes the ages in the development classes. When F = DELT/RT, 'continuous' simulation, the residence time in the preclass is negligible but then very small time steps are necessary and this requires too much computer time.
Waste of computer time is prevented by choosing the number of classes not too close to that number with which continuous simulation mimics the dispersion correctly.
In this way growth and development of organisms is simulated with incorporation of the dispersion in development, due to the underlying physiological processes, and without losing any accuracy in the age structure of the population.

3.2 Time constants of processes

As shown in Section 3.1 where the simulation technique was introduced by describing the simulation of population development, the rates of change are integrated numerically. The time step used was 0.01 day and it was kept constant during the process. However within a rather complex simulation model of the system, processes with differ-

ent relaxation times occur. Relaxation time is defined as the time needed to recover from small disturbances. The physical processes determining the microweather in the laminar layer around the leaf, for example, are much faster than the ageing process of the female fruit-tree red spider mite.
A characterization of the time scale on which such changes occur is the time constant of a process. The time constant can be estimated, when the rate of change of a state variable is approximated by a differential equation of the form:

$$\frac{dA}{dt} = \pm A/\tau$$

in which τ is the time constant with dimension time. The dynamic behaviour of a system is correctly simulated when the time intervals of integration are much smaller than the time constant of that system. If not the postulate that the rate of change of the system does not change during that interval is invalid. The time constant of the fastest process therefore determines the time interval to be employed in the simulation. When the time constants are more than a factor 10^3 apart, an hierarchical approach can be used to avoid handling of several levels of resolution in parallel in one model (van Keulen, 1975).
For this system the predation process (Section 4.2) is treated in this way.

4 Relational diagrams

Process simulation models should be based on quantitative data on the sub-processes of the system to be simulated. But before formulating the quantitative aspects, the main interrelations within the system are given in relational diagrams. The biology of the fruit-tree red spider mite and its natural enemies, given in Chapter 2, paves the way for an analysis of the system which results in these diagrams. For the symbols used see Appendix I.

The simulation model on the population fluctuations of the fruit-tree red spider mite and its natural enemies consists of four parts:
the fruit-tree red spider mite, its natural enemies, the interrelations between prey and predator, and the abiotic factors.
A detailed analysis of the sub-processes made clear that the predation process (4.3) and the weather, especially temperature (4.4), required more detailed simulation models.

4.1 Fruit-tree red spider mite (P. ulmi)

A relational diagram of the population growth and development of *P. ulmi* is given in Fig. 7. The development is lumped into five groups: the eggs, the juveniles insensitive to diapause-inducing conditions, juveniles sensitive to diapause-inducing conditions, and adults; males and females.
Two conditions of the teleiochrysalis and deutonymph can be distinguished, the summer and the winter form, so that there are at least four adult forms: females and males both in winter and summer form. After copulation summer females lay summer eggs that may hatch after a short period; winter females lay winter eggs that may hatch next spring. The arrows with the crosses indicate death due to abiotic and biotic factors. Each group of physiological stages, distinguished in this relational diagram is presented in more detail in the next diagrams.

Fig. 8 shows the hatching of winter eggs.
A train with two boxcars is sufficient to mimic the dispersion. The winter eggs start hatching after a cold period (winter), when a certain sum of mean daily temperatures above the development threshold has

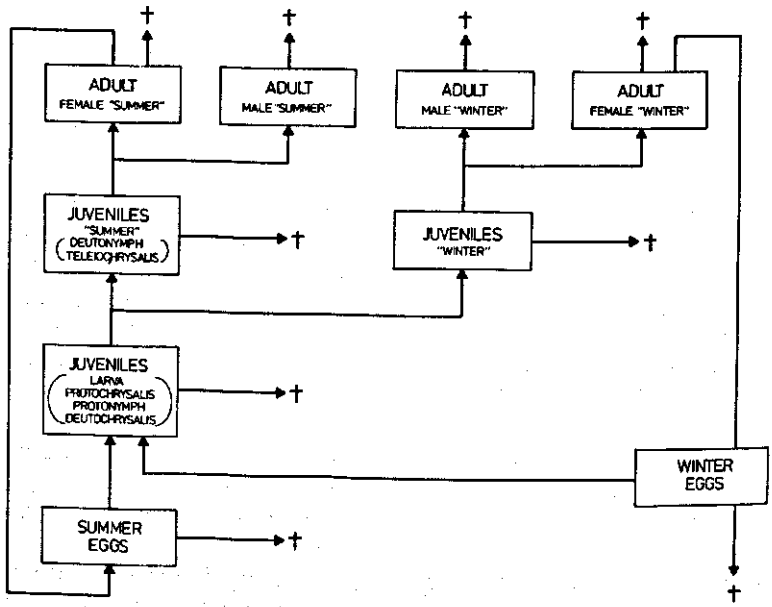


Fig. 7 | Life cycle of *Panonychus ulmi*.

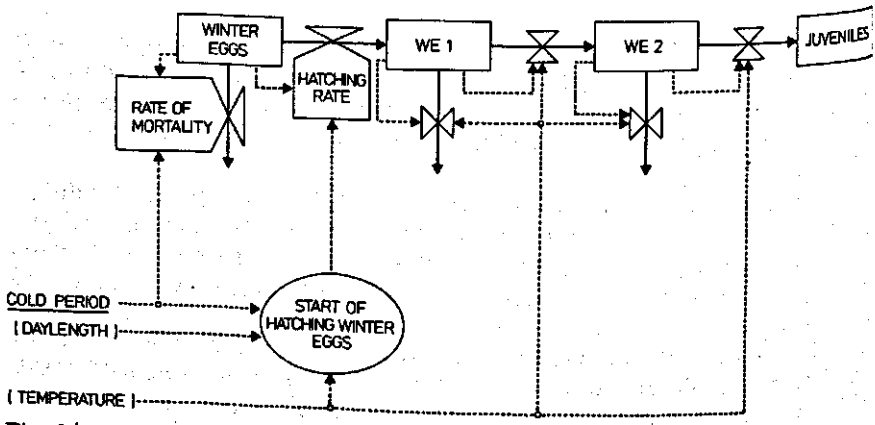


Fig. 8 | Development and hatching of winter eggs of *Panonychus ulmi*.

cumulated (incubation period). From then on the rate of hatching is determined by the actual temperature as are the rates of transfer to the next stages.
Winter mortality depends on the length and the intensity of the cold period. Since all intrinsic rates are given in relative terms (day^{-1}), the rates of transfer also depend on the number of individuals in each state.

Fig. 9 represents the growth and development in the juvenile stages. Six juvenile stages are considered, except for stage zero which must be introduced to synchronize the transfer of one stage to the other, a technical detail which was discussed in Chapter 3.
This number is sufficient to mimic the dispersion and to distinguish the different growing and quiescent juveniles. This distinction is necessary because the predator prefers young active juveniles and does not accept the quiescent stages or eggs. The rate of transfer from one boxcar to another depends on temperature, relative humidity and food quality. The mortality due to abiotic factors depends on temperature only, because even with closed stomata the relative humidity near the leaf is high enough to prevent death due to this factor (Section 5.4).
The mortality by predation acts only in the stages J0, J1, J2, J4, and J5, the other stages representing quiescence. Whether the animals in J6 are transferred to the state of summer (JS0) or winter (JW0) juveniles depends on daylength, daily mean temperature and food condition of the plant.
Fig. 10 shows the development and growth of the juvenile stages sensitive to diapause-inducing conditions. Here four stages are sufficient to mimic the dispersion and to distinguish the juveniles acceptable to the predators from those not eaten. Only JS1 and JS2 (deutonymph) are consumed; JS3 and JS4 represent the quiescent stage teleiochrysalis, which is not eaten at all.
Because of the reversibility of the diapause process, there is a flow of animals from winter form to summer form and vice versa. The rates of flow depend on daylength, daily mean temperature and food condition of the plant. The transitions to the next stage depend on temperature and food supply, and the mortality rates due to abiotic factors depend on temperature and relative humidity. As the relative humidity in the laminar layer around the leaf, where the animal is living, never has values above or below the lethal thresholds, this driving variable does not play a role in the simulated situations. The rate at which the JS5 and JW5 become males or females depends on sex ratio and temperature (AFS0 and AMS0, or AFW0, and AMW0). The sex ratio is considered to be constant unless very high population densities are

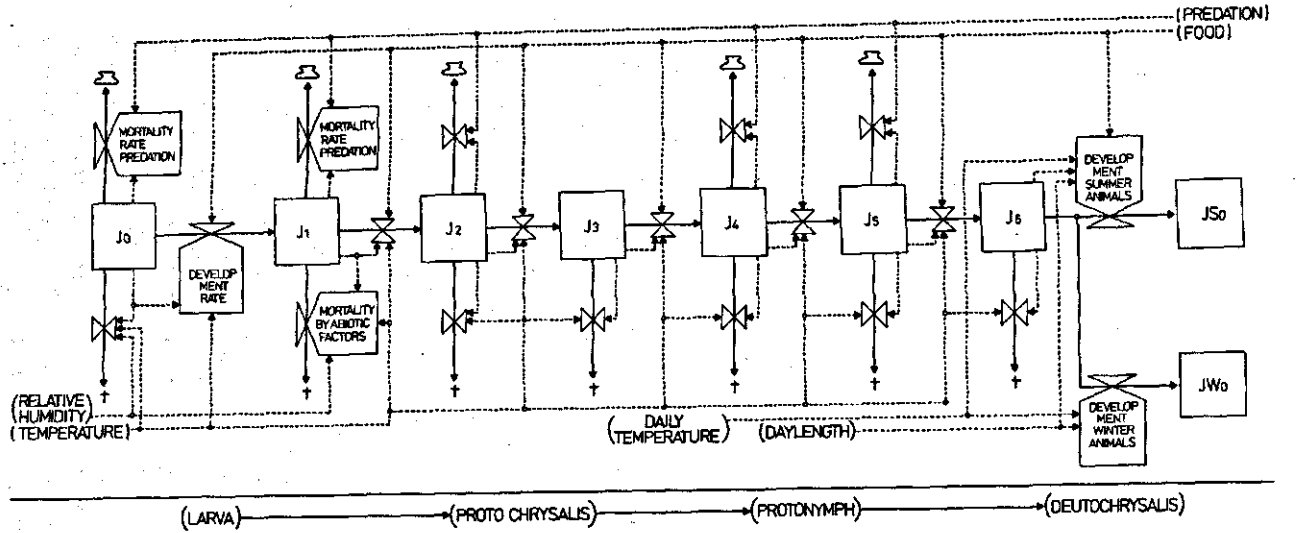


Fig. 9 | Growth and development in the juvenile stages of *Panonychus ulmi*. (larva, protochrysalis, protonymph, deutochrysalis).

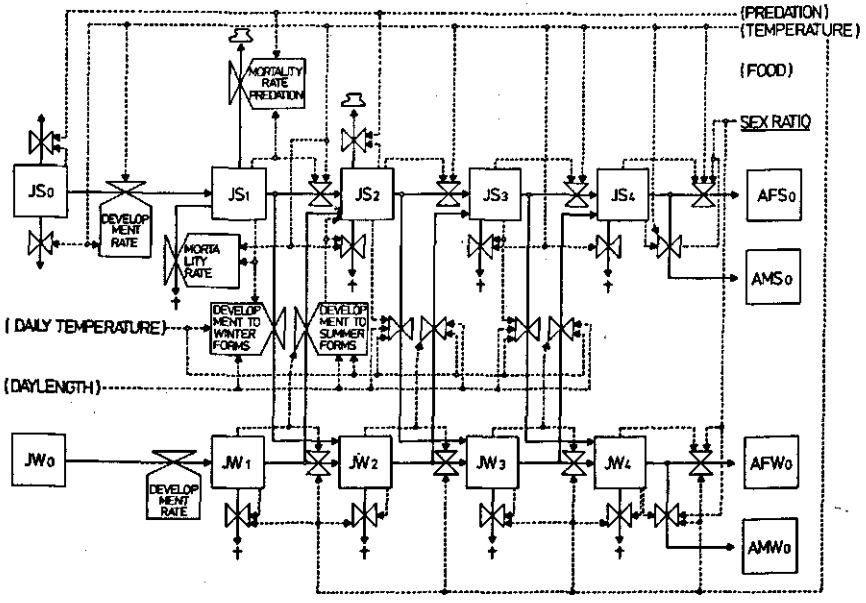


Fig. 10 | Growth and development in the juvenile stages sensitive to diapause-inducing conditions of *Panonychus ulmi* (deutonymph, teleiochrysalis).

reached. Therefore this factor is introduced here as a constant parameter.

The development, growth and ageing of the adult females (only summer forms) is given in Fig. 11. During the life of adult females three phases can be distinguished; the pre-oviposition females, the ovipositing females and the post-oviposition females. The pre-oviposition females are simulated with a boxcar train of only two boxcars and since relative dispersion in the pre-oviposition period is nearly constant, the method of 'continuous' simulation is applied. After maturation, oviposition and senescence will follow and since both ageing and fecundity are dependent on temperature, ten cohort groups of different ages are considered. Predators accept females as food but prefer the younger stages. Thus the predation of the older stages is neglected. The rate of change through the different boxcars is simulated by the method without dispersion. Mortality rates are continuous and depend on temperature and age. Ageing can also be correctly simulated by the

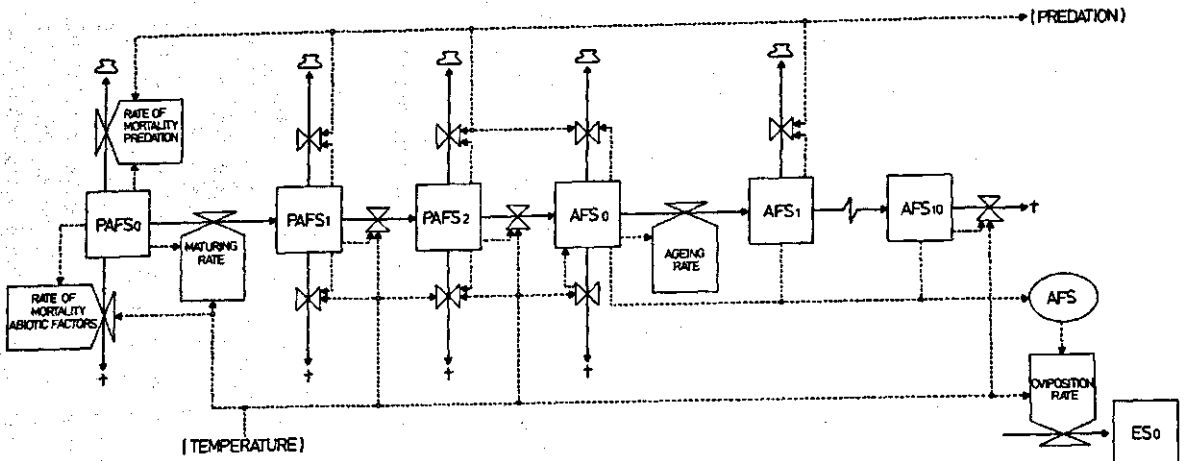


Fig. 11 | Ageing of the adult females of *Panonychus ulmi*.

method of controlled dispersion. However as this method is based on the calculation for the mean adult female, the mean rate of oviposition for the whole life-span should then be taken.
Rate of oviposition dependent on age can only be simulated by the method of ageing without dispersion.
In both methods oviposition rate depends on the number of females available and on the relative oviposition rate, an auxiliary variable dependent on temperature and food quality. The food quality is assumed to be within narrow limits and therefore this effect is neglected. There is no lack of food because these models work below the economic damage level.

In Fig. 12, the ageing of the males is given. In males the duration of the last juvenile stage is half a day to a day shorter than that of females. Here the only function of the males is copulating with the females. Several matings by one male are possible without any effect on the fertilization of subsequent females. Males die by ageing or from predation by the adult predators. Rate of ageing, mortality rates and predation rates are temperature dependent.
A separate description of the same sequence of development, ageing and dying in 'winter' animals is not necessary.
The summer and winter eggs will hatch if certain conditions are fulfilled.
The hatching process of winter eggs has already been described. In

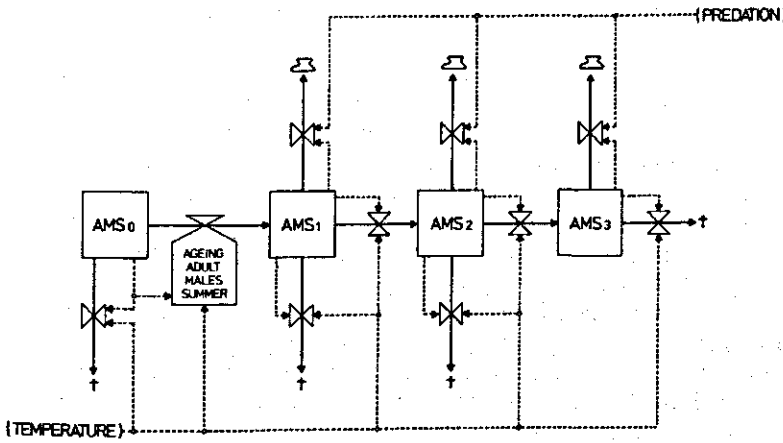


Fig. 12 | Ageing of the adult males of *Panonychus ulmi*.

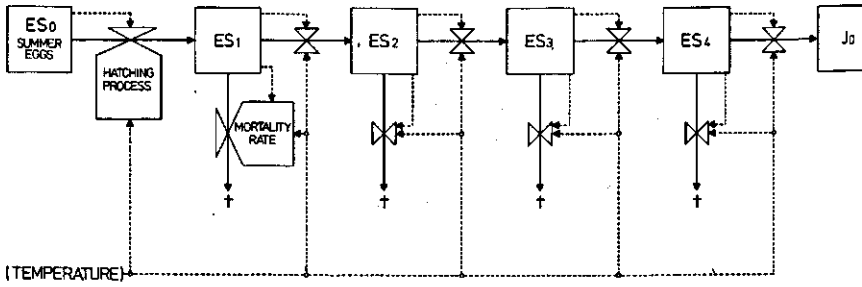


Fig. 13 | Development and hatching of summer eggs of *Panonychus ulmi.*

Fig. 13 the hatching process of the summer eggs is represented. After oviposition the egg passes into a quiescent state that lasts several days. The length of this period depends on hatching rate; mortality and hatching rate depend on temperature.
The juveniles from winter and summer eggs are not distinguishable and are therefore lumped.

4.2 The predatory mites

As the life cycles for the predatory mite species considered are similar, the description of merely one species, *Amblyseius potentillae* will suffice. In Fig. 14, a relational diagram for the population growth and development of *A. potentillae* is given. Again the stages are lumped into five groups: eggs, juveniles insensitive to diapause-inducing conditions, juveniles sensitive to diapause-inducing conditions, and adults: males and females.
In the adult stage a distinction is made between summer and winter forms, resulting in four adult forms: females and males, both in winter and summer form. Although 'winter males' do not exist, Section 2.2, they appear in the relational diagrams for reasons of simplicity. In the computer models, Chapter 8, they are absent. After copulation summer females start laying eggs, winter females do not immediately oviposit but start ovipositing after a cold period on the branches and the twigs of the trees.
The arrows with the crosses again mean mortality due to abiotic and biotic factors. Two groups are sufficient to discriminate between summer and winter forms. Development is faster when sufficient preferred food is available. The influence of the prey on the rate of mortality can practically be neglected because alternative food sources are always present (see Section 9.4).

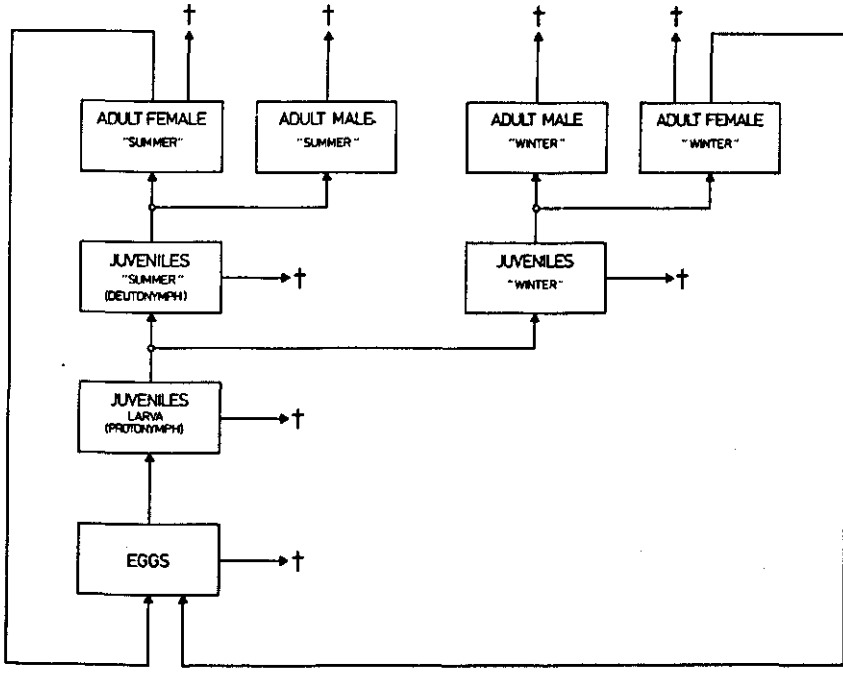


Fig. 14 | Life cycle of *Amblyseius potentillae.*

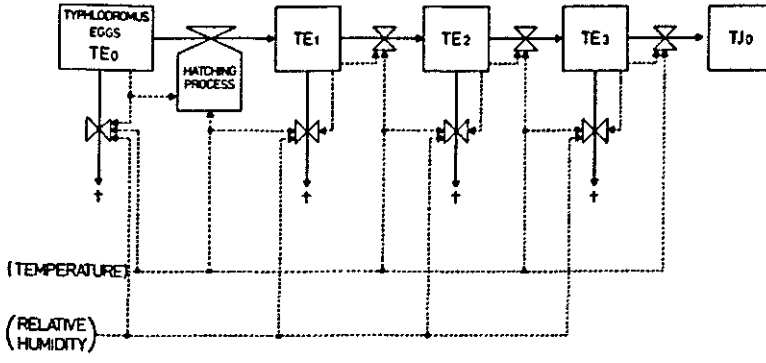


Fig. 15 | Development and hatching of eggs of *Amblyseius potentillae.*

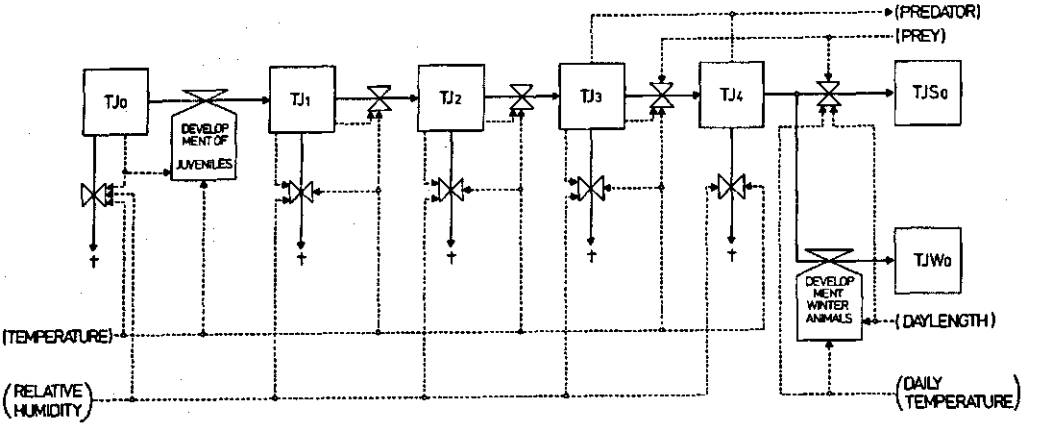


Fig. 16 | Growth and development of juveniles (larva and protonymph) of *Amblyseius potentillae*.

Fig. 15 represents the development of the eggs, which depends, as do mortality rates, on the temperature. Four stages suffice to mimic the dispersion in the hatching process of the eggs. A zero class is again added to synchronize the age in the different stages.

In Fig. 16 the growth and development of the juveniles (larva, protonymph) are given. Four boxcars are sufficient to mimic the measured dispersion and to distinguish the different developmental stages. The mortality in the different stages depends on temperature and relative humidity, although the influence of the last driving variable is limited because the lethal level is practically never reached. The rate of development in the last two boxcars is affected by the auxiliary variable, prey, expressing the influence of prey on development. At last juveniles sensitive to diapause-inducing conditions appear: the summer and winter juveniles. The rate of development of winter and summer forms depends again on daylength and daily temperature and on prey density.

The induction of summer and winter forms is assumed to be similar to that in the fruit-tree red spider mite. Fig. 17 shows the development

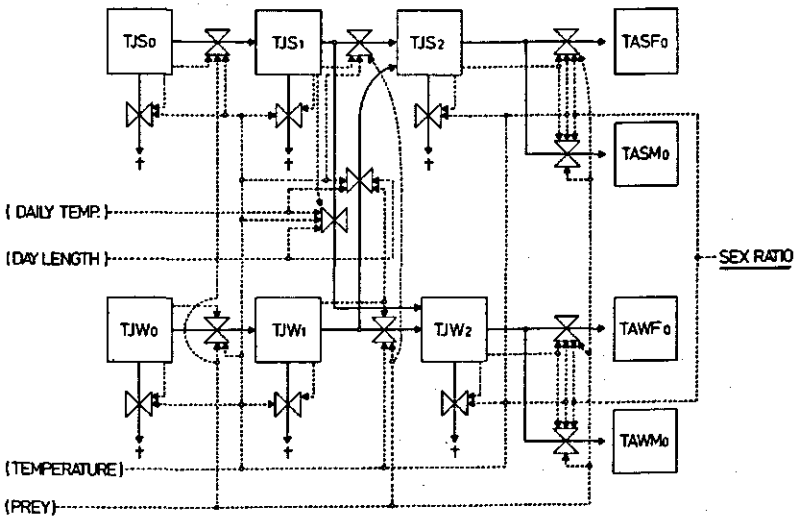


Fig. 17 | Growth and development of juveniles sensitive to diapause-inducing conditions (deutonymph) of *Amblyseius potentillae.*

and growth of the juvenile stages sensitive to diapause-inducing conditions (deutonymph). The rate of development is again influenced by temperature and prey, the mortality rates being influenced by temperature only. The number of age classes is chosen in such a way that the dispersion is well mimiced.

Fig. 18 shows the growth, development and ageing of the adult summer females. Because of their similarity the relational diagrams for the adult winter females and the summer and winter males are not given. The only difference is that winter females overwinter and all the other adult forms die in autumn.
The pre-oviposition female is described with two boxcars, development rate and mortality rate considered to be affected by temperature only. The reproductive and senescent female is described with ten boxcars and again the simulation method of boxcars without dispersion is applied. Ageing is simulated as for the fruit-tree red spider mite with relative mortality rates dependent on age and temperature. The rate of oviposition is age dependent so that not all boxcars contribute to reproduction. Besides the summer females, the winter females contribute to the production of eggs in spring. So the birth rate of eggs is the total number of egg-laying females multiplied by their temperature-dependent relative rate of oviposition, which is influenced by the auxiliary variable prey, expressing the number and composition of prey.

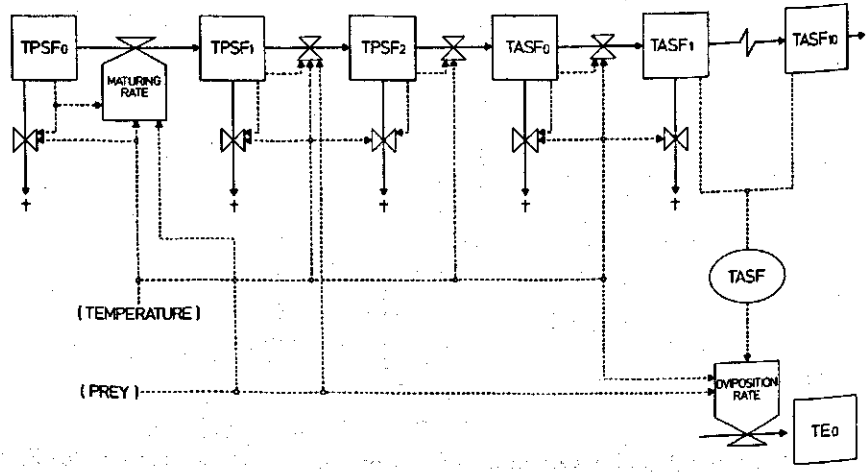


Fig. 18 | Ageing of the females of *Amblyseius potentillae*.

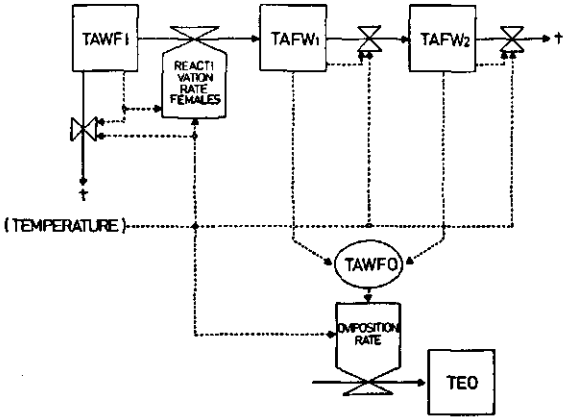


Fig. 19 | Reactivation of adult females of *Amblyseius potentillae* after the winter.

In Fig. 19, the reactivation of the overwintered females is given. The initial number of winter females depends on the number of females that were present in the preceding autumn and the mortality during the winter.
The start of the activation is synchronized with the development of the winter eggs of *P. ulmi* for simplicity. Before this time there is also some activity during warm periods in winter but this has no influence on the prey population. Prey eggs are not eaten. Two boxcars suffice to describe different stages and to mimic the dispersion. Temperature influences the activation rate. Since no oviposition occurs winter activity is completely neglectable. Because of lack of information about the overwintering process for both prey and predator, the models had to be initiated in another way (section 8.1.).

4.3 Interference between predator and prey

The interference between predator and prey population are shown in Figs. 9–18, and are represented by dotted lines to and from the auxiliary variables, (prey), (predator) and (predation). Five developmental stages of the prey (larva, protonymph, deutonymph, adult female and adult male) and four of the predatory mites (protonymph, deutonymph, adult female and adult male) are involved in the predation process because larvae of the predator do not feed and eggs of the prey are not eaten. The preference of predators for different stages of

prey depends on the state of the predators and their size. Juvenile predatory mites do not accept the adult stages of the prey and show a clear preference for the younger stages. Adult predatory mites attack all mobile stages of the prey, but also show preference for the younger stages, depending to a large extent on the satiation level of the predator.

The complexity of these interrelationships requires a detailed analysis of the predation process. Situations with very large numbers of predators and prey per unit (> 25 females of the prey per leaf) of surface are not considered. This is a realistic hypothesis as the model only presupposes situations in which regulation may occur.

Fransz (1974) presented a detailed analysis of a predator-prey system. With this detailed analysis it is possible to formulate simply the relations between predator and prey in population models of higher order. Only a short description of this modelling and experimenting on predation at the individual level will be given here.

The predator-prey system analysed in detail by Fransz (1974) was maintained on leaf disks of 5 cm^2 of lima bean. These were placed upside down on wet cotton wool in Petri dishes, with a number of fresh eggs of *T. urticae* or adult males and one *T. occidentales* female between three and ten days old. In Fig. 20 a relational diagram is given of the simplest situation of one predator and a fixed number of preys on a standard surface, all being kept constant. The number of captures per time unit (predation rate) depends on the number of encounters per time unit (encountering rate) and the success ratio (number of successful encounters to the numbers of encounters). The success ratio is influenced by the satiation level of the predator, the degree of filling of

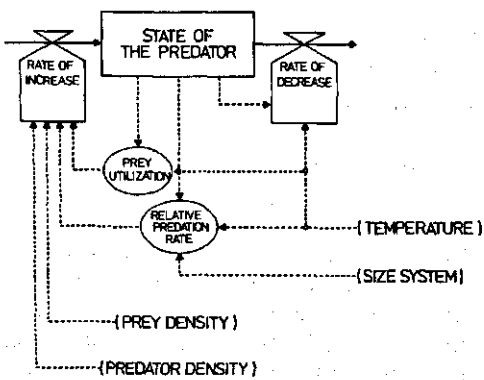


Fig. 20 | A prey-predator system one predator versus a fixed number of prey of one stage.

the gut or the predator's state, and the frequency of encounters that may induce response waning, which Holling (1966) called inhibition by prey. These processes occur only at very high densities and then the population model does not work properly.
The increase of the degree of filling of the predator's gut is affected by the predation rate and prey utilization. The degree of filling of the gut is used by Fransz as a measure of the predator's state; this is allowed as the maximum content of the gut is constant and the food consumed has a constant nutritive value. Prey utilization expresses the size of a prey and the degree of emptying of a prey; it is influenced by the predator's state.
Fransz also assumed that the ingestion rate is proportional to the difference between the actual gut content (A) and the maximum gut content (M). So

$$\frac{dA}{dt} = c \times (M - A)$$

c being a positive constant.
Catching and abandoning of prey were observed to be random processes. Irrespective of the handling time the number of prey caught in Δt has a Poisson probability distribution, with average values $sxEx\Delta t$, s being the success ratio, E the average number of encounters per time unit. This number depends on the actual number of eggs on the leaf disk, the coincidence in space, the locomotion velocity of the predator and the activity of the predator.
During each time step there is a small probability that the predator leaves its prey. This probability seems to be primarily determined by the predator's state (satiation) since hungry predators continue feeding on empty prey while satiated predators abandon their prey even before it is empty. In a stochastic model the variables handling, searching, catching and abandoning represent conditions and events. In a deterministic simulation of the predation process, these variables are considered as proportions on a continuous scale of individuals in a population, which is subjected to these events or conditions. Then all other variables represent population means. Stochastic models, give good results but require an excessive amount of computing time. The deterministic simulation model for the predation process requires much less computing time, but its results are wrong because of the many curvilinear relationships involved. The advantages of a new method, compound simulation, outweigh the disadvantages. It is a deterministic model which gives the expectation values of the stochastic model, but takes much less computing time.

Basically, at every time step the deterministic model is applied to homogeneous classes of individuals which are then de-homogenized, but reclassed again and again (Fransz, 1974).

With this model the functional response of the predator to the prey density can be explained by the underlying physiological and ethological processes. Thus the model on the predation process provides the basis for its incorporation in the population models in which the expectation values of the numbers of prey and predator are calculated. Calculations with the complex compound model show that the system reaches equilibrium, i.e. that the state of the predator fluctuates with a small amplitude on a level depending on predator and prey density and the temperature of the system.
Because of this equilibrium it is not necessary to use this complex model in population models at a higher hierarchical level. It suffices to work with the expectation values of relative predation rates and prey utilization as function of the state variable, that characterizes the state of the predator, and the temperature in a system of a well defined size. Relative predation rate multiplied by the number of preys and predator gives the predation rate. Prey utilization, for instance, in units of gut content per killed prey, expresses the size and degree of emptying of a prey.
The system: fruit-tree red spider mite – *Amblyseius potentillae* comprizes the same elements as Fransz' system. In an experimental analysis the correspondence and the similarity in predator's behaviour is shown (Section 6.1). Therefore Fransz's results can be used in the population models for fruit-tree red spider mite and its predatory mites.
The satiation level of the predator is easily quantified for *A. potentillae*, because a well-fed predator is dark reddish, while hungry predators are whitish and transparant. A colour scale was developed which relates the behaviour of the predator (success ratio) to the quantity of leaf and animal pigments in the predator that cause the colour (Section 6.2.2). The influence of temperature on the relative digestion rate is quantified in thermocabinet experiments and the effect of temperature on relative predation rate is found by determining the relations between relative predation rate and predator state at different temperatures. Prey utilization expresses the size of the prey, its utilization and its nutritive value.
Fig. 21 presents one predator with preys belonging to two prey stages; the temperature is kept constant. Both stages have the same relations with the predator as described for one prey stage. The decrease of the predator state is influenced by temperature and level of

the state only. The increase of the predator's state depends on predation rates 1 and 2, and prey utilization 1 and 2. The utilization of the prey is only influenced by the state of the predator. Predation rates 1 and 2 are determined by the success ratio and the encountering rates. For simplicity the factors that influence encountering rate (Fig. 21) are omitted here. Besides the number of prey present, temperature is the only driving variable.
In Fig. 22 a still more simple way of presenting the predator-prey relation for one predator stage and two prey stages is given: the predation rate is influenced by the relative predation rate and the number of prey present. This relative predation rate is affected by the temperature of the system and the state of the predator. The predator's state again is influenced by the rate of digestion and the rate of ingestion. The latter rate depends on the predation rates and the prey utilization.

If the temperature is not kept constant, predation rate, digestion and ingestion will fluctuate. Therefore all rates should be known at various temperatures. When several prey species are present the same approach is applied. Then several predation rates and prey utilizations influence the increase of the predator's state. How these relations are quantified is described in Chapter 6. When several predators of one stage are considered the same approach holds. Predation rates are multiplied by the number of predators present; the state of the predator is found by dividing the total state, i.e. the total amount of satiation level units per considered surface, by the number of predators. Relative predation rate and prey utilization are related to this variable.
When predators of different stages are involved the same approach works. For each predator stage the characteristic relations between predator state and relative predation rate or prey utilization are introduced.
All relative predation rates are given for a standard surface. Enlargement of the surface reduces the relative rate of predation so that for other apple cultivars a multiplication factor for the difference in surface structure should be introduced.
It is well known that also the different rates in the predator are affected by its satiation level. In *Amblyseius potentillae* the oviposition and development rates are strongly determined by its physiological condition. Section 6.3 describes the experiments on these relations.

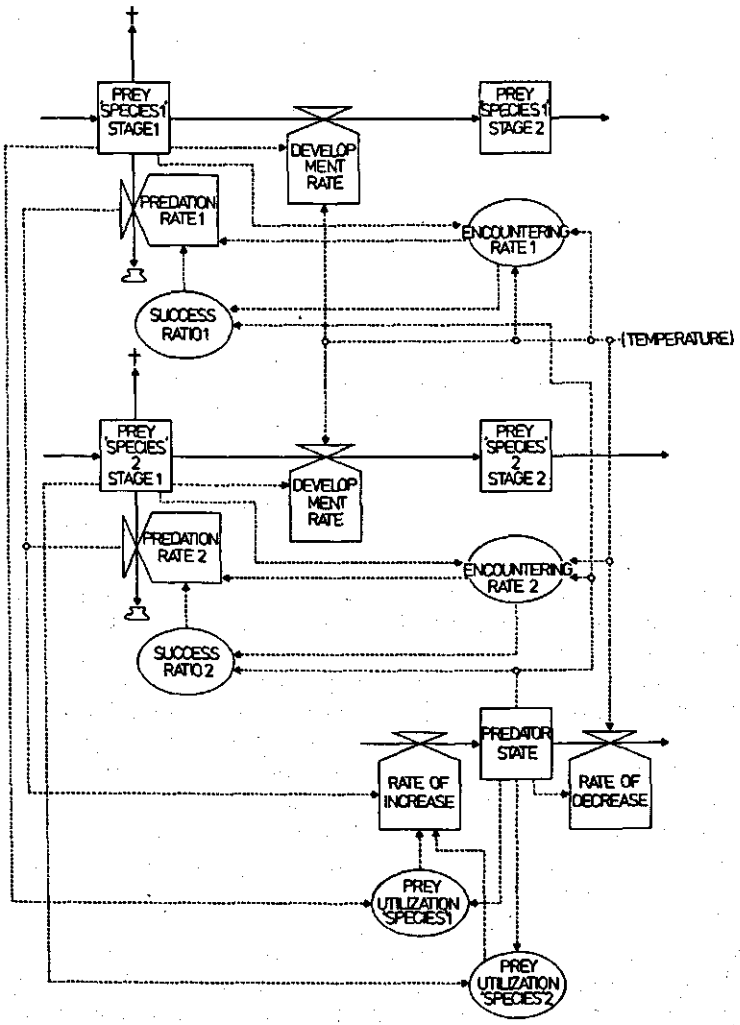


Fig. 21 | A prey-predator system one predator versus a fixed number of prey of two 'species', in this case the word 'species' represents different development stages of the prey.

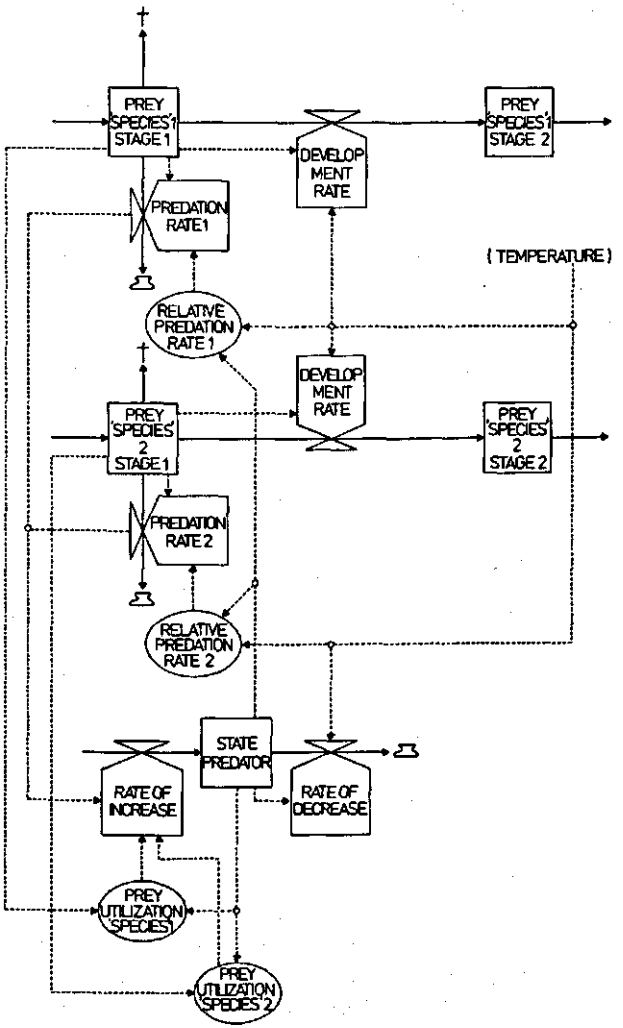


Fig. 22| A prey-predator system, simplified situation of Fig. 21.

4.4 The orchard and the weather

Nearly all modern apple orchards are of the spindle bush type described in Section 2.3. The orchard has three effects on the population models of fruit-tree red spider mite:

1. A direct effect on the rates such as oviposition, development and mortality (food quality).
2. An indirect effect on the rates by influencing the microweather around the leaves where the predator and prey are living (microweather).
3. Another indirect effect is the effect on the predation rates because the relative predation rate is influenced by the surface structure of the leaves and the ratio leaf area index–mean leaf surface (leaf area and structure).

Several studies on the relation between mite and host plant (Kuenen, 1949; Post, 1962; Storms, 1969) have shown that the nitrogen level of trees has an important influence on the population growth of the fruit-tree red spider mite. Post (1962) and Storms (1969) proved that the rates of oviposition, development and mortality are affected by different nitrogen dressings. But since the differences in nitrogen level in the leaves that they induced, were large in comparison with present field situations and because of the big standard deviations in their results the quantitative meaning of their data is rather small.

In Section 7.1 water culture experiments will be described to quantify the effect of nitrogen treatment on the photosynthetic activity of the trees and their influence on the fecundity and the oviposition rate of the fruit-tree red spider mite.

Besides the substrate on which the animals live, microweather factors such as temperature, relative air humidity and wind are the most important driving variables of the system. The 0.3–0.7 mm mites live in the very thin laminar layer around the leaves and here the abiotic conditions should be determined. Measuring these conditions requires sophisticated instruments and a very extensive sampling procedure because of the many different leaf positions within the tree. To make accurate measurements therefore is very time-consuming and may not give the right answer to the required accuracy. Another approach is simulation, i.e. the microweather at the leaf surface is simulated from the independent driving forces at the meso-level. The meso-level means here the temperature, wind, and air humidity in a Stevenson screen at 1.50 m and the incoming total global radiation above the crop.

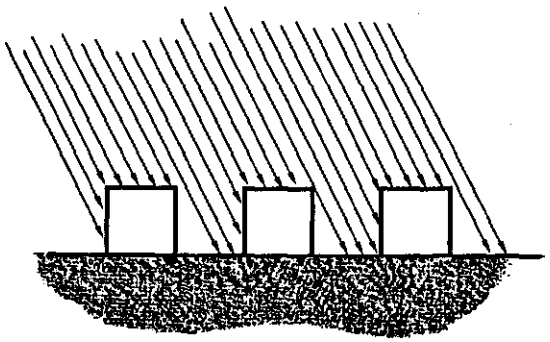


Fig. 23 | Hedgerowed crops and incoming sun beams.

Goudriaan & Waggoner (1972) described such a model for a closed crop and this model is transferred to a system of hedgerow crops. A complete description of the micro-weather models is given elsewhere (Goudriaan, in prep.); in Section 7.3 a short introduction to the approach is given. The canopy is described by its geometrical, optical and physiological properties, the soil underneath by its thermal and hydraulic properties. However, some assumptions were made to simplify the calculations. The main assumption was an optimum condition of the soil, with no water shortage. This is reasonable as most apple orchards in the Netherlands are situated on heavy clay soils, where shortage of water is very rare. Moreover many orchards are provided with a rain installation which guarantees optimum water conditions throughout the year. Another important assumption in the micro-weather models is the absence of vertical temperature and humidity profiles, based on the experimental experience that vertical air temperature differences within the 2.5–3 m high canopy are negligible. (Landsberg et al., 1973; see Section 7.3). The reason for this difference with the indian corn microclimate (Stigter et al., 1976) is the open hedgerow crop system. This crop structure, however, causes the problem of sidewards incoming sunrays (Fig. 23) with its influence on the sunlit area.

5 The bionomics of prey and predator

5.1 Introduction

The model description in Chapter 4 shows that much quantitative information on basic processes is needed, especially the influence of temperature, humidity, rain, wind and daylength on the rates of development, mortality, oviposition, ageing and diapausing of both the spider mite and the predatory mite. Since food supply may affect these rates, experiments have been done with abundant food of good quality; the influence of nutritive conditions will be treated in Chapters 6 and 7.

Many different kinds of experiments are discussed in this chapter. Some are straightforward, and give accurate results without much trouble; others require prohibitive amounts of time and labour to achieve the same accuracy. For instance the length of the hatching period of summer eggs of the spider mite is easily measured with an accuracy of 0.1 (defined as standard error/mean), but the determination of the oviposition rate of the spider mite with the same accuracy requires considerable effort. It is, however, not very useful to carry out all experiments with the same accuracy because the influence of each input relation on the end result of the simulation is different. Small differences may have a large effect on the end result and large differences a small effect, depending on whether their influence is magnified by positive feedback relations or damped by negative ones. It is of little use when models give end results of a much higher accuracy than the results of the independent experiments of higher order for verification of the simulation model. Hence, the accuracy of these verification experiments is a measure of the accuracy of the end results of the model. Thus it is possible at an early stage to form an idea about the required accuracy of the model. The preliminary models which are at first available are parameterized as well as possible and the influence of variation in the parameter values is evaluated. Then the first experiments on the input relations are planned in such a way that the accuracy of their results may be of the right magnitude. Since the model improves gradually, the necessary accuracy is reevaluated and those experiments which did not provide parameter estimations of an

acceptable accuracy are repeated to increase the data set or are executed in an improved fashion. This iterative procedure was continuously followed in the phase of model development and experimentation. Not all necessary input relations could be treated in sufficient detail, because equipment or time was lacking. Then the implication of this lack of information was evaluated with the same procedure.
The results of the last sensitivity analysis with the final and verified models are discussed in Chapter 10.
The literature data on the bionomics of the spider mite and the predatory mite were often not too useful because they were collected under different conditions that were not always specified and with other purposes in mind. Hence more experiments were done than was originally planned. The bionomics of the prey and predator are particularly affected by temperature and most attention was given to the analysis of its influence on the various processes. The necessary experiments were numerous because they concerned two species and because many processes like diapausing, oviposition, predation and so on are dependent on the developmental stage.
As an example of the treatment of the experimental data the hatching process of Section 3.1 will be considered again. This process can be described by two variables, the relative rate of hatching and the fraction of the individuals that had to be transferred from one box to the next in order to mimic correctly the dispersion. These variables can be calculated from experiments in which the duration of the hatching period is recorded in such detail that besides its average, the standard deviation may be estimated. To determine the average hatching period it may be sufficient to record the day on which the egg was laid and the day on which it was hatched, but to determine the standard deviation, observations should be made at intervals of some hours. This procedure may have been followed for the moment of hatching, but in most experiments reported in the literature batches of eggs laid during a 24-hour period were used. Therefore it was necessary to record the moment of the laying of the eggs with an accuracy of less than one hour. This laborious procedure was adhered to throughout all experiments. The mean and the standard deviation were obtained by plotting the frequency distribution of developmental periods cumulated with respect to time on probability paper (Fig. 24) because the normality of the distribution can be conveniently evaluated in this way. This evaluation was necessary because the modelling technique implies the assumption of a normal distribution for the duration of developmental stages.
In practically all cases the data were sufficiently close to a straight line

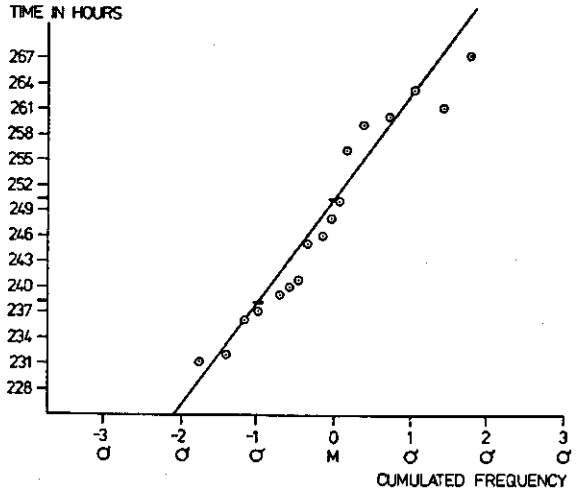


Fig. 24 | An example of a plot on probability of a frequency distribution of developmental periods cumulated with respect to time. The plots are used to determine mean and standard deviation and to test for a normal distribution of the data.

so that the assumption of normal distribution is justified. The effect of temperature was observed at various temperatures, which were the same throughout an experimental series. The results were used in situations where the temperature varied and this use implies that the (relative) rate under consideration reacts instantaneously and shows no after-effects. Van Keulen (1975) showed that this assumption is valid for the development rate of plants. Jansen (1974) and many others showed, however, that the process of seed germination is considerably enhanced by varying temperatures. This result is explained by the assumption that there are at least two catenary processes involved of which one has an optimum at a lower temperature than the other. For insects Uvarov (1931) described several examples of development rates at alternating temperatures that deviate from the rate to be expected on the assumption of an instantaneous reaction. Hence such an assumption has to be verified both for the spider mite and the predatory mite. Most determinations were made in situations where measurable responses occur so that any threshold value above which the process ceases to manifest itself has to be found by extrapolation. Putman (1970) did careful threshold experiments on red spider mites and his

results are practically the only literature data which could be used without much further experimentation.

5.2 Experiments

5.2.1 Fruit-tree red spider mite

Experiments on development rate were done in a serial cabinet at the Institute of Plant Protection Research, Wageningen. The duration of the different developmental stages was determined at constant temperatures of 10, 15, 17, 20, 25 and 30°C, and at alternating temperatures of 10 and 20 and 15 and 25°C. Temperature was measured continuously during the experiments with copper-constantan thermocouples in the zones where the animals were living.
The mites were reared on leaves of the apple rootstock M9 or the apple cultivar Golden Delicious on M9, both grown in the glasshouse at 15°C, and a relative humidity between 70 and 90%. The leaves were placed upside down on wet cotton wool in plastic boxes with the stalks pressed in the wet cotton wool to provide water. Although the leaves could remain fresh for some weeks at low temperatures, they were changed at least every four days to eliminate effects of food quality on the developmental period (Hamstead & Gould, 1957; Post, 1962). A small-scale experiment at one temperature with leaves attached to the tree was done for comparison.
Mortality during the experiments due to too low humidity (Mori, 1957) was neglected, as the wet cotton wool prevented lethal values below 60%. Too high humidities (>90%) did not occur in the cabinets. The mites were observed from the egg-stage up to the adult stage in a small ring of Tangle Foot (the trade name for a type of insect glue) applied to a leaf with a hypodermic syringe. Females were taken from colonies reared on small Golden Delicious trees (on rootstock M9) in the glasshouse.
The development of individual mites was observed at intervals of 8 hours. More frequent observations would have interfered with the experiments too much. The age at the beginning of the experiment was known with an accuracy of half an hour. Some mites died due to the transfer to fresh leaves and several others died by becoming stuck to the ring of glue. These mites were replaced by new eggs. Some mites died during development for unknown reasons. This mortality was lower than 5% in the considered temperature range, but above 30°C mortality increased abruptly.
Mortality rate during development in different stages was measured by

placing series of 10 eggs, larvae, protonymphs or deutonymphs for 24 hours on leaf disks of the apple cultivar Golden Delicious, floating upside down on water in Petri dishes with river sand. The experiments were done in cabinets at constant temperatures of 5, 10, 15, 20, 25, 30, 33 and 35°C and at alternating temperatures of 10 and 20 and 15 and 25°C. Food effects could be neglected in these experiments since the experimental period was very short and the leaf disks were always taken from fresh leaves. Since extreme temperature conditions above 33°C and below 5°C only occur for very short periods in Dutch orchards, observations were at 4-hour intervals. Thus the relative rate of mortality within these short periods could be compared with the relative rate of mortality during longer exposition periods (24 hours). Oviposition rate, pre-oviposition period, oviposition period, life-span and fecundity were also determined at constant temperatures of 10, 15, 20, 25 and 30°C and at alternating temperatures of 10 and 20 and 15 and 25°C, with relative humidity between 70 and 90% and a daylength of 16 h. The experimental set-up was the same as in development experiments, only the Tangle Foot was omitted. Females isolated as teleiochrysalids (final quiescent stage) were placed on the experimental leaves, immediately after moulting and copulation. Oviposition and mortality were observed at 8-hour intervals, the eggs laid in those periods being removed. Again food effects (Kuenen, 1949; Post, 1962; Rodriquez, 1972) were eliminated by frequently refreshing the leaves. A small-scale experiment with leaves attached to trees grown under optimum nutritive conditions was done for comparison. In the experiments on rate of oviposition and ageing, extreme temperatures above 30°C and below 10°C were not considered. Therefore some additional short-term experiments were done to determine relative mortality rate and oviposition rate at 5, 10, 30, 33 and 35°C.
Mortality rate was determined with intervals of observation of 2 hours and total experimental periods of 24 hours.

5.2.2 Predatory mites

The duration of the different developmental stages was measured in thermo-cabinets. Development of the mites from the egg until the adult stage was observed at constant temperatures of 10, 15, 20, 23, 25 and 30°C and at alternating temperatures of 10 and 20 and 15 and 25°C. Relative humidity in the cabinets was kept within the range 70–90% and temperature fluctuated not more than 1°C. Trials were started with fresh eggs in Munger cells. These were 5 x 10 x 1 cm pieces of plastic with a round hole in the middle, one side covered with wet filter

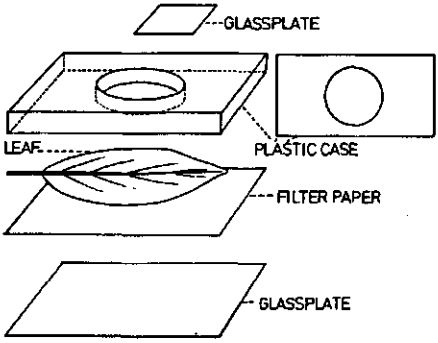


Fig. 25 | Munger cells, as used for determinations of developmental period of *Amblyseius potentillae*.

paper and a glass slide, the other with a small glass slide attached to the plastic with rubber bands, Fig. 25. Continuous measurements within the cells with small (0.1 mm) copper-constantan thermocouples showed that the temperature in the cells did not differ from the cabinet temperature, provided that the cells were placed at least 30 cm from the light source. Again development was observed for each individual separately. Observations were done every 8 hours and more than sufficient living food was given daily, consisting of all stages of the two-spotted spider mite. The eggs were laid by females taken from predatory mites mass reared on two-spotted spider mites in plastic boxes in cabinets at a constant temperature of 20° C, a daylength of 16 h and a relative humidity between 70 and 90% (McMurtry & Scriven, 1966). During experiments on rate of mortality, in different developmental stages, the mites were kept on leaf disks, in the same way as described for the spider mite. These experiments were done in constant temperature cabinets; eggs, larvae, protonymphs and deutonymphs were again taken from mass cultures of the predators.

Reproduction capacity, rate of oviposition, pre-oviposition period, oviposition period and life-span were determined in similar cabinets. Observations were made at 10, 15, 20, 23, 25 and 30°C (relative humidity between 70 and 90%, daylength 16 h) and at alternating temperatures of 10 and 20 and 15 and 25°C. Experiments were started with female deutonymphs taken from the mass cultures, each being placed with a male in Munger cells. Immediately after moulting and copulation, the female was transferred to another cell and placed under the experimental conditions. Observations were done every 8 hours

and every day more than sufficient food was added to the cell. Oviposited eggs were removed daily to prevent double countings. Mortality rate at extreme temperatures (below 10°C and above 30°C) was again determined according to the method described for the spider mite. Series of males and females taken from the mass culture were subjected to the extreme conditions and observed every 4 hours.

5.3 Results

5.3.1 Fruit-tree red spider mite

Table 2 presents the developmental period and its standard deviation for the different developmental stages at various temperatures. The embryonic development in the egg takes about the same time as the total juvenile period. Developmental periods of the different active stages (larva, protonymph, deutonymph) equal those of the quiescent stages (protochrysalis, deutochrysalis, teleiochrysalis) except at temperatures above 25°C where the quiescent stages are slightly shorter. The same table presents developmental periods of juveniles sensitive (deutonymph, teleiochrysalis) and insensitive to diapause-inducing conditions (larva, protochrysalis, protonymph, deutochrysalis). The standard deviations of these periods are smaller than the sum of the standard deviations of the separate developmental stages. This difference may be due to the size of the time interval of observation (8 hours) or to sequential dependence, i.e. a short larval stage is compensated by a long juvenile stage and vice versa. Sequential dependence was tested with Spearman's rank correlation test (Table 3). As no significant negative correlation was found between the duration of successive stages, there was probably no compensation. Therefore the necessarily long intervals between observations may have caused these differences in standard deviation. The average and standard deviation of the duration of juvenile periods sensitive or insensitive to diapause-inducing conditions determine the number of age classes within these groups (Tables 4, 5 and Section 4.1). The simulated dispersion is distributed proportionally to the duration of the developmental stages included. This assumption is confirmed by the results of the measurements presented in Table 2. The average developmental periods given in this table are subsequently used to calculate the corresponding age classes.

In the experiments the number of developmental stages was the same for females and males, this confirms the results of Putman (1970), Herbert (1970) and Parent & Beaulieu (1957) rather than those of

Table 2. Duration of different developmental stages of fruit-tree red spider mite in days at various temperatures.

	Duration of development at temperature of									
	15°C		18°C		20°C		25°C		30°C	
	$\bar{x}$	$s(x)$	$\bar{x}$	$s(x)$	$\bar{x}$	$s(x)$	$\bar{x}$	$s(x)$	$\bar{x}$	$s(x)$
Egg	17.4	0.96	10.4	0.97	8.3	.	5.53	0.24	4.95	0.18
Larva	2.49	0.46	2.03	0.49	.	.	1.03	0.48	0.64	0.09
Protochrysalis	2.78	0.56	1.51	0.41	.	.	1.03	0.37	0.48	0.19
Protonymph	2.51	0.47	1.61	0.72	.	.	1.07	0.4	0.66	0.23
Deutochrysalis	2.30	0.41	1.77	0.51	.	.	0.82	0.4	0.61	0.18
Deutonymph	2.55	0.67	1.83	0.69	.	.	1.14	0.42	1.03	0.4
Teleiochrysalis	3.0	0.29	2.32	0.27	.	.	1.13	0.38	0.8	0.3
J[1]	10.1	0.95	6.9	1.05	4.7	.	3.95	0.7	2.39	0.56
JS[2]	5.55	0.72	4.2	0.85	3.45	.	2.27	0.43	1.8	0.5
Active stages (L, PN, DN)[3]	7.55		5.47				3.25		2.3	
Quiescent stages (PC, DC, TC)[4]	8.0		5.6				2.98		1.9	

1. J = juveniles insensitive to diapause-inducing conditions
2. JS = juveniles sensitive to diapause-inducing conditions
3. L, PN, DN = larva, protonymph, deutonymph
4. PC, DC, TC = protochrysalis, deutochrysalis, teleiochrysalis

Table 3 Test on sequential dependence of duration of the developmental stages in *Panonychus ulmi*.

Developmental stages	Spearman's rank correlation coëfficient			Null hypothesis on concordance
	calculated	5% level	1% level	
Larva				
- Protochrysalis	0.221	0.514	0.641	rejected
- Protonymph	0.582	0.514	0.641	accepted at 5% level
- Deutochrysalis	0.435	0.514	0.641	rejected
- Deutonymph	- 0.086	0.514	0.641	rejected
- Teleiochrysalis	0.185	0.514	0.641	rejected
Protocrysalis				
- Protonymph	- 0.025	0.514	0.641	rejected
- Deutochrysalis	0.193	0.514	0.641	rejected
- Deutonymph	0.407	0.514	0.641	rejected
- Teleiochrysalis	0.557	0.514	0.641	accepted at 5% level
Protonymph				
- Deutochrysalis	- 0.096	0.514	0.614	rejected
- Deutonymph	- 0.153	0.514	0.641	rejected
- Teleiochrysalis	0.3	0.514	0.641	rejected
Deutochrysalis				
- Deutonymph	0.007	0.514	0.641	rejected
- Teleiochrysalis	- 0.203	0.514	0.641	rejected
Deutonymph				
- Teleiochrysalis	0.107	0.514	0.641	rejected
Juveniles				
- Juveniles sensitive to diapause-inducing conditions	0.207	0.514	0.641	rejected

Geijskes (1938) who described 5 juvenile stages for the male and 6 juvenile stages for the female. Only the teleiochrysalid stage is slightly shorter for males than for females. However, this small difference is neglected in the simulation model, as it has no effect on population growth, since the males only play a role as prey for the predatory mite and as a mate for the females.

In Table 6 the threshold values according to Putman (1970) are given for the various stages. Two threshold temperatures are given, at the

Table 4 Development rate per day for different developmental stages of *Panonychus ulmi* at various temperatures.

Developmental stage	Rate of development at temperature of				
	15°C	17°C	20°C	25°C	30°C
Larva	0.4	0.5	.	0.6	2.0
Protochrysalis	0.35	0.6	.	0.9	2.0
Protonymph	0.4	0.6	.	0.7	0.9
Deutochrysalis	0.4	0.5	.	1.1	2.1
Deutonymph	0.4	0.5	.	0.9	0.9
Teleiochrysalis	0.3	0.4	.	1.0	1.4
Juveniles	0.1	0.15	.	0.24	0.42
Juveniles sensitive to diapause conditions	0.18	0.24	.	0.51	0.55
Pre-oviposition adult females	0.29	0.35	0.42	0.6	0.7
Oviposition adult females	0.04	0.04	0.08	0.11	0.13
Life-span adult females	0.03	0.03	0.07	0.09	0.11

Table 5 Number of boxcars, required when 'continous' simulation is applied to mimic dispersion during development in *Panonychus ulmi*.

Development stage	Rate of development at temperature of				
	15°C	17°C	20°C	25°C	30°C
Juveniles	112	42	.	30	18
Juveniles sensitive to diapause conditions	59	25	.	28	13
Pre-oviposition adult females	25	52	.	20	6
Oviposition adult females	2	6	6	9	19
Life-span adult females	4	7	9	12	33

higher temperature (permissive) all animals completed the development process and at the lower temperature (inhibitive) none of the animals completed the process. In Figs 26 and 27, the data of Tables 2 and 6 are presented for eggs and juveniles that are sensitive and insensitive to diapause-inducing conditions. Developmental period and development rate of eggs (the inverse of developmental period) are

Table 6 Threshold temperature for the various stages, the permissive temperature is the temperature where all mites complete development, the inhibitive temperature is the temperature where none completed the process. (Putman, 1970).

	Temperature (°C)	
	inhibitive	permissive
Hatching of eggs		
1 day old	.	10.8
7 days old	6.3	7.2
Larva		
feeding and growth	7.2	8.3
moulting	6.3	7.2
Deutonymph		
feeding and growth	7.2	8.3
moulting	6.3	7.2
Complete post-ovarial development	9.2	11.7
Oviposition		
females eclosed at 7.2°C	10.7	11.7
females eclosed at 24°C	10.7	11.7
Insemination	.	8.3

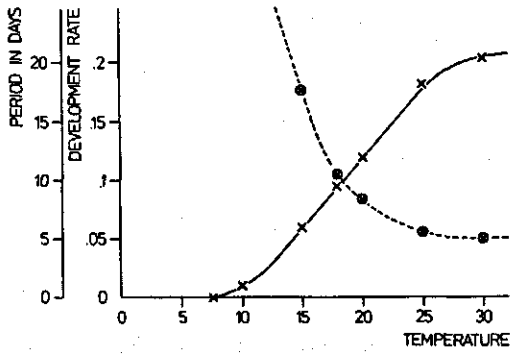


Fig. 26 | Developmental period in days and development rate of eggs of *Panonychus ulmi* per day against temperature in °C.

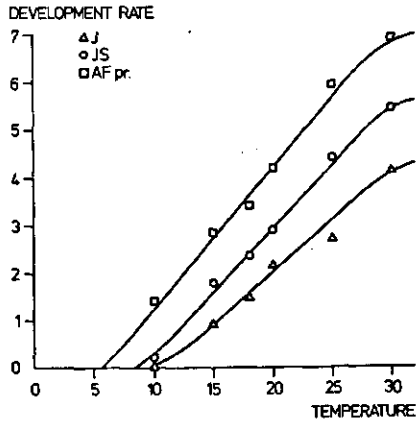


Fig. 27 | Development rate of juveniles insensitive to diapause-inducing conditions (J), of juveniles sensitive to diapause-inducing conditions (JS) and pre-oviposition females (AFP) of *Panonychus ulmi* per day against temperature in °C.

given in Fig. 26. In Fig. 27 development rates of the two distinguished juvenile groups are given. From the threshold temperatures up to 10°C there is nearly no development. Then the relation of development rate with temperature, linear till 25°C, starts flattening above 25°C and reaches a maximum at 33°C.

In all results of Table 2 the standard error of the developmental periods was less than 10 percent of the mean. With deviations of 10 percent in developmental periods, the results of the simulation model are within the confidence interval of the results of the verification experiments (Section 9.3). The required accuracy is therefore obtained and so it was not considered necessary to continue the observations.

In Table 7 literature data on development are given. A description of the experimental conditions is lacking in most cases. Several workers made observations under field conditions and interpolation in Fig. 26 and 27 suggests that most data are collected at an average temperature of 15–18°C. Since these temperatures are common during summer where the experiments were performed, these results from literature confirm the experimental laboratory data. This correspondence between laboratory data and field data suggests that food effects can be

Table 7 Developmental period of *Panonychus ulmi* in days.

	Blair & Groves (1952)	Newcomer & Yothers (1928)	Andersen (1947)	Kuenen (1946)	Post (1962)
Egg	11	8.29	15.4	17	
Larva	4	2.72	8–10		
Protochrysalis		2.27			
Protonymph		1.52		± 10	7.9–11.2[1]
Deutochrysalis		3.25	♂ 16.0		
Deutonymph	8	1.66	♀ 16.6		
Teleiochrysalis		4.21			
Temperature (°C)	25	field	field	field	field

1. Depending on generation.

neglected in the laboratory experiments. Nevertheless at one constant temperature, the duration of development was measured for mites on leaves attached to the tree. The results, Table 8, confirm the assumption that food conditions have no effect on the experimental results. The mean relative mortality rate between time t and $t + \Delta t$ is defined as:

$$Y_{t+\Delta t} = Y_t \exp(-\text{rmor} \times \Delta t)$$

Table 8 Comparison of methods for measuring duration of developmental stages in fruit-tree red spider mite.

	Substrate	
	leaves on wet cotton wool	leaves attached to tree
Egg	10.4	10.6
Juvenile	6.8	7.0
Juvenile sensitive to diapause-inducing conditions	4.2	4.5
Pre-oviposition period of female	2.9	2.7

in which

Y_t = number of animals at time t
$Y_{t+\Delta t}$ = number of animals at time $t+\Delta t$
Δt = time interval between observations.
rmor = mean relative mortality rate.

Hence this mean relative rate is calculated as;

$$rmor = (\ln y_t - \ln y_{t+\Delta t})/\Delta t$$

The results of the relative mortality rates in all stages in day^{-1} are given in Table 9. Relative mortality rate is negligible at temperatures for which the curve development rate against temperature is linear, but it increases abruptly above 25°C, Fig. 28. Temperatures, above 35°C, are lethal but these values are never reached at the sites where the animals occur. The relative mortality rates are about the same in different stages. Table 9 shows that the relative rate of mortality for 4-hour periods is the same as that for a 24-hour period when the temperature is below 30° C. Exposition to temperatures above 30° C for 24 hours causes much higher mortality. Since these extreme temperatures occur in the field only for short periods, the mean relative rates of mortality determined for 4-hour periods are introduced in the model.

Table 9 Mean relative rate of mortality in day^{-1} of some developmental stages of the fruit-tree red spider mite.

Temperature (° C)	Developmental stage						
	Egg[1]	Larva exposed for		Protonymph exposed for		Deutonymph exposed for	
		24h	4h	24h	4h	24h	4h
35	1.15						
33	0.335	0.77	0.195	0.387	0.118	0.979	0.152
30	0.017	0.1	0.05	0.07	0.03	0.05	0.03
25	0.013	0.05	0.04	0.03	0.03	0.03	0.03
20	0.0012	0.04	0.04	0.03	0.03	0.03	0.03
15	0.0006	0.04	0.04	0.02	0.02	0.02	0.02
10	0.01	0.124	.	0.15	.	0.1	.
5	0.05	0.15	.	0.18	.	0.13	.

1. Data from Putman (1970) and Mori (1957).

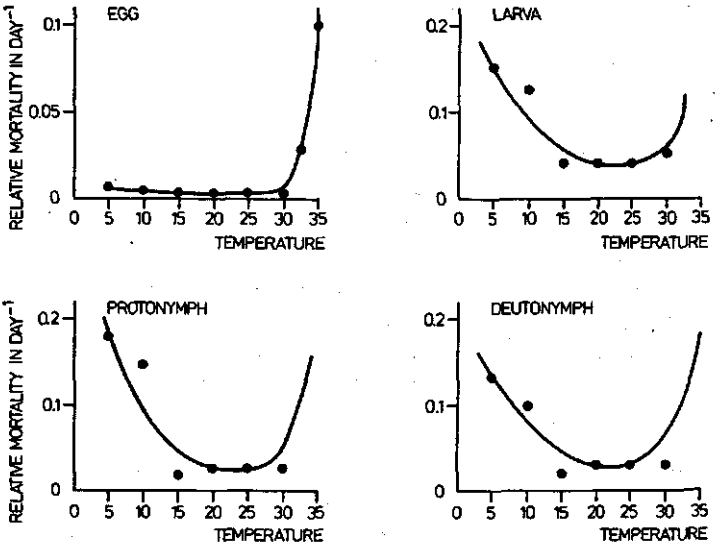


Fig. 28 | Relative mortality in day^{-1} in different developmental stages of *Panonychus ulmi* against temperature in °C.

Table 10 presents pre-oviposition period, oviposition period and total life-span of females in days at various temperatures, and their standard deviations. The relative dispersion (standard deviation divided by mean) of pre-oviposition period at different temperatures is about constant (ranging from 2.1 to 2.6), and since the data on pre-oviposition period are normally distributed as are all the other data on development and ageing, the method of continuous simulation with $(2.1)^2 \approx 4$ age classes can be applied (Section 3.1). In Fig. 29 the pre-oviposition period and maturation rate in relation to temperature are given; the latter relation is linear except at temperatures above 30°C. Figure 30 presents the mean rate of ageing at different temperatures, again in the region 12.5–25°C, this relation is linear.

Section 4.1 describes how to model ageing; the method of discontinuous simulation was applied with N boxcars or age classes, the size of the age classes being determined by the maximum period of living and the number of boxcars. The maximum period of living is now defined as the mean period of living plus $3 \times \sigma$; the number of boxcars is chosen such that the age dependency of oviposition is well described.

The mean relative rate of mortality in each age class only depends on

Table 10 Pre-oviposition period, oviposition period and life-span of *Panonychus ulmi* in days, rate of oviposition in eggs per day and fecundity in eggs at various temperatures.

	Temperature														
	10°C			15°C			20°C			25°C			30°C		
	$\bar{x}$	$s(x)$	$s(\bar{x})$	$\bar{x}$	$s(x)$	$s(\bar{x})$	$\bar{x}$	$s(x)$	$s(\bar{x})$	$\bar{x}$	$s(x)$	$s(\bar{x})$	$\bar{x}$	$s(x)$	$s(\bar{x})$
Pre-oviposition period	8.0	3.6	0.9	3.4	1.7	0.2	2.3	1.0	0.2	1.7	0.6	0.16	1.5	0.5	0.14
Oviposition period	24.1	17.9	4.8	25.5	10.6	2.3	13.0	4.7	1.0	8.9	3.0	0.8	7.5	1.7	0.5
Life-span	31.7	16.4	4.2	28.7	10.6	2.3	14.4	4.7	1.1	10.6	3.0	0.8	8.9	1.5	0.4
Fecundity	12.7	10.9	2.9	28.8	17.4	3.7	25.1	11.1	2.5	25.8	10.7	2.9	30.4	10.6	3.1
Oviposition rate	0.5	0.2	0.05	1.1	0.2	0.1	1.9	0.7	0.1	2.9	0.8	0.2	3.9	1.1	0.31

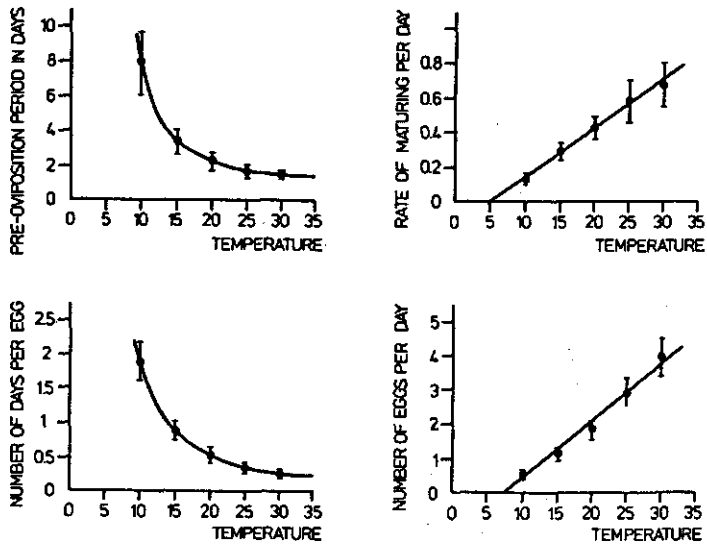


Fig. 29 | Pre-oviposition period in days and maturation rate per day of *Panonychus ulmi* at various temperatures in °C and rate of oviposition in number of eggs per day against temperature in °C.

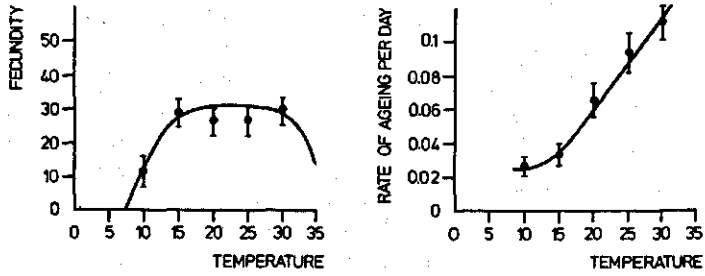


Fig. 30 | Mean rate of ageing per day and fecundity of females of *Panonychus ulmi* against temperature in °C.

temperature and is calculated as:

$$\text{rmor} = (\ln y_n - \ln y_{n+1})/\Delta t, \text{ in}$$

which y_n is the number of females at the front and y_{n+1} he number at the end of the age class, Δt being the size of the age class in days. The

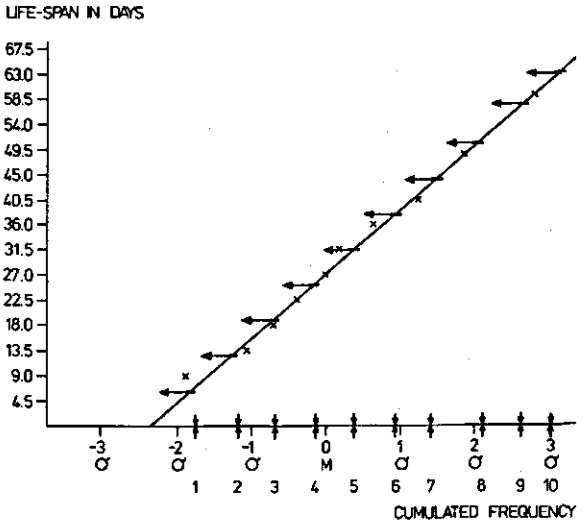


Fig. 31 | Frequency distribution of life-span of *Panonychus ulmi* adult females cumulated with respect to time on probability paper and used to calculate relative mortality rate in day^{-1} at one temperature in different age classes.

numbers y_n and y_{n+1} are found as follows: The data on life-span are expressed on probability paper, (Fig. 31), and a straight line is drawn through the data so that the mean coincides with the inverse of the mean ageing rate of Fig. 30. The number of days on the ordinate, (Fig. 31), is divided in N equal classes in such a way that at the end of the Nth class $3 \times \sigma$ on the abscissa is reached. The numbers y_0, y_1, y_2, y_3,... y_n are then read from the abscissa and are used to calculate the relative rate of mortality, (Table 11). With this rather complicated procedure to calculate the relative rate of mortality the mortality curves are smoothed without losing valuable characteristics.

Table 10 also presents rate of oviposition and oviposition capacity at different temperatures. The average rate of oviposition has a linear relation with temperature, Fig. 29, and the mean oviposition capacity is nearly constant between 15 and 30°C (Fig. 30). Fig. 32 shows that the rate of oviposition is age dependent and especially at high temperatures these effects cannot be neglected. Ten age classes suffice to obtain a good resemblance between simulated birth and death curve and measurements. Because of the linear relation between average ovi-

Table 11 Mean relative rate of mortality in day^{-1} of adult females of *Panonychus ulmi* in different age classes at various temperatures calculated from the mean and standard deviations of life-span.

Age class	Relative mortality rate (d^{-1}) at temperature of				
	10°C	15°C	20°C	25°C	30°C
1	0.01	0.0048	0	0	0
2	0.0157	0.0119	0	0	0
3	0.0277	0.0227	0.018	0.018	0.01
4	0.0484	0.0443	0.044	0.071	0.056
5	0.0699	0.0784	0.108	0.178	0.279
6	0.0916	0.110	0.194	0.152	0.413
7	0.127	0.129	0.313	0.396	0.71
8	0.152	0.156	0.472	0.60	1.14
9	0.152	0.156	0.472	0.646	1.46
10	0.152	0.156	0.472	1.09	1.5

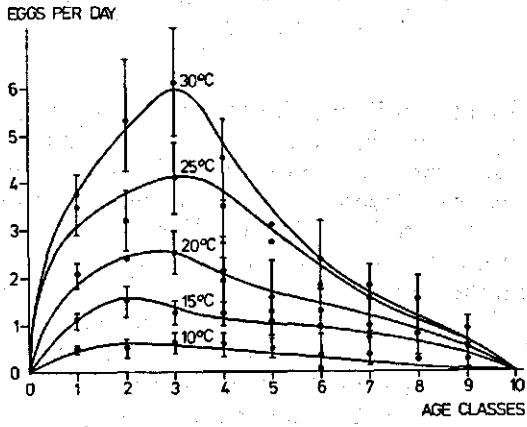


Fig. 32 | Age-class dependent oviposition rate of *Panonychus ulmi* in eggs per day at various temperatures in °C, mean and confidence interval.

position rate and temperature, it is assumed that this linearity operates in each age class. Fig. 33a presents the oviposition rate per age class against temperature; the third age class deviates but this deviation is only caused by the high oviposition rate at 30°C. However the large

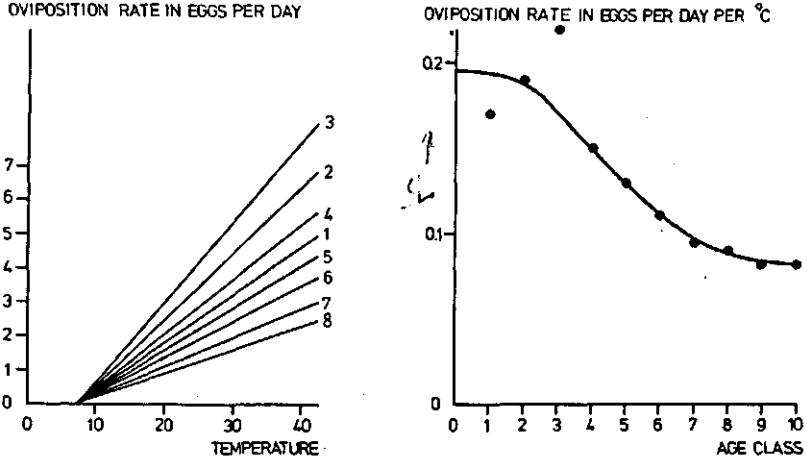


Fig. 33 | Left: Oviposition rate of *Panonychus ulmi* in eggs per day against temperature for different age classes (1–8).
Right: Oviposition rate per day per °C against age classes.

variance enables further smoothing. Thus the slopes of the lines, eggs per day per °C, are plotted against the age classes, Fig. 33b. The points obtained are then described with a sigmoid curve and this levels the extreme value in the third age class at 30°C. The oviposition rate per age class is then given by:

$$(TEMP - TT) \times SL_i,$$

in which TEMP is the actual temperature, TT is the temperature threshold for oviposition, here 7.5°C, and SL_i is the slope of the line read from the sigmoid curve. Since oviposition rate and relative mortality rate are calculated more or less independently, the measured total oviposition capacity may be incorrectly calculated by the simulation model. Therefore runs with a small simulation model that describes ageing and oviposition were done to verify and improve the input data. In Fig. 34 the results of these simulations at different temperatures are given. Two iterative runs with the model were sufficient to obtain a correct birth and death curve and fecundity at 15–30°C that was about constant and in agreement with the measurements.

The data on ageing and reproduction were obtained from cultures maintained on leaves placed on wet cotton wool, and although leaves

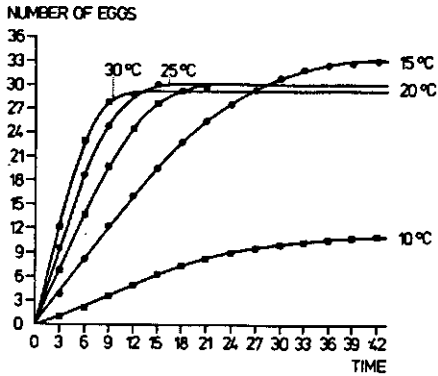


Fig. 34 | Simulated cumulated egg production of *Panonychus ulmi* against time in days at various temperatures in °C.

were renewed at least every four days, the quality of food may have changed during the observations. Observations at one temperature with leaves attached to well fertilized trees given in Table 12, do not indicate this.

Although all mites were transferred carefully and damaged mites were replaced, the possibility of adverse effects of manipulation on mortality cannot be disregarded. However the average oviposition capacity in

Table 12 Oviposition rate, fecundity, oviposition period and life-span of *Panonychus ulmi*, determined on different substrates. Null hypothesis that both methods are correlated, is accepted ($P < 0.02$) Spearman correlation coefficient is 0.786.

	Substrate			
	leaves attached to tree		leaves on wet cotton wool	
	15°C	25°C	15°C	25°C
Average oviposition rate (eggs per day)	1.14	3.07	1.15	2.85
Average fecundity	27.7	31.6	29.8	22.6
Mean oviposition period	23.6	10.2	26.5	8.3
Mean life-span	27.4	11.7	29.4	10.0

Table 13 Data on rate of oviposition per day and fecundity of *Panonychus ulmi*. All mites were collected in the field.

Reference	Oviposition per day	Fecundity		Temperature	Generation	Place experiment
		average	maximum			
Andersen, 1947	2.1	27	45	.	1	field
Andersen, 1947	1.3	16	32	.	2	field
Andersen, 1947	1.0	14	32	.	3	field
Balevskey, 1967	.	29	52	.	.	lab.
Blair & Groves, 1952	.	11.2	46	.	.	lab.
Cagle, 1946	.	18.8	69	.	.	insectary
Gilliat, 1935	.	6.6–34.9	69	.	.	field
Kuenen, 1946	.	.	37	.	.	insectary
Leski & Predki, 1947	.	25–48	75	.	.	lab.
Musa & Dosse, 1966	.	71.8	.	24–28	3	lab.
Musa & Dosse, 1966	.	44.2	.	24–28	4	lab.
Musa & Dosse, 1966	.	36.5	.	24–28	4	lab.
Musa & Dosse, 1966	.	27.0	.	24–28	6	lab.
Musa & Dosse, 1966	.	7.4	.	24–28	7	lab.
Newcomer & Yother, 1929	.	.	83	.	1	field
Newcomer & Yother, 1929	.	.	91	.	2	field
Newcomer & Yother, 1929	.	.	59	.	3	field
Parent & Beaulieu, 1957	.	10–35	90	.	.	lab.
Post, 1962	.	10.7–16.2	.	.	.	insectary
Ross & Robinson, 1922	.	15–16.2	.	.	.	field

Table 14 Mean relative rate of mortality (day^{-1}) of *P. ulmi* and *A. potentillae* adult females at extreme temperatures.

Temperature	*P. ulmi* exposed for			*A. potentillae* exposed for		
	4h	8h	24h	4h	8h	24h
10 °C	0.04	0.05	0.07	0.1	0.1	0.1
33 °C	0.7	0.9	5.0	0.1	0.3	0.4

the determinations described is in agreement with many literature data, Table 13, so that the assumption that these effects are negligible is acceptable.

The effect of extreme temperatures, below 10° C and above 30° C, on the relative rate of mortality of females is given in Table 14. Again a longer period of exposition may increase the rates, but since the periods with these extreme conditions are never longer than 4 hours, the relative mortality rate per day determined in the 4-hour experiments are introduced in the model.

5.3.2. Predatory mites

Because many literature data were available on the bionomics of the fruit-tree red spider mite, the number of experiments for parameterization of the simulation model should have been reduced. However these data have little value for modelling because they were collected for a completely different purpose and the abiotic and biotic conditions are poorly represented. Literature data about the predatory mite suitable for modelling are still scarcer. Therefore all data on the predatory mite had to be collected from experiments as described in Section 5.3.1 or they were estimated.
Table 15 presents the data on the duration of the different developmental stages at various temperatures in terms of mean and standard deviation. The embryonic period of the egg and the total juvenile period are much shorter than for the fruit-tree red spider mite, Table 3, so that the number of generations per year may exceed that of the prey manifold. The correspondence between the embryonic period in the egg and the total juvenile period, present in fruit-tree red spider mite, does not exist for the predator. The duration of the egg period nearly equals that of the juveniles insensitive to diapause-inducing conditions,

Table 15 Duration of developmental stages of *Amblyseius potentillae* in days at various temperatures.

	Temperature (°C)									
	10		15		20		23		25	
	$\bar{x}$	$s(x)$	$\bar{x}$	$s(x)$	$\bar{x}$	$s(x)$	$\bar{x}$	$s(x)$	$\bar{x}$	$s(x)$
Egg	7.0	2.5	3.25	0.9	2.0	.	1.58	0.25	1.38	0.4
Larva	3.2	.	1.4	.	.	.	0.7	.	0.6	.
Protonymph	3.2	.	1.5	.	.	.	0.8	.	0.7	.
Deutonymph	4.5	.	2.4	.	1.5	.	1.24	.	1.10	.
J[1]	6.4	1.2	2.9	0.9	1.75	.	0.8	.	1.31	0.3
JS[2]	4.5	1.6	2.4	0.8	1.5	.	1.23	0.4	1.10	0.3

1. J = juveniles insensitive to diapause-inducing conditions
2. JS = juveniles sensitive to diapause-inducing conditions

larva and protonymph. The deutonymph period, juveniles sensitive to diapause-inducing conditions, is slightly shorter. Again sequential dependence of the length of the stages is absent, so the number of age classes applied in the model are calculated from the mean and standard deviation of the length of both juvenile periods. Since the relative

Table 16 Calculated number of classes required for 'continuous simulation' and relative dispersion of eggs, larvae and protonymphs, and deutonymphs of *Amblyseius potentillae* at various temperatures.

	Temperature (°C)			
	10	15	23	25
Egg				
number of classes	8	13	40	12
relative dispersion	0.36	0.28	0.16	0.29
Larva and protonymph				
number of classes	29	11	4	19
relative dispersion	0.19	0.31	0.53	0.23
Deutonymph				
number of classes	8	9	10	14
relative dispersion	0.35	0.33	0.32	0.27

dispersion at various temperatures is not constant, Table 16, the method of controlled dispersion is applied to mimic the dispersion.

In Fig. 35 the developmental period in days and development rate day^{-1} against temperature are given for eggs, juveniles sensitive and juveniles insensitive to diapause-inducing conditions. Between 10 and 25°C the rates and temperature are linearly related and above 25°C there is a flattening of the curves. The temperature threshold for development in the different stages has not been determined exactly. Observations at 5°C showed that no development occurs, but at 10°C the egg develops into an adult. Below 10°C the relatively low contributions to development and the linearity of the rates between 10 and 25°C allows a simple extrapolation to determine a threshold value that may be not completely correct but only causes negligible deviations and saves considerable experimenting. Again the required accuracy of the data should be determined by the accuracy of the measurements of the verification experiments, Section 5.1, but since the experiments for a first estimation of the developmental period provided data with an accuracy of 0.1 (standard error divided by mean) and this is more than required, further experiments were superfluous. The normality of the

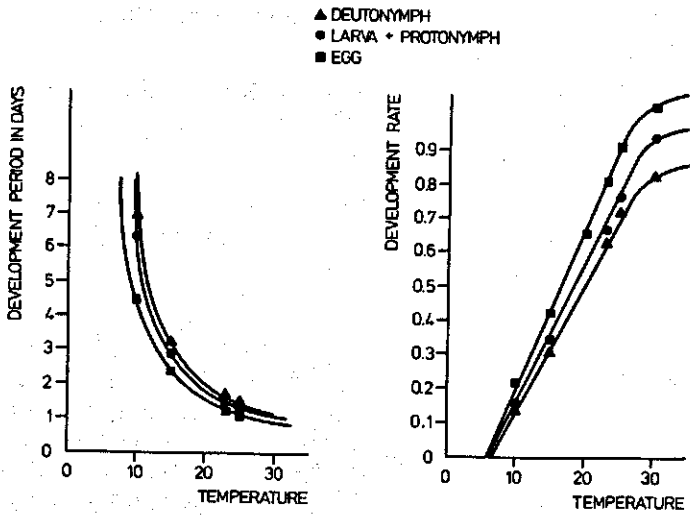


Fig. 35 | Duration in days and development rate per day of different developmental stages of *Amblyseius potentillae* against temperature in °C.

Table 17 Mean relative rate of mortality (day^{-1}) of *Amblyseius potentillae* at different developmental stages and temperatures.

Temperature	Relative mortality rate of			
	egg	larva	protonymph	deutonymph
5 °C	0.16	0.1	0.08	0.08
10 °C	0.05	0.051	0.045	0.045
15 °C	0.03	0.02	.	.
20 °C	0.02	0.02	.	.
25 °C	0.05	0.02	0.01	0.01
30 °C	0.05	0.02	0.02	0.02
33 °C	0.16	0.08	0.07	0.07

data on development was tested with probability paper which also gave the mean and standard deviation.

The results of the experiments on mortality due to abiotic factors are given in Table 17; again they are expressed as the mean relative mortality rate. Between 10 and 30°C this mortality is nearly negligible. Above 30°C the relative mortality rates per day calculated from the 4-hour experiments rather then the 8-hour experiments are used in the model, since under field conditions temperatures are extreme only for very short periods. The experimental method of determining mortality was the same as for fruit-tree red spider mite, but it should be emphasized that food was abundant and that the possibility for escape was minimized by the water barrier around the leaf disks.
Table 18 presents the data on oviposition period, pre-oviposition period and life-span at various temperatures in days. Although the developmental period of the predatory mite is much shorter than that of the prey, life-span and oviposition period last at least the same time or are even longer. Again oviposition rate is age and temperature dependent, so that the simulation technique with no dispersion has to be used to describe the ageing process of the females, the number of age classes being determined by the age dependency of oviposition.
Again 10 age classes were sufficient to obtain a good description of birth and ageing curve.
Fig. 36 gives the relations maturation rate against temperature, the inverse of maximum life-span against temperature and mean ageing

Table 18 Oviposition rate in eggs per day, fecundity in eggs and pre-oviposition period, oviposition period and life-span in days of *Amblyseius potentillae* at various temperatures (Data from van de Vrie pers. commun.).

	Temperature (°C)									
	10		15		20		25		30	
	$\bar{x}$	$s(x)$	$\bar{x}$	$s(x)$	$\bar{x}$	$s(x)$	$\bar{x}$	$s(x)$	$\bar{x}$	$s(x)$
Pre-oviposition period	> 15	.	7.4	1.1	4.0	0.9	1.9	0.9	2.9	0.8
Oviposition period	> 30	.	32.8	.	26.8	.	23.1	.	17.0	.
Life-span	> 30	.	32.8	.	28.2	.	25.0	.	18.0	.
Fecundity	9.0	.	20.0	.	27.8	.	29.1	.	16.0	.
Oviposition rate	0.2	.	0.63	.	1.04	.	1.25	.	0.9	.

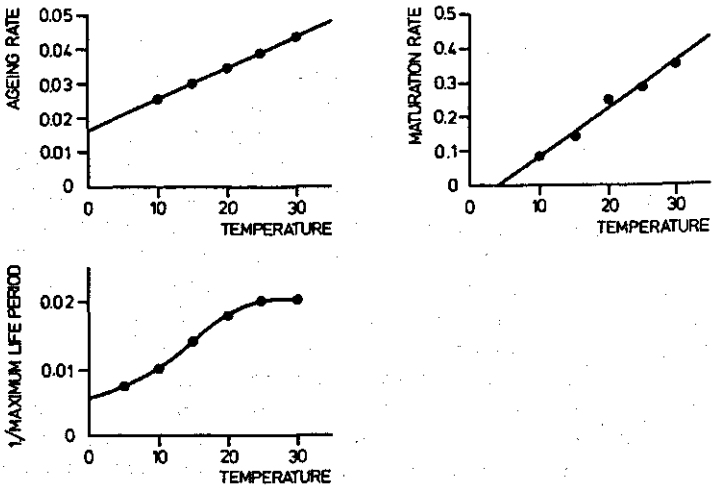


Fig. 36 | Ageing rate and maturation rate per day of *Amblyseius potentillae* against temperature in °C.

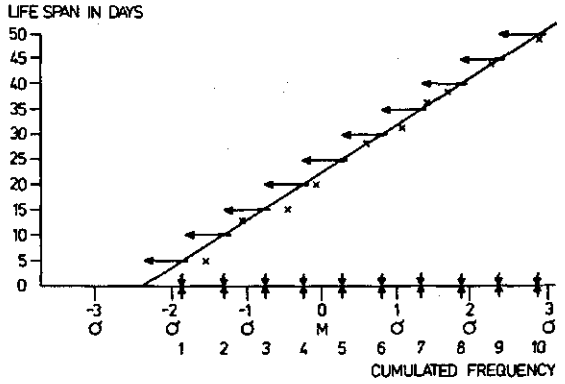


Fig. 37 | Frequency distribution of life-span to calculate age-dependent relative mortality rate of *Amblyseius potentillae* in day^{-1}, in different age classes.

rate against temperature. All these relations are linear and this characteristic is used to calculate the relative rates of mortality dependent on age and temperature in the same way as described for fruit-tree red spider mite, Fig. 37. In Table 19 the results of these calculations are given.

Table 19 Mean relative mortality rate in day^{-1} of adult females of *Amblyseius potentillae* in different age classes at various temperatures, calculated from the mean life-span and its standard deviation.

Age class	Temperature (°C)				
	10	15	20	25	30
1	0.0068	0.0057	0.0009	0.002	0.006
2	0.0111	0.0105	0.0009	0.007	0.015
3	0.0213	0.0219	0.0075	0.0186	0.029
4	0.0327	0.0375	0.022	0.043	0.052
5	0.0533	0.0662	0.055	0.067	0.081
6	0.0632	0.0816	0.079	0.109	0.119
7	0.0891	0.127	0.156	0.160	0.158
8	0.1078	0.136	0.222	0.212	0.241
9	0.145	0.186	0.293	0.301	0.22
10	0.223	0.223	0.301	0.301	0.22

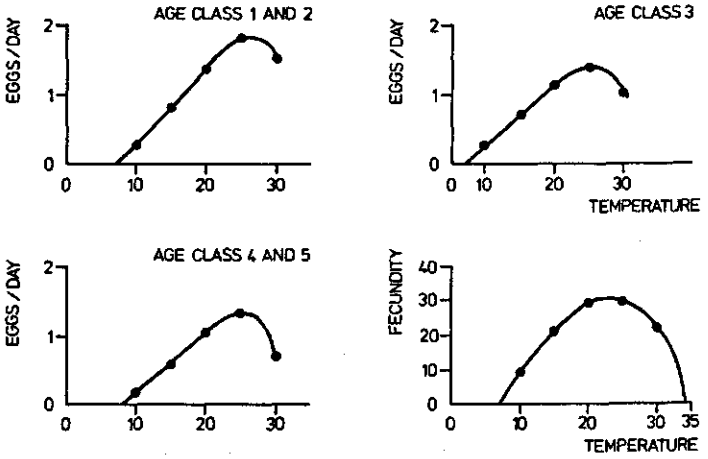


Fig. 38 | Oviposition rate in eggs per day in different age classes and fecundity of *Amblyseius potentillae* against temperature in °C.

Table 18 also presents the data on oviposition capacity and oviposition rate. The maximum oviposition capacity is about the same for the predatory mite and fruit-tree red spider mite but the range is 20–25°C instead of 15–30°C. At this maximum the average oviposition rate per day is much less than that for the fruit-tree red spider mite, so that the oviposition period is much longer. Fig. 38 gives the relations of mean oviposition rate and oviposition rate of females in age class 1, 2 and 3 (eggs per day) with temperature. Up to 25°C these relations are linear but then a fast decrease of the oviposition rate occurs. Because of this deviation from linearity above 25°C and the small optimum region for oviposition capacity it is impossible here to apply the calculation technique of oviposition rate that was used for the fruit-tree red spider mite. Therefore the age and temperature dependency functions are introduced in the model with tabulated functions between oviposition rate and temperature in each age class. Table 14 presents also the data on relative mortality rates of females at the extreme temperatures. The method of determination is the same as that for the fruit-tree red spider mite and again the relative mortality rates per day based on the 4-hour experiments are used in the model, Table 14. The same iterative procedure with a small simulation model, as applied in the fruit-tree red spider mite was applied to adjust rates of oviposition, relative rates of mortality and oviposition capacity.

Development, oviposition and mortality were measured with abundant food present. A more detailed description of these experiments and their ecological implications will be given by Rabbinge & van de Vrie (in prep.).

5.3.3 Varying temperature

The graphs on development, oviposition and ageing show clearly that in the fruit-tree red spider mite and in predatory mites, the rates are linearly related with temperature in the region of normal summer and spring temperatures, 10–25°C. In Section 5.1 the assumption on momentaneous temperature reaction was made, so that measurements at constant temperatures could be applied in situations with fluctuating temperatures. The assumption has to be verified because even in cases

Table 20 Test on momentaneous reaction. Average rates of development, oviposition and ageing of *Panonychus ulmi* and development of *Amblyseius potentillae*. For both species nulhypothesis on non-momentaneous reaction is rejected (student's t-test, $\alpha = 0.05, P<0.05$).

	Temperature (°C)			Calculated
	15	25	15–25	
Panonychus ulmi				
Development rate per day				
egg	0.06	0.154	0.092	0.106
juveniles insensitive to diapause-inducing conditions	0.099	0.253	0.181	0.176
juveniles sensitive to diapause-inducing conditions	0.180	0.44	0.31	0.31
adult female pre-oviposition	0.285	0.688	0.49	0.487
Oviposition rate eggs per day	1.13	2.93	2.06	2.03
Ageing rate	0.038	0.096	0.083	0.07
Amblyseius potentillae				
Development rate per day				
egg	0.308	0.631	0.382	0.46
juveniles insensitive to diapause-inducing conditions	0.345	0.66	0.427	0.50
juveniles sensitive to diapause-inducing conditions	0.416	0.80	0.518	0.61

where all relations are linear, fluctuating temperatures may give deviating results. Basically these may be caused by the involvement of two catenary processes that have different relations with temperature, so that other development rates or ageing rates result when fluctuating temperatures with the same average are applied.
In Table 20 the results of measurements on development, ageing and oviposition with fluctuating temperatures are compared with measurements at average temperatures. In all cases the hypothesis of an influence of fluctuating temperatures was rejected (Table 20).

5.4 Humidity, rain, wind and daylength

The relational diagrams, Figs 7–19 showed where relative humidity and daylength may affect the rates.
Daylength together with temperature and food induce diapause in both fruit-tree red spider mite and predatory mites. Many good data for fruit-tree red spider mite are available, (Lees, 1953) so that the process of diapausing could be modelled without further experimentation. Section 8.1.3 describes this modelling and how the literature data are processed. No literature data on diapausing in predatory mites were available. Field observations showed that only females overwinter and that diapause is induced in the deutonymph stage. Since a detailed analysis of this process requires an exhaustive amount of experimenting time and the predator's correspondence with the fruit-tree red spider mite is very clear, the assumption was made that the diapausing process is about the same as in the fruit-tree red spider mite. This implies a similar way of modelling.

Effects of relative humidity on fruit-tree red spider mite were investigated by Putman (1970) and Mori (1957). They found a delayed development and an increased mortality of eggs when relative humidities were above 92% or below 60%. Relative air humidities below 50% occur very seldom in Dutch summers, 4 times in 1974, 5 times in 1975, and for only very short periods, whereas the measured effects occurred when the whole development took place under extremely humid conditions. Moreover relative air humidities of 40–50% imply a relative humidity of at least 55–60% in the laminar layer around the leaf where the animals are living, Section 7.3.1.
Humidities above 92% are more frequent, but field observations showed that mortality and delay effects due to these conditions are absent in Dutch orchards. Even eggs lying in condensed water on the leaves during most of their life hatched undelayed and the resulting

larvae showed no visible damage. These considerations justify neglecting effects of relative humidity on mortality and development of the spider mite eggs. Quantitative data on the effect of relative humidity during the juvenile period were not available and experiments with low relative humidities were not feasible. Since living leaves should be used as substrate for the animals, and humidities lower than 50% cause rapid withering of leaves the effects measured are food effects rather than humidity effects. Still some small-scale experiments with the Zwölfer technique (Mori, 1957), were done and showed no effects on mortality and development with relative humidities between 60 and 95%. Humidities above 95% increase mortality rate (Kuenen, 1946), but these effects are absent during short periods of exposition comparable with field conditions. Therefore both the low and the high humidities may have a negligible effect on the mortality and the development rates. Because predatory mites hide under veins etc. the effects of humidity on the eggs, juveniles and adults of these species are still more unlikely. Small scale experiments with the different juvenile stages have shown that there are no effects on either mortality or development when relative air humidity is above 50%. Eggs are still more insensitive to humidity. The adults as well as the juveniles need water to keep alive and when reared in Munger cells on dry paper many animals die. When living material, apple leaves, are used as the substrate the hairs of the leaves provide sufficient water. Water requirement under natural conditions can therefore be neglected.

Although preliminary experiments have shown that effects of relative humidity may occur, quantitatively these effects may be neglected under Dutch summer conditions because of the frequency and the length of the periods with extreme humidity conditions.

Effects of wind and rain are still more difficult to establish. In 1946, Kuenen made field observations and found effects of heavy rain and wind on the juvenile mortality of fruit-tree red spider mite; but these effects were not well assessed. In 1970, Putman found in laboratory experiments that direct effects of wind on mortality are negligible, but that indirect effects due to friction of leaves may be considerable, with very strong winds, Table 21. However the wind within the orchards is only a fraction of the wind above the orchard, Section 7.3.2, so that windspeeds of 10–20 metre, causing mortality, are hardly reached. Moreover the effects are smaller when the animals are on the underside of the leaves. Therefore the quantitative effect of wind as a mortality factor is neglected. Again the hidden way of living by the predatory mites, especially during bad weather conditions makes it unlikely that the effect of wind on the predatory mite mortality is quantitatively

Table 21 Mortality in fruit-tree red spider mite in percentage of those present, attributable to wind of different velocity (data from Putman, 1970).

Developmental stage	Side of leaf	Air velocity in $m.s^{-1}$			
		10	20	30	40
Larva					
resting	upper	0	8	18	20
walking	upper	4	26	56	72
Juvenile					
resting	upper	0	18	16	28
walking	upper	2	40	84	98
quiescent	upper	0	0	0	14
Adult female					
resting	upper	0	2.5	32	54
resting	lower	0	8.5	0	0
walking	upper	12	33.0	90	100
walking	lower	0	61.2	0	0

important.

Several authors reported on the effect of rain on mortality. Kuenen (1946) assessed the mortality of females in red spider mite juveniles after heavy rain (> 20 mm $hour^{-1}$) at 40 percent, and other authors give higher but also lower estimations, ranging from 2 to 50%. This wide range and the further scarce quantitative data makes an incorporation of a rain effect based on these data impossible.

However an investigation of these effects is rather cumbersome and requires much experimenting time. It was therefore omitted.

6 Predator-prey relations

6.1 Introduction

The predator-prey relation described in Section 4.1.3 was restricted to the relation between *Amblyseius potentillae* and *Panonychus ulmi*. The number of 'prey species' amounts in this particular example to 5 and the number of 'predator species' to 4, because different development stages of prey and predator are involved, each with their own preference and attractiveness. The field situation is still more complicated as two other predatory mites, *Typhlodromus pyri* and *Amblyseius finlandicus* often occur, even more frequently than *Amblyseius potentillae*. However because of the correspondence in the behaviour of the predatory mites and the small differences in their bionomics, it is justifiable to consider only one predatory mite species in a first simulation model. In Chapter 10 the implications of these simplifications and the ecological meaning of different properties of predatory mite species will be discussed.
Literature data and own investigations made it clear that the effects of alternative food, for instance, apple pollen, apple powdery mildew spores, honey dew and gall mites may also be very important, but these food sources are considered in the results of the population model in Section 9.4.
This chapter describes the experiments required for the quantification of the functional and the numerical relations between *Amblyseius potentillae* and the fruit-tree red spider mite. From the system description in Section 4.1.3 it is clear that the following relations should be experimentally determined for each of the predator - prey combinations (theoretically 5 x 4 = 20):
- Predation rate at several constant prey densities at various temperatures,
- Predation rate dependent on the satiation levels of the predator at various temperatures,

and for each predator:
- Calibration of the colour scale that is used as a measure for the satiation level of the predator,
- The relative rate of decrease in the satiation level at various temperatures,

- Rate of development of the predator at various satiation levels of the predator; this only holds for the protonymphs and deutonymphs of the predator,
and for the adult female:
- Relative rate of oviposition of the predator dependent on the satiation level at various temperatures.

These relations should all be determined for the equilibrium situation of the predator, Section 4.3, i.e. in the situation where the rate of ingestion equals the rate of digestion. So the satiation level of the predator oscillates at a certain level with a small amplitude.
Prior to the experiments on the functional and numerical relations some experiments were done to establish a standardization technique of the predator and to estimate the time required at various temperatures for adjustment to equilibrium. These experiments showed that, for instance, in the adult female predator, the equilibrium situation at 25° C is reached within 6–8 hours, but that at 15° C more than 36 hours are required.
This long period of acclimatization makes the experiments time and labour consuming so that the experimental work was restricted as much as possible. A more detailed description of experiments, their results and meaning in predator-prey systems will be given by Rabbinge et al., (in prep.).

6.2 Functional response

The description of the experiments on the functional relations and the processing of the data will be limited to the situation adult female predator versus young larvae of the prey. The other prey-predator relations were determined in the same way, but from these only the final results are given. The experimental method is for all experiments the same and is given in Section 6.2.1. In this section the assumed correspondence between the *Tetranychus urticae* - *Typhlodromus occidentalis* system and the *Panonychus ulmi* - *Amblyseius potentillae* system is verified. Very high densities (> 25 ♀♀ per leaf) at which predators mutually interfere are not considered since these densities are above the economic damage level for which chemical treatment is required.

6.2.1 *Methods*

Experimental conditions
All experiments were done under controlled conditions in climate rooms at 18°C and at 5, 10, 15, 20 and 25°C on leaf disks of Golden Delicious with an area of 5.0, 3.8 or 2.67 cm², floating upside down on wet river-sand in Petri dishes, the water barrier preventing the preys and predators from escaping.
The animals, preys and predators were taken from mass cultures described in Section 5.2. The adult female predator was isolated as a deutonymph and placed after moulting and copulation on a leaf disk without food for 24 hours at 20°C. These predators were then placed on a leaf disk under the experimental conditions for a period necessary for the system to reach equilibrium. During this period the prey density was kept constant, i.e. every four hours the killed or moulted preys were replaced. The hungry predator started eating very rapidly and its colour reached high values in a short time. Then the predator rested for a long period and it became paler in colour. Thus a damped oscillation starts with a period that is determined by the temperature and the prey density. At 15°C it takes minimally 36 hours and at 25°C maximally 8 hours to reach the equilibrium situation where the amplitude of the oscillations never exceeds 1 colour unit (see Section 6.2.2).

Correspondence with the acarine system Typhlodromus occidentalis – Tetranychus urticae
Fransz (1974) analysed non-stationary predator-prey systems, and showed that these approach the stationary state relatively rapidly. In this state the analysis to construct a functional response curve can be greatly simplified. Since his observations were done with the *Tetranychus urticae – Typhlodromus occidentalis* system (two-spotted spider mite with a predatory mite), its correspondence with the present system has to be shown so that his suggestions can be applied to simplify the analysis. A correspondence analysis was done at 18° C.
The following events, states and time periods were recorded:
- the number of encounters between prey and predator,
- the number of successful encounters between prey and predator,
- the time of activity of the predator,
- the state of the predator, its colour value,
- the activity of the predator.

These observations were done at prey densities of 1, 2, 5 and 25 prey larvae per leaf disk of 2.67 cm². The results of these experiments, given in Table 22 show that *Amblyseius potentillae* has the same behaviour

Table 22 Succes ratio, relative predation rate and predation rate of the adult female predator at various colour values for different densities of the prey (larvae) counted in areas of 2.67 cm² at 18°C.

	Colour value of predator			
	2.0	3.5	4.5	5.0
Prey density (number per 2.67 cm²)	1	2	5	25
Success ratio	0.95	0.86	0.67	0.1
Relative predation rate (day⁻¹)	4.5	3.79	1.95	0.78
Predation rate (day⁻¹)	4.5	7.6	9.7	19.4

as the *Typhlodromus occidentalis.*
When the prey density increases, the number of encounters increases and the number of successful encounters increases until a certain stationary predation rate is reached; so the success ratio decreases. It was also shown that the search behaviour of *Amblyseius potentillae* is at random like that of *Typhlodromus occidentalis* and that the relation between the length of the resting period and the satiation level is also the same for both. The correspondence of both systems proves that also in this situation continuous observation of behaviour is not necessary, but that it suffices to determine directly in the equilibrium situation (ingestion = digestion), the relation between colour (i.e. gut content) and the relative rate of predation, the relation between colour and the utilization of the prey, and the relative rate of decrease in the colour, all these at various temperatures.

Methods
Observations were made at 15, 18 and 25°C and at prey densities of 0.5, 1.0, 5.0 and 10 larvae per 3.8 cm². At 5°C and 10°C some small-scale experiments on the predation activity were done.
The observation interval ranged from 0.25 hour at 25°C to 1 hour at 15°C. These intervals were so small that the density of the prey did not change numerically. At each observation the killed and moulted preys were, of course, replaced.
Temperature fluctuations in the climate rooms at 5, 10, 15, 25°C were not more than 0.5°C, but in the climate room at 18°C these fluctuations were maximally 1.5°C. The temperature on the surface of the

small leaf disks with animals was continuously measured with thermocouples and occasionally with a Heyman infrared thermometer. Although in the experiments at 25° C 8 fluorescent tubes were used for illumination, the temperature where the animals were living did not differ from the temperature in the climate room. At 15° C glass-fissel optics were used for illumination, to prevent heating by illumination. All observations were done with a binocular microscope, magnification 16x. The characteristics observed were the mortality of the prey, the colour of the predator and the oviposition of the predator.

6.2.2 Satiation of the predator

Holling (1966) used the gut content of the preying mantids as an operational definition of the satiation level. Fransz could not determine the absolute gut content but succeeded in measuring the rate of ingestion and digestion and thus in calculating the gut content. In the predatory mite *Amblyseius potentillae* an operational definition of the satiation level is possible because this mite is transparent and the content of its gut can be seen. Mites with a white to pale red colour had a high success ratio > 0.8 and those with a low success ratio < 0.5 were dark red.
Although the colour of the animal has been used to determine the composition of the food of the predator, (Gilliatt, 1935; Anderson & Morgan, 1956; Chant, 1959) it was never used for the determination of the satiation level, so that a scale had to be developed. This colour scale ranges from 0 to 7, and for the female predator is as follows:

0 *Amblyseius potentillae* is completely transparent, gut colourless
1 Predator is pale yellow, gut is invisible
2 Predator is sandy yellow, gut is scarcely visible
3 Gut is clearly visible as a thin pale red H-form
4 Gut is wider and more intensively red
5 Gut is still wider and pure red
6 A dark red or brownish H fills the abdomen of the predator
7 The gut nearly fills the abdomen and is totally brown.

This colour pattern is slightly different for the other prey and predatory stages, but this can easily be accounted for. For more objective work with this colour scale it is necessary to use the same magnification of the binocular microscope and two independent observers.
The colour of the predator is caused by the pigments chlorophyll a and b and carotenoid α and β. These pigments are partly of animal and partly of vegetable origin and can be analysed by spectrophotometry

(Veerman, 1970). Such a quantitative determination is required for calibration of the colour scale in terms of quantity of food in the gut. Hence animals of a certain colour value could be used for a spectrophotometric analysis. This was only done for adult females of *Amblyseius potentillae* and repeated 5 times. 200 adult females were divided into two groups: one provided with an abundant amount of food, all stages of *Panonychus ulmi*, and the other provided with a limited amount of food of the same composition. After one day feeding on this food 75 animals with a colour value of 5–6 were taken from the first group and 75 animals with colour 2–3 from the second group. These animals were put in 2 ml ethanol, ground, homogenized and centrifuged (10 min at 4000 rev/min).
The supernatant was then spectrophotometrically analysed in the light range 370–700 mμ, the surface under the absorption curve being determined planimetrically, Fig. 39. Separately a spectrometric analysis was done of the prey used and of the two-spotted spider mite used by Fransz, the results being presented also in Fig. 39. Obviously the composition of the pigment in the three species is the same, which suggests that the colour scale can be used independently of the prey species.

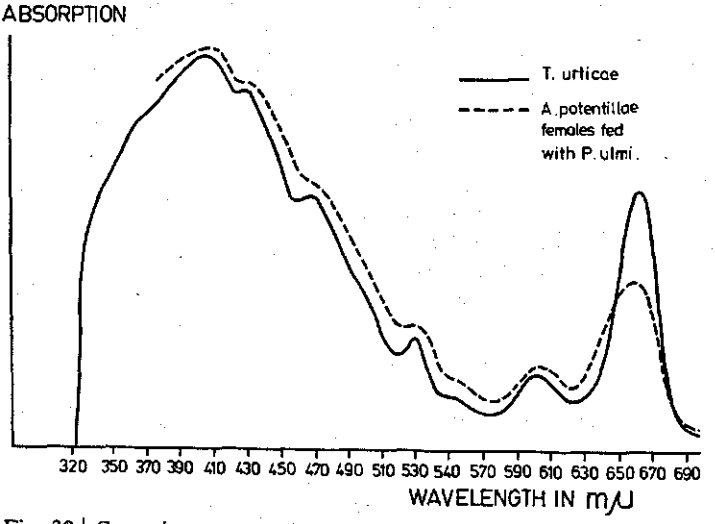
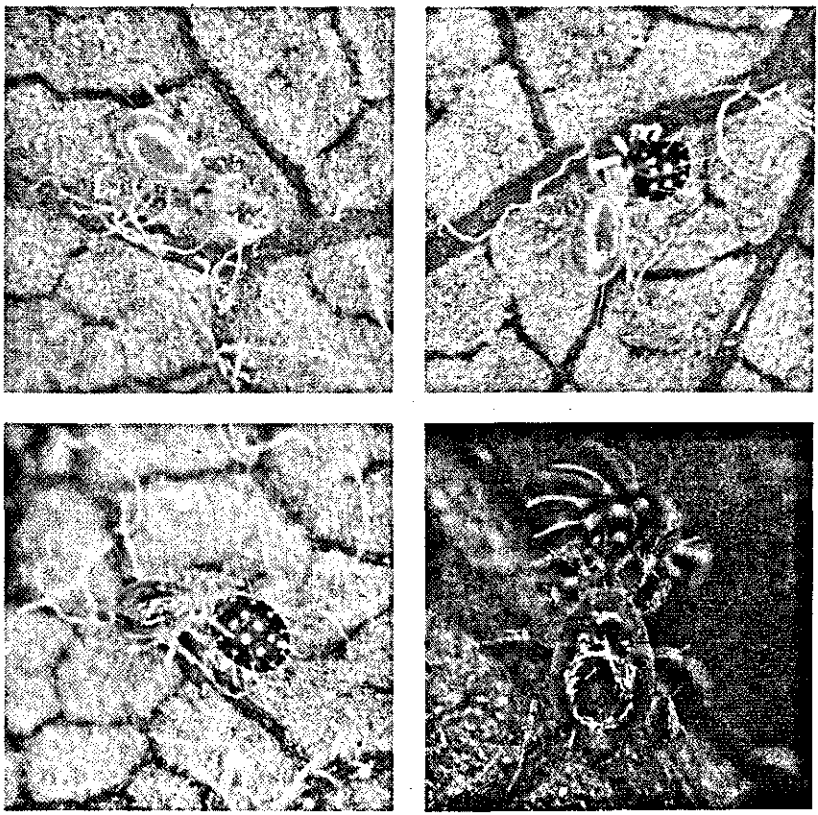


Fig. 39 | Scanning spectrophotograms, wavelengths from 300 mμ — 700 mμ for *Tetranychus urticae*, and *Amblyseius potentillae* fed with females of *P. ulmi*.



Female A. *Potentillae* feeding on *P. ulmi*
Upper Left: coulour value 2, male of prey; upper right: colour value 3, female of prey; lower left: colour value 6, female of prey

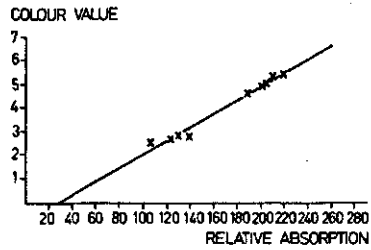


Fig. 40 | Relative absorption against visually determined colour value.

The relation relative absorption against visually determined colour value was linear, (Fig. 40 correlation coefficiënt 0.96) so that each colour unit of the visual scale represents the same amount of pigment consumed. Hence, the scale units 1–7 of the colour scale are used without any further transformation as a relative measure for the amount of food.
Fransz found that the gut content of a predator when kept without food, decreases exponentially with time at constant temperature. In Fig. 41, it is shown that this is also so for the decrease in colour. The relative decrease, c, being defined as

$$\frac{dA}{dt} = c.A$$

in which A is the colour value (0–7), the mean relative rate of decrease being estimated with

$$c = \frac{\ln A_{t+\Delta t} - \ln A_t}{\Delta t}$$

In Table 23 the results at various temperatures are given with the 90% confidence interval and Fig. 42 shows that the relative decrease in colour depends linearly on temperature.

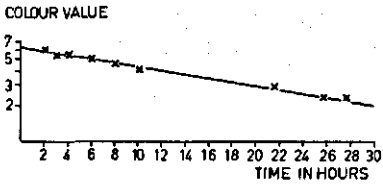


Fig. 41 | Exponential decrease in colour value of adult female predators with respect to time.

Table 23 Relative rate of decrease in colour value of the adult female predator in day^{-1}, mean and 90% confidence interval, at various temperatures.

Temperature °C	Number of replicates	Relative rate of decrease in colour value	
		x	± confidence interval
5	14	0.054	± 0.007
10	10	0.075	± 0.02
15	33	0.45	± 0.04
18	36	0.68	± 0.08
20	14	0.78	± 0.016
25	14	1.01	± 0.09
30	14	1.46	± 0.2

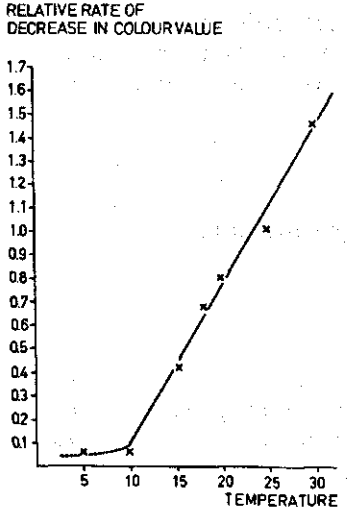


Fig. 42 | Relative decrease in colour value in day^{-1}, against temperature in °C.

Further experimentation showed that as with development, the data determined at constant temperature may be used in situations with fluctuating temperatures.

6.2.3 *Relative rate of predation*

The results of the experiments described in Section 6.2.1 for the adult female predator and the larvae of the prey are given in Table 24 for various temperatures and prey densities. Since there was no predation at 5°C, the temperature threshold for predation lies somewhere between 5 and 10°C. Since it was shown by the Run test that hourly observations are independent, confidence intervals were based on these data. The colour values of the predator are not sequentially independent. Thus the confidence interval is based on the average colour value for one observation period.
Since the data always had a normal distribution, the Student's *t*-value

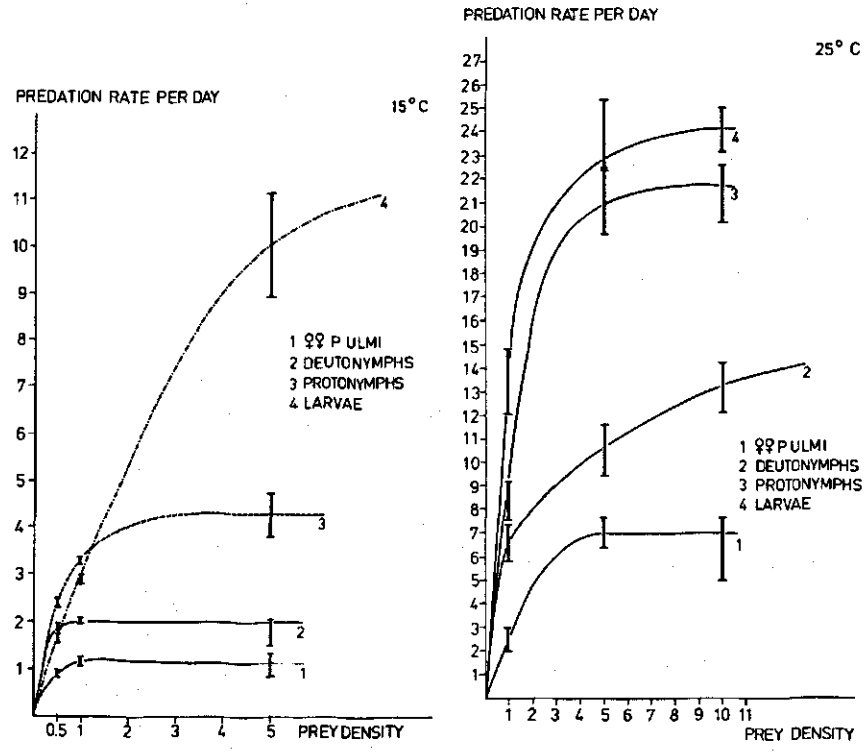


Fig. 43 | Functional response curves of the adult female predator for various prey stages of *P. ulmi* at 15° C and at 25° C, mean and confidence 95% interval.

Table 24 Predation rate per day and colour value (mean[2] and standard deviation) of adult female predator at various prey densities (larvae) and temperatures.

Temperature (°C)	Prey density (number per 3.8 cm²)	Number of replicates	Total time observed[1]	Predation rate		Colour value	
				$\bar{x}$	$s(x)$	x	$s(x)$
10	10	12	313	2.34± .	.	3.85± .	0.50
15	0.5	16	608	1.66±0.12	1.45	2.34±0.46	0.86
15	1	24	693	2.70±0.1	1.15	3.5 ±0.33	0.79
15	5	10	125	9.98±1.1	6.2	5.1 ±1.33	1.75
18	1	2	4	6 ± .	.	2.9 ± .	.
18	2	8	35	7.7 ±3.0	10.1	3.6 ±0.9	1.1
18	5	8	35	9.7 ±3.5	10.2	4.5 ±0.6	0.7
18	10	5	22	12.0 ±3.4	7.6	4.4 ±1.5	1.23
18	25	4	17	19.4 ±5.8	11.4	5.0 ±2.1	1.34
25	1	20	160	13.4 ±1.4	9.1	4.5 ±0.6	1.39
25	5	12	121	23.0 ±2.4	13.1	5.3 ±0.8	1.34
25	10	8	64	24.0 ±1.0	3.9	6.0 ±0.3	0.34

1. Equilibration period excluded.
2. With 95% confidence interval.

was used to calculate the 95% confidence intervals.
Fig. 43 presents the functional response curves of the adult female predator for various prey stages at various temperatures. The preference for the younger stages is clearly demonstrated with these curves. The higher predation of the older juvenile stages, protonymph and deutonymph, than the young juvenile stage, larva at low prey densities (< 1.0 per 7.6 cm^2) and at low temperatures may be due to the behaviour of the larvae. At that temperature they are immobile and hidden under veins etc. whereas the older juveniles are still active.
The relation between the colour value of the predator and the predation rate is given in Fig. 44, together with a 95% confidence interval, here calculated with logarithmic transformation.
The results of Figs. 43 and 44 are used to compute the relation between relative predation rate and temperature at various colour values of the predator, which are used in the simulation models (Section 8.2). The calculation procedure is given for the adult female predator and larvae of the prey.
Mathematically the functional response is described by:

$$MORT = \frac{E \times D}{E \times D + M} M \qquad (6.1)$$

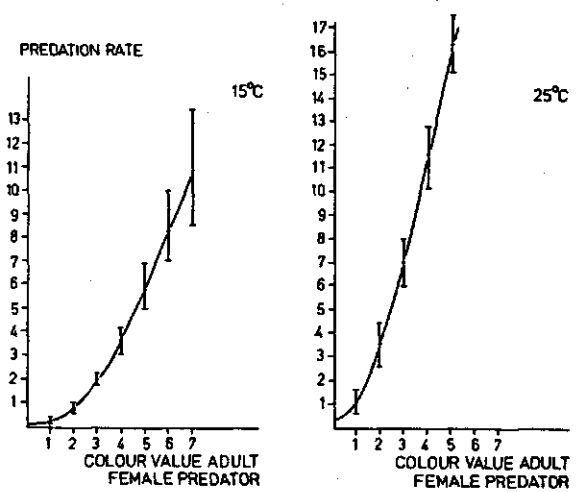


Fig. 44 | Predation rate of the adult female predator in larvae of the prey per day against colour value at 15°C and at 25°C.

in which D is prey density, here per 3.8 cm² and M is maximum predation rate. If $D \rightarrow \infty$, predation rate MORT equals M. E in day^{-1} expresses predation efficiency, if $D \rightarrow 0$, then $MORT = ED$. The relative rate of predation is $RRP = MORT/D$, and ranges from E at $D = 0$, to 0 at D is infinity, it being assumed that effects of response waning at very high densities are outside the range of interest. E and M are most conveniently estimated with graphs of the inverse of prey density against the inverse of the predation rate, Fig. 45.
The resulting relation is linear according to Eq (6.1) since

$$1/MORT = \frac{E \times D + M}{E \times D} \times \frac{1}{M} = \frac{1}{E \times D} + \frac{1}{M}$$

The calculations are done for the limits of the confidence interval of the functional response curve so that the extremes: the maximum predation rate, M and the predation efficiency E are found, Fig. 45. The calculated corresponding relative rates of predation are given in Fig. 46.
Fig. 44 shows the relation between predation rate and colour value. The predation rate at a certain colour value (0–7) was found from this graph and used in Fig. 45 to find the corresponding prey density. Then the relative predation rate was calculated and Fig. 46 was constructed which shows the relation between colour value of the predator and relative predation rate.
The same procedure was followed at all experimental temperatures, thus enabling the construction of a graph in which the relation between relative predation rate and temperature is given at different colour

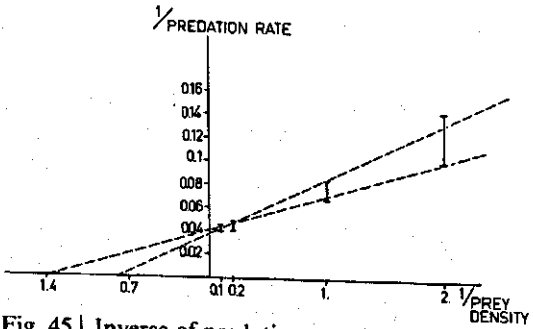


Fig. 45 | Inverse of predation rate (day prey^{-1}) against inverse of prey density (prey^{-1} 3.8 cm²) for larvae of *P. ulmi* and one adult female predatory mite at 25 °C to calculate M (intersection with y axis) and 1/E (slope of the curve).

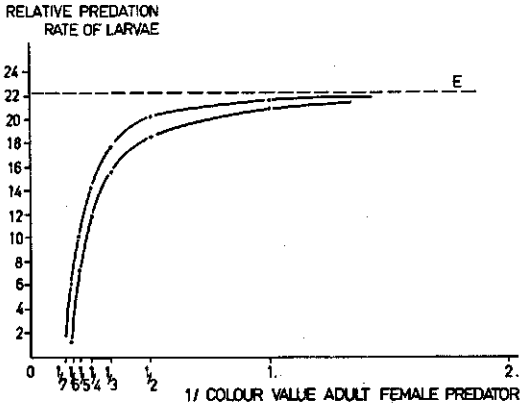


Fig. 46 | Relative predation rate of larvae in day^{-1} against inverse of colour value of the adult female predator at 25°C.

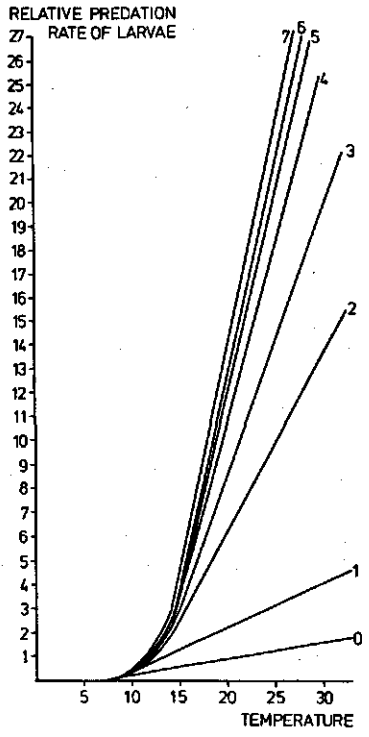


Fig. 47 | Relative predation rate of larvae in day^{-1} against temperature at various colour values (0–7 = ~~1/7, 1/6, 1/5~~ 7–0 .) of the adult female predator.

values of the predator, Fig. 47.
The estimate of these relations may be considerably improved by an iteration procedure. For this purpose a small simulation model for the predation process was written. This model was used to calculate the curves in Fig. 44 from those in Fig. 47 and to estimate anew the functional response curve and the relation between colour and predation rate within the confidence interval. This iteration was repeated 2 to 4 times until the resulting relation in Fig. 47 was sufficiently smooth in all aspects but with the original curves all within their 95% confidence interval.
All these observations and calculations were also done for the other predator and prey stages, although less thoroughly, because the life period of the juvenile stages is much shorter than the life period of the adult female. Thus their contribution to the predation is considerably smaller. The results of these small-scale experiments with the juvenile predators made clear that the relative predation rates of the young stages and the adult males may be calculated from the well determined relative predation rates of the adult female predator. Thus these relative rates are multiplied by factors that are the values of the quotient predator stage size to prey stage size related to these values for the adult female predator. The factors equal 0.33, 0.66 or 1.0, the regularity in the factors being due to the allometric growth of both prey and predator.
Comparisons will be made in Section 9.3 where verification experiments are discussed.

6.2.4 Prey utilization

As described in Section 4.3.1 the relative rate of predation determines the number of prey killed and prey utilization determines the increase in colour value for the predator due to consumption of the killed prey. The prey utilization accounts for the size of the prey, its content, its nutritive value and the fraction that is consumed. The latter parameter depends mainly on the colour value of the predator. The first three are characteristic for each prey species, and are therefore considered independent of temperature and of the predator's condition.
All calculations are again done in the equilibrium situation, so that the rate of ingestion equals the rate of digestion: INCAF = DECAF.
INCAF = increase in colour of adult female,
DECAF = decrease in colour of adult female.
Since

$$DECAF = RDCV \times CAF$$

and

$$INCAF = PU \times RRP \times PL \times AAF$$

in which

RDCV = Relative rate of decrease in colour value of predator
CAF = Colour of adult female,
PU = Prey utilization
RRP = Relative rate of predation,
PL = *Panonychus ulmi* larvae,
AAF = *Amblyseius potentillae* adult female

Hence

$$RDCV \times CAF = PU \times RRP \times PL \times AAF$$

$$PU = \frac{RDCV \times CAF}{RRP \times PL \times AAF}$$

RDCV, CAF, RRP, PL and AAF are all known, Sections 6.2.1 and 6.2.2, and thus PU may be calculated at a certain colour with the corresponding RRP and PL. Fig. 48 presents the results of these calculations in terms of averages at 15, 25°C and average of all

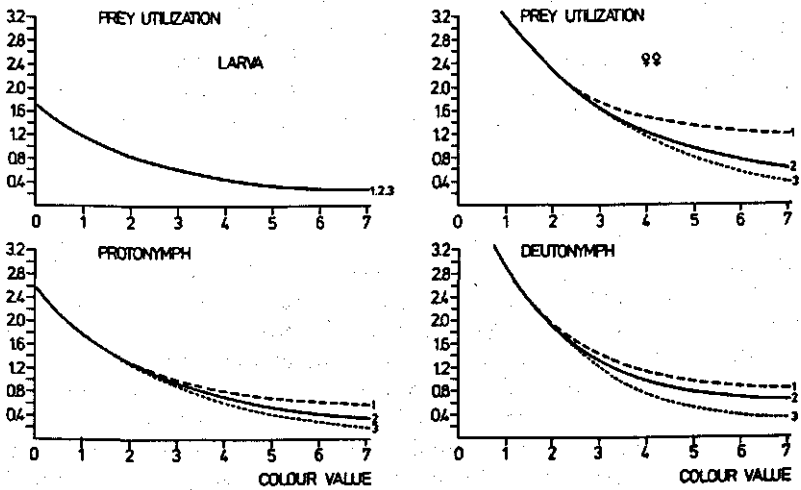


Fig. 48 | Prey utilization of different prey stages against colour value of the adult female predator at 15°C (1), at 25°C (3) and when all data are averaged (2).

measurements. The results indicate that there may be a temperature effect on prey utilization especially at the higher colour values and in the more advanced prey stages. The importance of differences in temperature response was evaluated with a small simulation model of the predation process. The predation rates with and without a temperature effect on prey utilization, were hardly different so that the temperature effect is further neglected, Section 8.2.
An additional reason for this simplification is that the effect on predation rate through small changes in the temperature-dependent relative predation rate in the same colour range, 3–7, was much more important.

6.3 Numerical response

Another important reaction of the predator on prey density is its numerical response, i.e. the numerical changes in predator density due to a changing prey density. Numerical changes may be caused by changing development, mortality or oviposition rates of the predator. In predatory mites it is widely known that development rate is delayed when prey densities are low, (Herbert, 1956, 1961; van de Vrie, 1973) and that oviposition rate diminishes when prey density decreases (Chant, 1961; Burnett, 1970; Fransz, 1974). Good quantitative data on these relations are scarce since most experiments have been done with changing prey densities or under changing abiotic conditions.
Instead of considering the indirect effect of prey density it is more sensible to determine directly the relation between the appropriate numerical rate and the colour value of the predator, and of course at various temperatures.

6.3.1 Development and mortality

Only when protonymphs and deutonymphs are kept at 15°C without food for more than 5 days does the mortality rate increase. This state of exhaustion seldom occurs under field conditions where water as well as vegetable and other alternative food sources are always available. Therefore effects on mortality are not of importance. In some preliminary experiments, van de Vrie (1973) found a strong delay in development and maturation when limited amounts of food were given to the predator. His data, Table 25 are transformed with the functional response curves, Fig. 43 and the relation between colour value and predation rate, Fig. 44 to the relation between colour value and developmental period. In Table 26 the results of these calculations are

Table 25 Developmental period of female *Amblyseius potentillae* at 23°C at various amounts of food (Table according to van de Vrie, 1973).

Number of prey consumed	Duration of development egg to adult (days) (range)	Duration of pre-oviposition (days) (range)
high (all stages)	6 (5–6.5)	2 (1.5–3.5)
10 day^{-1}	6 (5–6.5)	2 (1.5–3.5)
4 day^{-1}	8 (7–9.5)	4 (3.5–5.5)
2 day^{-1}	12 (10–18)	8 (7–10.5

Table 26 Multiplication factor of the development period of different stages of *Amblyseius potentillae* at various colour values of these predatory stages.

Colour value	Multiplication factor of duration of		
	protonymph	deutonymph	pre-oviposition female
0	5.0	5.0	10.0
1	4.0	4.0	5.0
2	2.5	2.5	2.75
3	1.25	1.25	1.5
4	1.0	1.0	1.0
5	1.0	1.0	1.0
6	1.0	1.0	1.0
7	1.0	1.0	1.0

given. Above a colour value of 4 units no effect on development is present, but at lower colour values there is a rapid increase in the development and maturation period. The value of this result is limited since the experiments were not done in the steady state of the predator. However a good quantification of these effects requires considerable study and this is only justified when sensitivity analysis with the computer model shows that this development effect of the predator's state plays a major role in the regulation of the population numbers of the fruit-tree red spider mite (Chapter 10).

6.3.2 *Oviposition*

All experiments for oviposition of *Amblyseius potentillae*, as described in Section 5.3.2, were done with abundant food of good quality, the colour value of the predator being 6.

The experiments of Section 6.2 on relative predation rate were, however, done at different colour values of the predator. In these experiments the oviposition rate was also measured so that the relation between oviposition rate and predator's colour could be determined at various temperatures. The results are presented in Table 27 in terms of average rate of oviposition per day and standard deviation at various temperatures and colours.

Fig. 49 presents the relation between oviposition rate per day and colour value (1–7) at 15 and 25°C. Whenever the predator is under suboptimum conditions, the oviposition rate decreases and the maximum oviposition capacity that was observed for abundant food is not reached at any temperature. Since these results were obtained with

Table 27 Average rate of oviposition of *Amblyseius potentillae* at different colour values and at different temperatures.

Time (h) of observation	Number of replicates	Average colour value	Average rate of oviposition (day^{-1})	Temperature (°C)
304	17	1.23	0.16	15
1116	37	2.02	0.12	15
1202	38	3.08	0.26	15
1522	50	4.05	0.27	15
1268	39	5.0	0.49	15
390	13	5.86	0.68	15
96	3	6.84	1.00	15
32	4	1.23	0	25
224	20	1.97	0.64	25
317	25	3.03	0.83	25
371	27	3.92	1.16	25
415	32	5.01	1.33	25
537	48	6.01	1.65	25
32	4	6.76	2.25	25

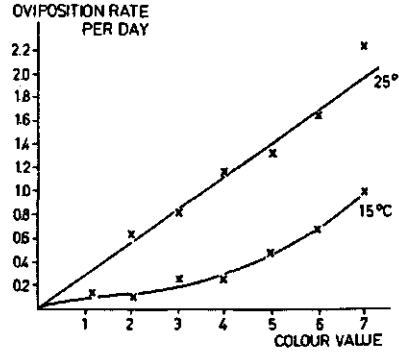


Fig. 49 | Oviposition rate of *Amblyseius potentillae* in eggs per day against colour values at 15°C and at 25°C.

standardized predators (Section 6.1), some additional experiments were done for predators of other age classes and these suggested that the relative reduction of the oviposition depends on colour only and is independent of age.

For further treatment the curves in Fig. 49 were linearized and transformed into those of Fig. 50, assuming as in Fig. 38 that the relation between temperature and oviposition rate is linear. In Fig. 50 the relation between temperature and oviposition rate of females in the second age class is given at various colour values. The reduction factors used in the computer models are the ratios of the slope of the line at colour value 6 to the slopes of the other lines. These factors are used for all age classes.

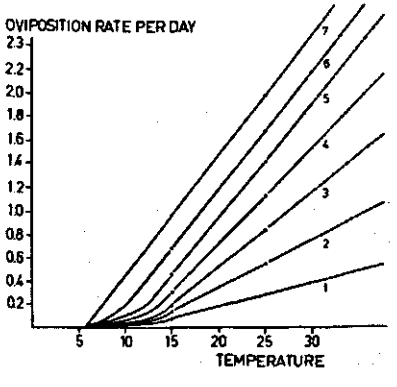


Fig. 50 | Oviposition rate of *Amblyseius potentillae* in eggs per day against temperature at various colour values (1 – 7) of the adult female predator.

7 Driving variables and forcing functions

7.1 Introduction

In Chapter 4 the driving variables temperature, humidity, rain, wind and quality of the host plant were distinguished. The host plant may affect the bionomics of the prey through the quality of the food. The micro-weather is influenced by morphological and physiological properties of the host plant. For instance the size of the leaves and the presence of hairs on the leaves affects the thickness of the laminar layer around the leaves thus influencing the transport of water vapour, heat and carbon dioxide in this layer, where the mites are living. The stomatal resistance and its response to light intensity also affects the vapour exchange and with that the energy balance of the leaves.
The effect of the host plant on the predation rates through its surface structure is not considered since all process experiments were done on the cultivar Golden Delicious and the simulation model was only applied to this cultivar. When the model is used for other cultivars, leaf size, position and surface structure should be compared with Golden Delicious and possibly multiplication factors should be introduced.

The microweather is not measured but computed from the meso-weather and the orchard properties. This modelling procedure was chosen because an existing microweather model for closed crops was easily adapted for the row-structured orchards and the results were shown to be sufficiently accurate (Goudriaan & Waggoner, 1973).

7.2 Host plant

Van de Vrie et al., (1973) discussed the effect of the host plant on different bionomic parameters of the prey. They showed that oviposition increases due to nitrogen fertilization and that development may accelerate. In detailed studies on these effects in fruit-tree red spider mite, Post (1962) Storms (1969) and van de Vrie & Boersma (1970) showed that the nutritive status of the plant and principally the nitrogen level affects the oviposition rate per female and the development from larva to adult. Several other authors have described experiments that confirm their findings. The experiments are often

done with apple trees grown in soil mixtures in pots and under these conditions the intended differences in nutritional status of the trees are often not reached. Instead, gravel or water cultures should be used. Storms (1969) succeeded in working with such cultures but his quantitative data on *Panonychus ulmi* were rather poor and therefore additional experiments had to be done. In these experiments the effect on the oviposition capacity, oviposition rate and life-span of different levels of nitrogen in the leaves in combination with the availability of other nutrients, was determined. Since the models are developed for normal field situations, the nitrogen levels in the leaves are adjusted to around the values occurring in commercial fruit orchards. A comprehensive study of Delver (pers. commun.) in commercial orchards showed that the nitrogen level ranges only from 2.2–2.8% N of the dry leaf matter, (Fig. 51). Unlike oviposition, development of *P. ulmi* is only quantitatively affected when much lower nitrogen levels are reached (Post 1962, and van de Vrie & Boersma, 1970). Therefore these effects are neglected.

7.2.1 Experimental

Apple rootstocks M9, still in the dormant winter conditions, were pruned down to 30 cm and placed in aerated water cultures. Eight different nutritional treatments were applied with respect to their nitrogen fertilization. The water in the 20 l containers was refreshed

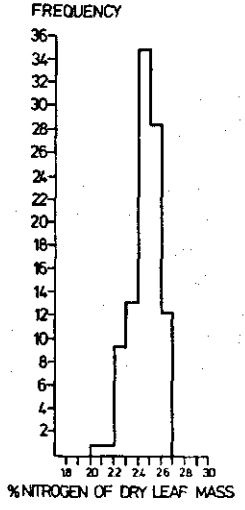


Fig. 51 | Frequency distribution of nitrogen percentages of total dry matter of the leaves for 200 commercial orchards in the Netherlands. (Delver, pers. comm.).

Table 28 Solutions for water culture experiments. Solutions 1A–1B, 2A–2B, 3A–3B and 4A–4B were equal in concentration of nitrogen: 0.202, 0.604, 1.812 and 5.44 mmol.litre^{-1}, respectively; 1B–2A, 2B–3A and 3B–4A were equal in osmotic pressure: 3, 8.5 and 25kPa, respectively; 1A–2A–3A–4A substance fraction of nitrate in total anions constant at 80%; 1B–2B–3B–4B substance fraction of nitrate in total anions constant at 25%.

	Concentration (mmol.litre^{-1}) of components in solution							
	1A	2A	3A	4A	1B	2B	3B	4B
$MgSO_4$	0.037	0.113	0.340	1.020	0.205	0.607	1.822	5.468
$Mg(NO_3)_2$	0.025	0.076	0.229	0.689				
KH_2PO_4	0.012	0.037	0.113	0.340	0.040	0.120	0.362	1.087
$Ca(NO_3)_2$	0.075	0.227	0.683	2.051	0.203	0.604	1.812	5.438
KNO_3	0.100	0.300	0.900	2.700				
KOH	0.001	0.004	0.012	0.037	0.004	0.013	0.039	0.118
$CaSO_4$					0.042	0.124	0.374	1.123
K_2SO_4					0.323	0.959	2.879	8.637

every three weeks. The cultures were placed in a climate room at 18°C for the 16-hour light period and at 12°C during the dark period. Relative humidity was kept constant at 70 percent and illumination was done by TLM fluorescent tubes, installed at density of 1407 watt m^{-2} and 50 cm above the top of the tree.

No sprayings against insects were needed and incidental leaf rollers were removed manually. Spraying against apple mildew, *Podosphaera leucotricha* had to be repeated every 15 days with Dionocton-4[1] which is harmless for spider mites.

The composition of the water culture according to Steiner (1961), was chosen such that all anions and cations were immediately available for uptake by the plant roots. Two series (A and B) with different nitrate percentages of the total anion concentration were used, each series consisting of four nitrate concentrations and therefore different osmotic values of the solutions. The lowest osmotic value was determined by the solution products of the sulphates and phosphates of calcium.

1. Synthesized by Murphy, England (Martin & Worthing, 1970)

Table 28 gives the different solutions and the characteristics that are compared, as will be described in Section 7.2.2. Aeration was done by pumping the water in a closed system. As continuous pumping caused mechanical damage of the roots, the pumping intervals were regulated so that the oxygen tension in the water measured with an electric oxygen meter, Type Ypsilon Si.54 R.C. Yellow Springs Instruments Co., was kept between 7.5 and 8. The pH was measured daily. At a pH above 5.8 precipitation of the calcium phosphate may occur and therefore the pH was kept below 5.8 by adding a water solution of the anions; pHs below 3.5 were prevented by addition of 1N KOH solution.

7.2.2 Results

The quality of the host plant is characterized by the nitrogen content of the leaves and their rate of photosynthesis. The nitrogen content of the fifth leaf from the top was measured according to Kjeldahl, and because its nitrogen content may vary during life time, (Storms, 1969), the measurement was repeated. In Table 29 the nitrogen and water contents in the leaves are given for the 8 treatments. The nitrogen contents in the leaves ranged from 1.6 to 3.5 percent of the dry matter, which is a much larger range than that of 2.2 to 2.8 in commercial fruit

Table 29 Nitrogen and water content of leaves of apple trees, Golden Delicious, grown on different water cultures.

Solution	Mass fraction of nitrogen in dry leaf (%)	Mass fraction of water in fresh leaf (%)
1A	2.11	70.35
2A	2.81	70.92
3A	3.27	70.55
4A	3.46	68.72
1B	1.83	69.61
2B	1.44	68.43
3B	1.67	69.44
4B	3.46	68.38

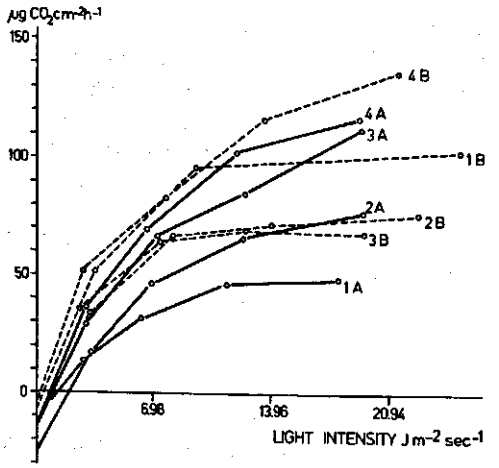


Fig. 52 | Assimilation in g CO_2 cm^{-2} leaf per hour (Golden Delicious) against light intensity in J m^{-2} sec^{-1} for trees grown on different water solutions.

orchards. The rate of photosynthesis was also measured to determine the metabolic activity of the plant and in that way the suitability as a food source for the mites. These measurements were done according to Louwerse & Van Oorschot (1969). In Fig. 52 the light response curves are given as an average of four replicates and with the photosynthetic activity in g CO_2 cm^{-2} leaf per hour and the light intensity in J cm^{-2} min^{-1}. Fig. 53 presents the relation photosynthetic activity in g CO_2 g^{-1} h^{-1} at a light intensity of 175 J m^{-2} min^{-2} and the percentage nitrogen. The relation is nearly linear with the exception of the 2B and 3B treatments that may be related to the abnormal composition of the water culture in those treatments.
Since the effects of P and K on rates of oviposition, development and mortality of *Panonychus ulmi* are negligible (Rodriguez, 1958; Mathys, et al., 1968), these elements are not determined in the leaves.

One female teleiochrysalid and one male isolated from the mass cultures were transported with small leaf pieces into Tangle Foot rings on the upperside of the leaves. Immediately after copulation the male was removed. Damage of the female due to handling was in this way prevented. The females stayed on the same leaf during their whole lives. Each day the eggs were counted and removed so that oviposition rate,

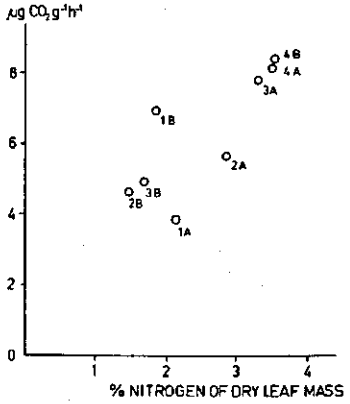


Fig. 53 | Assimilation in $\mu g\ CO_2\ g^{-1}$ leaf per hour (Golden Delicious) against nitrogen percentage of leaf dry matter.

fecundity and life-span were measured, Table 30. Females that walked into the ring of glue were replaced except when more than 20 days old. For each of the 8 treatments 20 replicates were started, but due to premature death not all data are statistically processed. Since treatments as well as replicates are statistically independent, analysis of

Table 30 Oviposition rate, life-span and fecundity of adult females of *Panonychus ulmi* in trees grown on different water cultures.

Solution	Average rate of oviposition (eggs day^{-1})	Average life-span (days)	Average fecundity (eggs)
1A	1.05	26.0	29.7
2A	1.08	24.8	21.3
3A	1.41	28.4	34.7
4A	1.62	21.9	28.9
1B	1.15	18.5	14.0
2B	1.26	20.2	17.8
3B	1.25	28.3	30.3
4B	1.77	24.7	46.5

variance was done for: the oviposition rate per day, the life-span and the total egg production. The egg production per day for treatments 1A, 2A and 1B is significant ($\alpha = 0.01$ and ($P < 0.05$)) lower than the mean and for treatments 4A and 4B significantly higher. So leaves above the range 2–3 percent nitrogen show a higher rate of oviposition and leaves below the range a lower oviposition rate than the mean. For life-span treatments 1B and 2B are significant below the mean and 3A and 3B above ($\alpha = 0.01$ and ($P < 0.05$)), so that also for this quality only extreme nitrogen levels give significant deviations from the mean. For some treatments that can be compared, Table 28, the contrasts and the confidence interval of the difference were calculated according to

Table 31 Contrast and confidence interval for different solutions. Only the contrast 3A - 1B is significantly larger than zero for life-span and fecundity ($\alpha = 0.1$).

Contrast between solutions	$\bar{x}$[1]	t value	
Oviposition rate			
2A - 1A	0.035 ± 0.557	0.063	P>0.3
2A - 1B	0.254 ± 0.545	0.466	P>0.3
3A - 2A	0.322 ± 0.514	0.628	0.1<P<0.3
4B - 1A	0.725 ± 0.585	1.239	0.1<P<0.3
4A - 2B	0.351 ± 0.545	0.644	0.1<P<0.3
Life-span			
2A - 1A	-1.17 ± 7.22	0.162	P>0.3
3A - 1B	9.88 ± 5.52	1.791	P>0.1
3A - 2A	3.54 ± 5.52	0.642	0.1<P<0.3
4B - 1A	-1.25 ± 7.80	0.160	P<0.3
4A - 2B	1.61 ± 6.40	0.251	P<0.3
Fecundity			
2A - 1A	- 8.33 ± 18.16	0.459	P>0.3
3A - 1B	20.75 ± 13.87	1.496	P>0.1
3A - 2A	13.42 ± 13.87	0.967	0.1<P<0.3
4B - 1A	16.83 ± 19.61	0.858	0.1<P<0.3
4A - 2B	11.11 ± 16.10	0.690	0.1<P<0.3

1. Second figure = confidence interval.

$$\hat{\alpha}_1-\hat{\alpha}_2-\sqrt{\text{var}\ (\hat{\alpha}_1-\hat{\alpha}_2)}\times t_R(^1/_2\times\alpha/5)<\hat{\alpha}_1-\hat{\alpha}_2<\hat{\alpha}_1-\hat{\alpha}_2+$$
$$+\sqrt{\text{var}\ (\hat{\alpha}_1-\hat{\alpha}_2)}\times t_R(^1/_2\times\alpha/5)$$

In Table 31 the results of these calculations are given. Only the effect $\alpha_3-\alpha_5$ (3A - 1B) is significant ($\alpha = 0.1$) for life-span and fecundity. The absence of significant differences for the other contrasts is principally due to the big standard deviations in the effects of the treatments that reduce the discrimination of the t-test.
It is concluded that no significant effects of food quality within the nitrogen range 2-3 is found. Therefore food quality effects can be neglected in simulation models applied in field situations.

7.3 Micrometeorology

The method to determine the required accuracy of the input data of the models was given in Section 5.1. This method is also applied for the temperature, the most important abiotic driving variable. Small deviations in temperature may cause considerable differences in the simulation results. Therefore an accurate knowledge of this forcing variable is required. The use of micro-weather simulators to evaluate the necessary detail on micro-weather was introduced in Section 4.4. The micro-weather simulators and the coupling of these with the population models will be given in this section.

The micro-weather models are not described in detail, for this the reader is referred to Goudriaan (in prep.).

7.3.1 Modelling

The micro-weather simulator is based on the experimentally verified assumption, Section 7.3.2.2, that temperature and humidity profiles within the orchard are absent and that a fixed relation exists between the wind within and outside the orchard, Section 7.3.2.1. The following distinctions are made for leaf exposure: leaves that are completely shaded; leaves that also receive diffuse light; leaves that receive both diffuse and direct light. Within the last group 10 subclasses dependent on the position of the leaves with respect to the sun are distinguished.

7.3.1.1 Calculation of the leaf temperature

With a formula that can be deduced from the energy balance of the leaf,

leaf temperature is calculated according to methods originally proposed by Penman (1948). The following relation is found for the difference between leaf (TL) and air temperature (TA):

$$TL-TA = \frac{((RA + RS) \times ABSRAD \times PSCH)/\rho c_p - (ES-EA)}{\frac{(RA + RS)}{RA} \times PSCH + S} \quad (7.1)$$

In this relation RA expresses the resistance of the laminar layer in sec m^{-1} around the leaf to transport of water vapour, heat and CO_2. This resistance is calculated with a formula according to Parlange et al., (1971): $RA = b \times \sqrt{WIDTH/WIND} \times 0.5$, in which b is a proportionality constant, WIDTH is the smallest size of the leaf in the direction of the wind and WIND is the wind speed in m $sec.^{-1}$; with the multiplication factor 0.5, it is implicitly assumed that both sides of the leaf are identical with respect to heat transport and that effects of hairs etc. can be neglected.

The other resistance in eqn (7.1), RS, stomatal resistance in sec. m^{-1} expresses the internal resistance of the leaf to transport of water vapour and CO_2 and, is found from a tabulated function of stomatal resistance to light intensity in J m^{-2} $sec.^{-1}$.

ES is the satiated vapour pressure at TA in mbar, S is the slope of the satiation curve, EA is the vapour pressure in the air in mbar, PSCH is the psychrometer constant in mbar $°C^{-1}$, ρc_p is the volumetric heat capacity of air in $Jm^{-3}\,°C^{-1}$, and ABSRAD is the absorbed radiation. ABSRAD is calculated with RAD–LWR, in which RAD is the net short-wave radiation and LWR the net long-wave radiation. RAD is found with:

$$RAD = (1.-SCAT) \times (DIRECT + DIFFUS)$$

in which

$$DIFFUS = 2. \times DIFCL \times (1.-FOV) + 1.7 \times DIFOV \times FOV$$

and

$$DIRECT = 2. \times SUNDCL$$

DIFCL and SUNDCL are the diffuse and direct visible light fluxes through a horizontal surface at the top of the orchard. DIFOV is the diffuse light flux with overcast sky. All three parameters are found with tabulated functions from the inclination of the sun, (de Wit, 1965). SCAT is the scattering coefficient of the leaf and comprizes transmission and reflection. FOV is the fraction of the sky which is overcast. A more detailed explanation of the formula is given by Goudriaan, (in prep.).

To include the position of the leaves with respect to the sun, the short-wave radiation from the sun (DIRECT) is multiplied by the sine of the angle of the sun and the leaf divided by the sine of the elevation of the sun relative to the horizontal. Ten inclination classes of leaves with respect to the sun are distinguished in this way. At night only one leaf temperature is calculated with the Penman formula, so that the following section only holds for daytime.

7.3.1.2 Calculation of the fraction of leaves per class

A diagram of the division of the leaf area index over the different classes is given in Fig. 54.
The sunlit leaf area index, SLLAI and the other leaf area indexes DLLAI and DARKLI are measured relative to the area of the row and the area of the shadow cast by the row upon the path, i.e. WROW + WPATH, in Fig. 55. It is assumed that leaves at the bottom are practically in the dark, DARKLI. Since their stomata are closed it is assumed that their temperature equals the air temperature.
The diffuse light is assumed to be evenly distributed over the higher leaves, a further distinction in radiation distribution of diffuse radiation not being necessary. The sunlit leaf area index SLLAI that determines the size of the other two fractions, DLLAI and DARKLI is calculated according to de Wit, (1965) and Goudriaan, (in prep.). They showed by application of simple geometrical and goniometrical formulas that the sunlit leaf area index SLLAI may be calculated with

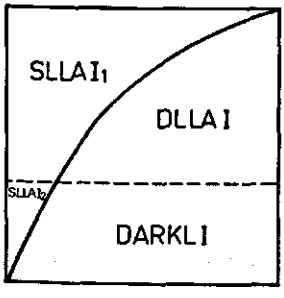


Fig. 54 | Distribution of the leaf area index over different classes, SLLAI1-Sunlit leaf area index1, leaves receiving both diffuse and direct light, SSLAI2-Sunlit leaf area index2, leaves receiving direct light only; DLLAI-Diffuse lit leaf area index, leaves receiving only diffuse light; DARKLI-Dark leaf area index, leaves completely in the shade.

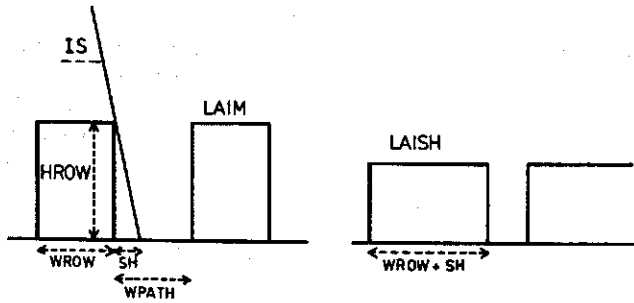


Fig. 55| Diagram of the row structure and its effect on light interception.

$$SLLAI = SIN(IS)/OPG \times (1 - \exp(-OPG \times LAIM/PROJ))$$

In this equation PROJ is the projection of the section radiated by the sun and is calculated with:

$$PROJ = \sin(IS) \times (WROW + SH)/WROW.$$

IS is the inclination of the sun and SH accounts for the shadow between the rows, Fig. 55, and is calculated with:

$$SH = AMIN1\ (HROW \times \cot(IS) \times \sin(RAZ), WPATH)$$

RAZ being the difference in azimuth between the sun and the rows, HROW is the height of the rows, and WROW is the width of the rows, Fig. 55.
LAIM is the measured leaf area index referring to the area of the rows only. OPG is the average projection of all leaves calculated from the measured leaf angle distribution with respect to the horizontal, Fig. 55. The leaf area index of the leaves receiving diffuse light only, but not completely in the dark, DLLAI, is now calculated with

$$DLLAI = TLLAI - SLLAI1,$$

in which TLLAI is the leaf area index of the leaves diffusely illuminated, including those which also receive direct radiation, DLLAI + SLLAI1.
TLLAI equals the ratio of the total absorbed diffuse radiation, DIFABS, and the absorbed diffuse radiation of the leaves, DIFL; so $TLLAI = DIFABS/DIFL = DLLAI + SLLAI1$.

DIFABS is calculated with:

DIFABS = DIFCL × 2. × AMIN1 (1., (WROW + HROW)/
(WROW + WPATH)) × (1. —exp (—0.7 × (LAIM ×
×WROW)/(WROW + HROW))) × ((WROW + WPATH)/
(WROW + SH))

in which

(WROW + HROW)/(WROW + WPATH)

gives the ratio between the diffuse radiation absorbed by the row area and the total incident diffuse radiation, it being assumed that the shaded area for diffuse radiation on both sides of the row is 0.5 × HROW.

(WROW + WPATH)/(WROW + SH)

converts the total soil area WROW + WPATH to the area WROW + SH used in the calculations.
The multiplication factor 0.7 gives the extinction for diffuse radiation and is about constant.
DIFL is calculated with

DIFL = (1. - SCAT) × DIFCL × 2.

so that

DIFABS/DIFL = AMIN1 (1., (WROW + HROW)/
(WROW + WPATH)) × (1. —exp (—0.7 × (LAIM × WROW)/
(WROW + HROW))) × ((WROW + WPATH)/
(WROW + SH))/(1. —SCAT)

SLLAI1, the leaf area index of the directly radiated leaves, that are also diffusely illuminated, is now calculated in the same manner as the SLLAI with

SLLAI1 = (SIN (IS)/OPG) × (1. —exp (OPG × (TLLAI/SIN(IS))))

Finally the leaf area index of the leaves completely in the shade is calculated by subtracting the leaf area indexes of leaves receiving direct and diffuse light, SLLAI, and the leaves receiving diffuse light only (DLLAI), from the total leaf area index LAISH, in which the row structure is accounted for. LAISH is calculated from the measured leaf area index with

LAISH = LAIM × (WROW/(WROW + SH) (Fig. 55)

so that

DARKLI = AMAX1 (0., LAISH - SLLAI - DLLAI)

The fractions of leaves are now calculated as follows:

fraction of leaves completely in the dark:

$$FDL = DARKLI/LAISH$$

the fraction of leaves receiving only diffuse radiation:

$$FDRL = DLLAI/LAISH \times (1. - FOV) + FOV \times \times((LAISH - DARKLI)/LAISH)$$

the fraction of leaves that receive direct and diffuse radiation:

$$FSRL = (SLLAI/LAISH)\ (1. - FOV)$$

The last fraction is subdivided into ten classes according to

$$FSRL'1\ .\ 10' = Z'1,\ 10' \times FSRL$$

in which Z'1,10' is the size of each of the 10 classes of Fig. 56, that describes the leaf position distribution function.
All the equations described are the result of a rather cumbersome geometrical analysis which will not be discussed here. Programs that describe the light distribution in the row-structured orchards and also some other types of orchards were also developed. These models will be described elsewhere by Goudriaan et al., (in prep.).

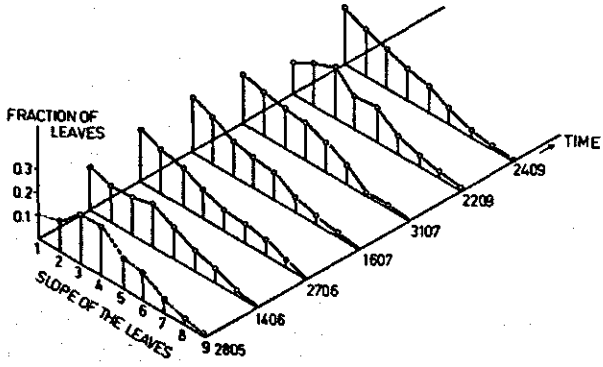


Fig. 56| Fraction of leaves in different leaf position classes, measured with respect to the horizontal, 9 classes.

7.3.2 *Experimental*

As with the population model two kinds of measurements and experiments are required for the micro-weather simulation.
The first concerns the parameterization of leaf area index, of the architecture of the orchard and the quantification of the relations between light intensity and stomatal resistance, and wind above and within the orchard. The second type of experiment concerns the comparison of model output with field measurements and the verification of simplifying assumptions, like the absence of temperature and humidity profiles in the orchard. For this purpose it is also necessary to measure the forcing variables, temperature, humidity and wind, 5 metre above the soil, and total global radiation. All field measurements were done in the hedgerow orchard at the Schuylenburg, described in Section 4.4.

7.3.2.1. Parameterization

The relation between light intensity and stomatal resistance was determined in a photosynthesis room for small Golden Delicious trees grown under optimum conditions. The CO_2-assimilation and transpiration were determined at various light intensities and with 8 replicates. The stomatal resistance was calculated from the transpiration data, according to Goudriaan, (1976). Moreover direct measurements with a diffusion porometer, Stigter, (1975), were done. There was reasonable correspondence between direct measured and calculated stomatal

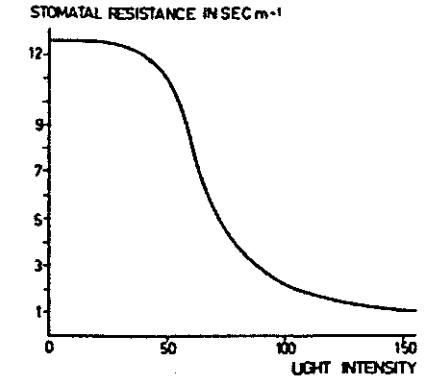


Fig. 57| Stomatal resistance of Golden Delicious leaves in sec m^{-1} against light intensity, values along the abcissa are found by multiplying the incoming radiation in J m^{-2} sec^{-1} with 0.7.

resistance, and the resulting relation between the stomatal resistance and light intensity (in J. m^{-2} sec^{-1}) is given in Fig. 57. A more detailed description of the experiments is given by Hopmans et al., (in prep). The relation between wind speed above and in the orchard at 2.5 metre height was determined by measurements at 0.2, 0.5, 1.0, 1.5, 2.0, 2.5 and 5 m. The wind profile was logarithmic and the wind in the orchard at 1.50 m was 30 percent of the macro wind. A more detailed description of the experiments is given by Lablans, (in prep.).
The leaf position with respect to the horizontal was determined with a leaf position marker (de Wit, 1968) at intervals of 10 degrees, from 0 to 90 degrees. It is further assumed that the leaves are distributed at random throughout the tree and do not have a preferred azimuth direction. Fig. 56 presents the leaf distribution function throughout the season, 70 percent of the leaves having a position between 0 and 40 degrees. The leaf area was determined by weighing fresh leaves and calculating the corresponding surface from a regression line, determined by subsampling, (regression coefficient 0.79, correlation coefficient 0.9). The leaf area per tree throughout the season stays the same from June to September, Fig. 58. The plant system of the Schuylenburgh is 1.5–2.5 m; the surface below the trees amounts to $1.5 \times 1.5 = 2.25$ m^2. The average leaf area per tree from June to August amounted to 8.06 m^2 so that the leaf area index for rows (LAIM) equals $8.06/2.25 = 3.6$.
Transmission and reflection coefficients from literature were used to estimate the scattering coefficient. Palmer, (1973) found a mean reflection in the visible light of 7–9 percent and a transmission of 1–4 percent. Shulgin et al., (1960), found a transmission of 1–3 percent for wavelengths of 400–500 nm, 12 percent for green light and 43 percent

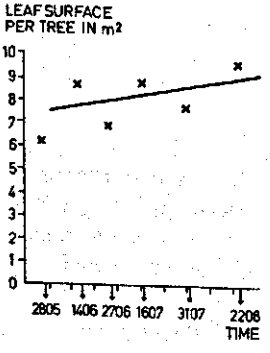


Fig. 58 | Leaf surface of the trees in m^2 throughout the season.

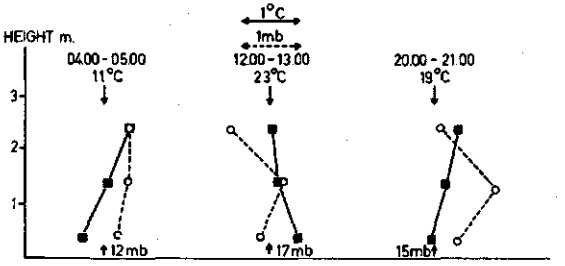


Fig. 59 | Temperature and air humidity with respect to height in a hedgerowed apple orchard, Landsberg et al. (1973).

for near infrared. Cowan (1968) gave a reflection for visible light of 5–10 percent and Gates (1962) stated that ultraviolet light is transmitted less than visible light. All these different data lead to an estimate of 0.4 for the scattering coefficient.

7.3.2.2 Verification

Temperature and humidity were measured continuously according to Stigter, (1976) at 20, 50, 150, 200 and 250 cm within and between the rows. The results of these measurements confirm Landsbergs' (1973) results that temperature and humidity scarcely vary with height in an open-structured orchard, Fig. 59.
Leaf temperatures at three measuring days were determined with Heyman's infrared thermosensors and that of Barn.
Three classes of leaves were distinguished: those completely in the shade, those in direct radiation perpendicular to the sun and the others randomly sampled. The size and composition of the classes changes continuously in the open structured canopy.
The leaf temperatures for these three classes were also simulated on basis of the input data and relations discussed in Section 7.3.2.1 and the meso-weather measured. Table 32 shows good correspondence between simulated and measured differences in leaf and air temperature for all three classes, further data on verification being given by Lablans, (in prep.).
The light distribution throughout the orchard was measured with photochemical radiation integrators (Bokhorst, 1970). With the more detailed simulation program of light distribution the blackening of the integrators was also simulated for 3 measuring days. The simulated and

Table 32 Measured and simulated leaf temperatures, results of one measure day, 3 July 1973, Schuylenburg, Lienden.

Time	Classes Leaves completely in the shade		Leaves perpendicular to the sun receiving direct radiation		Leaves randomly sampled	
	simu-lated	meas-ured	simu-lated	meas-ured	simu-lated	meas-ured
7.12	13.8	–	21.4	–	13.8–20.6	–
9.36	19.3		26.9			
11.10	21.5	20.5	–	–	–	–
12.00	21.1	–	30.8	29	24.6–29.8	26
14.20	26.6		31.4	29.5	26.4–28.8	27
16.50	25.3	–	29.7	–	22.5–28.8	23

measured results show good correspondence. A more detailed description of these verifications will be given by Goudriaan et al., (in prep.).

7.3.3 Coupling micro-weather simulator and population model

With the micro-weather simulator the leaves are divided in 12 temperature classes and the fraction of the leaves in each of the classes is calculated. The assumption is now made that the mites are distributed uniformly over the leaves and that the fraction of mites at a certain temperature corresponds with the fraction of leaves at that temperature. Moreover it is assumed that the size and composition of the fractions continuously change so that mites with a constant relatively high or low temperature do not exist. In the first approximation this latter assumption is justified by the results of the verification measurements in the open-structured orchard. The first assumption is not valid but its effect is negligible, Section 11.1. The micro-weather simulator is coupled with a simple population model of the spider mite as follows: The rate of flow from one class to another, for eggs, juveniles or adults, is determined by the number in the outgoing class multiplied by a relative rate that depends on temperature. For each of the twelve temperature classes the corresponding relative rates are read from tabulated functions and multiplied by the fraction of leaves belonging to this class. The sum of these products is then used as the relative rate of transfer. Thus the population movement of the spider mites is

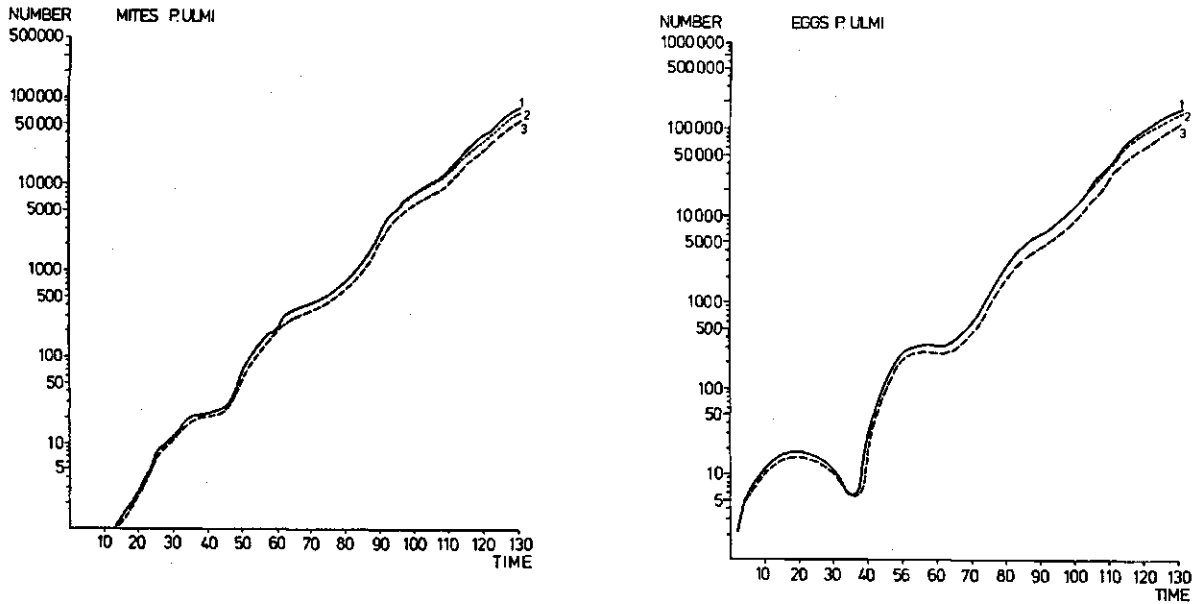


Fig. 60 | Population growth of *Panonychus ulmi* throughout the season for eggs and mites (all developmental stages and adults together).

1. population model with air temperature;
2. population model with leaf temperatures;
3. population model with air temperature with oviposition rate X 0.9.

Day 0 = 25 May; weather data from the Schuylenburgh, Lienden, the Netherlands.

simulated, taking into account all the various temperatures that may occur in the orchard.
The calculations with this population model may be compared with a model that uses only air temperature as a driving variable. The differences between these two population simulators are compared with results of the air-temperature model in which the oviposition rate against temperature is multiplied by a factor 1.1 or 0.9, within the confidence interval of this relation. The results of these calculations, Fig. 60 show that the differences between population fluctations of *P. ulmi* in the air-temperature model and the leaf-temperature model are smaller than the differences due to a small change in the oviposition rate.
From these results it is concluded that detailed information about micro-weather is not necessary for simulating the population fluctuations of the fruit-tree red spider mite and that it suffices to work with the air temperature as the driving variable.
With this model a sensitivity analysis was done for orchards with other characteristics: LAI, leaf position, row distance, scattering coefficient. The results of these calculations are discussed in Section 10.2.

8 Computer models

In Chapter 4 the system was described qualitatively with relational diagrams. The relations and the effects of the driving variables were quantified in Chapters 5, 6 and 7.
Here a description of the computer models and the processing of literature data is given. Three models are presented: a model that describes the population growth of prey and predator during the season, a model that describes the predation of one predator in replacement series of prey stages, and a micro-weather simulator.
The population model is divided into three submodels that can be run separately. The first submodel concerns the hatching process of the winter eggs of fruit-tree red spider mite, the second describes the population growth of prey and predator during the season and the third the diapausing process in the autumn.
Since there was not enough time for experiments on hibernation of prey and predator, the incomplete and inaccurate data of Cranham (1972) and Putman (1970) were used for the construction of a first simulation model on this process and the hatching of winter eggs in spring.
The rudimentary character of this submodel makes its use in the population model doubtful. For this reason the population model is initialized when adult females of prey and predator appear. This appearance in time and number can be observed in the field.

8.1 Population models

The treatment of the physical factors influencing population growth is the same for each of the submodels. Section 1 of Fig. 61 presents the listing of this part of the computer program. The actual temperature, TEMP, is calculated from a sinusoid through the daily minimum and maximum temperatures. The average daily temperature, VALAV, the amplitude of the temperature, VALAMP, and the time of sunrise and sunset are considered. The time of sunrise is calculated from the latitude of the site, LAT, and the number of the day, DAY. The daily minimum and maximum temperatures are read from tabulated functions, MNTT and MXTT. The daylength is calculated from the calculated time of sunrise and sunset increased by one hour for the twilight.

Fig. 61 | Computer program for population model.

```
TITLE RABBINGE
TITLE PANONYCHUS ULMI AND AMBLYSEIUS POTENTILLAE

*         IN THIS SIMULATION MODEL THE METHOD OF SIMULATION DEPENDS ON
*         THE RELATIVE STANDARD DEVIATION OF THE DESCRIBED PROCESSES
*         (CONTINUOUS SIMULATION OR DISCONTINUOUS SIMULATION)

*         THE RELATIVE DEATH RATE IS SIMULATED CONTINUOUSLY
*         WITH A FIXED FACTOR, A POISSON PROCEDURE IS UNNECESSARY.
*         THE PREDATION CHARACTERISTICS FOR THE ADULT MALE OF
*         P.ULMI ARE SET EQUAL TO THOSE OF THE DEUTONYMPHAE

*         CALCULATIONS ARE DONE FOR THE STANDARD SAMPLE OF 100 LEAVES


*MACRO CT,C,DEC,RATE,EQT=PRAEDA(UL,TT,RDCV,SEMC,INC,EQTI)
*       CT=1./C
*       C=LIMIT(UL,7.,EQT/(NOT(TT)+TT) )
*       DEC=AFGEN(RDCV,TEMP)*INSW(EQT-CHECK,0.,EQT) *SEMC
*       RATE=INSW(EQT+(INC-DEC)*DELT,-EQT*DELX,INC-DEC)
*       EQT=INTGRL(0.,EQTI*PUSH*DELX+RATE)
*ENDMAC

FIXED I1,I2,I3,I4,I5,I6,I7,I8,I9,I10,I11,I12
INCON I'1,12'=0
STORAGE AY(8),XY1(8),XY2(8),XY3(8),XY4(8),XY5(8),XY6(8),XY7(8), ...
        XY8(8),XY9(8),XY10(8),XY11(8),XY12(8)
TABLE AY(1-8)=.142,.166,.2,.25,.333,.5,1,100.

INCON ZE=0.,     RTE=0.,    PUSHE=0.,   ER0=0.,ER'1,4'=0., ...
      ZJ=0.,     RTJ=0.,    PUSHJ=0.,   JR0=0.,JR'1,6'=0., ...
      ZJS=0.,    RTJS=0.,   PUSHJS=0.,  JSR0=0.,JSR'1,6'=0., ...
      ZPAFS=0.,  RTPAFS=0.,  STPU=0.,   RPFS'1,2'=0., ...
      ZAMS=0.,   RTAMS=0.,   PUAMS=0.,  RAMS0=0.,RAMS'1,3'=0., ...
      TOMOR=0.,  RTAFS=0.,   PUAFS=0.,  RAFS'1,10'=0., ...
      ZTE=0.,    RTTE=0.,    PUTE=0.,   RTE0=0.,RTE'1,3'=0., ...
      ZTJ=0.,    RTTJ=0.,    PUTJ=0.,   RTJ0=0.,RTJ'1,4'=0., ...
      ZJTS=0.,   RTTJS=0.,   PUTJS=0.,  RTJS0=0.,RTJS'1,2'=0., ...
      ZTSF=0.,   RTTSF=0.,   PUTSF=0.,  RTPSF0=0.,RTPSF'1,2'=0., ...
      ZTSM=0.,   RTTSM=0.,   PUTSM=0.,  RTSM0=0.,RTSM'1,3'=0., ...
      TOMOF=0.,  RTTSFF=0.,  PUTSFF=0., RTAS'1,10'=0.

*         ALL RATES ARE SET TO ZERO WHEN THE PROGRAM STARTS


*         INITIAL CALCULATIONS
*         FOR LOCATION AND TEMPERATURE
INITIAL
      DLONG=AMOD( (LONG+360.)/15.,1.)
*         DLONG IS DIFFERENCE IN HOURS WITH THE STANDARD SOLAR TIME
PARAM LONG=5.

      CSLT =COS(RADL*LAT)
*         COSINE LATITUDE
      SNLT =SIN(RADL*LAT)
*         SINE LATITUDE
PARAM LAT=52.
*         LATITUDE LOCATION
      RADL=PI/180.
CONST PI=3.1415927

      DTEMI=(AFGEN(MXTT,STAR )+AFGEN(MNTT,STAR ) )*0.5
*         INITIAL AVERAGE DAILY TEMPERATURE
      DELX=1./DELT
*         RECIPROCAL OF DELT TO AVOID DIVISIONS


*         INITIAL NUMBERS OF PANONYCHUS ULMI AND
*         OF AMBLYSEIUS POTENTILLAE

INCON TPE=0.
*         EGGS PANONYCHUS ULMI
```

```
INCON IPAFS=4.
*         ADULTS PANONYCHUS ULMI
INCON TAFWI=0.
*         ADULTS AMBLYSEIUS (TYPHLODROMUS) POTENTILLAE

*         SENSITIVITY FACTORS USED AS
*                              MULTIPLICATION FACTORS FOR RATES
PARAM SENB'1,10'=1.
PARAM SENC'1,8'=1.
PARAM SEN'1,33'=1.
PARAM SEN9'1,4'=1.,SE15'1,9'=1.,SE34'1,10'=1.
PARAM SENA'1,10'=1.
PARAM SENF'1,12'=1.
PARAM CHECK=0,10



DYNAMIC

*         TOTAL NUMBERS IN THE DIFFERENT MORPHOLOGICAL STAGES
          PANONYCHUS ULMI

      TPE=E1+E2+E3+E4+E0
*         EGGS
      TPL=J0+J1+.5*J2
*         LARVAE
      TPPC=.5*J2+J3
*         PROTOCHRYSALIS
      TPPN=J4+J5
*         PROTONYMPHAE
      TPDC=J6
*         DEUTOCHRYSALIS
      TPDN=JS0+JS1+JS2
*         DEUTONYMPHAE
      TPIC=JS3+JS4
*         TELEIOCHRYSALIS
      TPAFSO=SUM1(AFS'1,10')
*         ADULT FEMALE OVIPOSITION AND POST-OVIPOSITION
      PAFST=PAFS1+PAFS2
*         ADULT FEMALE PRE-OVIPOSITION
      TPAFS=TPAFSO+PAFST
*         TOTAL ADULT FEMALES
      TPAMS=AMS1+AMS2+AMS3+AMS0
*         TOTAL ADULT MALES

*         AMBLYSEIUS POTENTILLAE

      TTE=TE1+TE2+TE3+TE0
*         EGGS
      TTL=TJ0+TJ1+TJ2
*         LARVAE
      TTPN=TJ3+TJ4
*         PROTONYMPHAE
      TTDN=TJS1+TJS2+TJS0
*         DEUTONYMPHAE
      TTAFS=TASF+TPSF0+TPSF1+TPSF2
*         ADULT FEMALE SUMMER
      TTAMS=TASM1+TASM2+TASM3+TASM0
*         ADULT MALE SUMMER

*         START  TIME AMBLYSEIUS POTENTILLAE AND PANONYCHUS ULMI

      PUSH=IMPULS(STA,FINTIM)
PARAM STA=14.
*         START TIME OF THE PREDATORS AFTER THE START OF THE MODEL
PARAM SPU=0.
*         START TIME P.ULMI
```

```
*******      SECTION 1          ******************************

*         CALCULATIONS OF THE ABIOTIC FACTORS

       DAY=TIME+STAR
*         CALCULATION START DATE
PARAM STAR =140.
*         START TIME OF THE MODEL 140 MEANS 20 MAY
      HOUR=AMOD(TIME,1.)*24.


*         ELEVATION OF SUN

      DEC=-23.45*COS(PI*(DAY+10.)/182.621)
*         DECLINATION OF SUN
      COSDEC=COS(RADL*DEC)
*         COSINE DECLINATION
      SINDEC=SIN(RADL*DEC)
*         SINE DECLINATION
      HA=PI*(HOUR+12.-DLONG)/12.
*         HOUR ANGLE
      SNHSS=SHLT*SINDEC+CSLT*COSDEC*COS(HA)
      SNHS=AMAX1(0.,SNHSS)
*         SINE ELEVATION


*         CALCULATION OF SUNRISE AND SUNSET

PARAM RISEI = 6.5
      RISE=RISEI+ZHOLD(AND(SNHSS,-LSNHS)=0.5,HOUR-SNHSS/ ...
          (NOT(SNHSS-LSNHS)+SNHSS-LSNHS)-RISEI)
*         TIME OF SUNRISE TODAY AND TOMORROW ARE TAKEN TO BE EQUAL
      LSNHS=INTGRL(-0.5,(SNHSS-LSNHS)*DELX)


*         SUN ELEVATION TODAY AT LAST TIME STEP

      DAYL=(12.+DLONG-RISE)*2.+1.
*         CALCULATION OF DAYLENGTH


*         AIR TEMPERATURE IS CALCULATED FROM MINIMUM AND
*         MAXIMUM TEMPERATURE

      MAXT = AFGEN(MXTT,DAY)
      MINT = AFGEN(MNTT,DAY)
      VALAMP = 0.5*(MAXT-MINT)
*         CALCULATION OF AMPLITUDE TEMPERATURE
      VALAV = 0.5*(MAXT+MINT)
*         CALCULATION OF AVERAGE TEMPERATURE
      TIM = INSW(HOUR-14.,HOUR+10.,HOUR-14.)
      VALSR = VALAV-COS(PI*(HOUR-RISE)/(14.-RISE) )*VALAMP
      VALSS = VALAV+COS(PI*TIM/(10.+RISE) )*VALAMP
*         CALCULATION OF VALUE AT SUNRISE AND SUNSET
      TEMP = INSW(AND(HOUR-RISE,14.-HOUR)-0.5,VALSS,VALSR) +SEN
PARAM SEN=0.

      TEMS=INTGRL(0.,TEMP)
*         CALCULATION OF TEMPERATURE SUM
      DTEMD=INTGRL(DTEMI,(TEMP-DTEMD)*.5)
*         CALCULATION FIRST ORDER AVERAGE OF TEMPERATURE WITH
*         A TIME CONSTANT OF 2 DAYS
```

```
*         TEMPERATURE DATA
*         MACRO=METEOROLOGICAL DATA, LIENDEN 1974
FUNCTION MNTT=136.,  .3,137.,  5.5,138.,  7.5,139.,  8.4,140.,12.4,  ...
              141.,11.2,142.,10.2,143.,11.4,144.,10.4,145.,  7.4,  ...
              146.,  5.3,147.,  9.8,148.,10.1,149.,10.5,150.,11.3,  ...
              151.,11.5,152.,10.4,153.,  6.1,154.,  7.4,155.,  6.0,  ...
              156.,  4.3,157.,  5.2,158.,  7.4,159.,  9.3,160.,  9.3,  ...
              161.,12.  ,162.,  7.2,163.,  4.5,164.,  5.4,165.,  1.6,  ...
              166.,  2.7,167.,  6.5,168.,10.  ,169.,11.4,170.,  7.3,  ...
              171.,14.1,172.,14.8,173.,11.9,174.,11.9,175.,13.2,  ...
              176.,11.8,177.,13.3,178.,17.8,179.,15.4,180.,12.4,  ...
              181.,10.  ,182.,11.6,183.,16.5,184.,12.8,185.,11.2,  ...
              186.,13.8,187.,15.5,188.,15.4,189.,10.9,190.,  6.6,  ...
              191.,  7.5,192.,14.4,193.,14.1,194.,13.3,195.,12.1,  ...
              196.,13.7,197.,13.7,198.,10.7,199.,10.7,200.,13.1,  ...
              201.,13.4,202.,12.5,203.,11.7,204.,  8.6,205.,  7.4,  ...
              20 6.,6.5,207.,12.4,208.,12.4,209.,14.3,210.,14.7,  ...
              211.,11.8,212.,11.8,213.,12.1,214.,13.4,215.,10.4,  ...
              216.,14.2,217.,12.5,218.,14.2,219.,12.5,220.,11.4,  ...
              221.,  6.9,222.,  8.2,223.,13.6,224.,12.5,225.,12.4,  ...
              226.,13.6,227.,14.4,228.,14.4,229.,12.3,230.,16.5,  ...
              231.,14.4,232.,11.8,233.,  6.8,234.,  2.9,235.,  8.7,  ...
              236.,  8.2,237.,  8.  ,238.,  8.9,239.,  8.5,240.,13.4,  ...
              241.,  9.8,242.,11.4,243.,  5.6,244.,13.7,245.,15.2,  ...
              246.,12.6,247.,10.3,248.,11.7,249.,13.7,250.,12.4,  ...
              251.,  9.5,252.,13.7,253.,11.4,254.,  5.5,255.,  3.  ,  ...
              256.,  6.7,257.,  3.8,258.,  8.3,259.,12.3,260.,11.  ,  ...
              261.,13.5,262.,12.5,263.,11.5,264.,11.1,265.,11.3,  ...
              266.,  5.2,267.,  3.8,268.,  6.8,269.,  4.4,270.,  8.6,  ...
              271.,11.2,272.,  7.7,273.,  7.7

*         MINIMUM TEMPERATURE
FUNCTION MXTT=136.,14.4,137.,17.8,138.,19.3,139.,20.2,140.,22.3,  ...
              141.,23.2,142.,20.7,143.,19.8,144.,15.2,145.,19.2,  ...
              146.,21.1,147.,22.5,148.,24.2,149.,18.7,150.,16.2,  ...
              151.,20.  ,152.,15.1,153.,13.5,154.,18.2,155.,17.6,  ...
              156.,17.7,157.,20.1,158.,19.  ,159.,20.2,160.,23.1,  ...
              161.,18.6,162.,18.8,163.,23.7,164.,19.5,165.,17.9,  ...
              166.,21.7,167.,23.1,168.,28.7,169.,23.3,170.,26.  ,  ...
              171.,26.4,172.,23.6,173.,23.7,174.,24.3,175.,26.  ,  ...
              176.,27.2,177.,29.2,178.,29.6,179.,23.5,180.,22.4,  ...
              181.,25.4,182.,29.2,183.,30.0,184.,24.2,185.,27.8,  ...
              186.,29.9,187.,26.6,188.,21.  ,189.,20.5,190.,21.3,  ...
              191.,23.9,192.,19.8,193.,20.6,194.,21.8,195.,23.9,  ...
              196.,19.3,197.,22.2,198.,19.8,199.,19.4,200.,20.3,  ...
              201.,19.6,202.,18.9,203.,18.8,204.,17.8,205.,19.7,  ...
              206.,19.1,207.,16.3,208.,15.3,209.,23.7,210.,19.5,  ...
              211.,18.  ,212.,21.7,213.,26.8,214.,26.2,215.,20.1,  ...
              216.,20.7,217.,19.4,218.,28.8,219.,19.7,220.,19.3,  ...
              221.,22.1,222.,26.6,223.,27.2,224.,25.6,225.,26.7,  ...
              226.,27.8,227.,27.9,228.,29.7,229.,28.8,230.,23.7,  ...
              231.,23.9,232.,23.2,233.,20.6,234.,20.3,235.,24.2,  ...
              236.,22.3,237.,22.9,238.,23.8,239.,26.2,240.,22.2,  ...
              241.,21.7,242.,18.1,243.,18.2,244.,20.3,245.,19.7,  ...
              246.,23.1,247.,26.2,248.,28.7,249.,20.3,250.,23.9,  ...
              251.,25.8,252.,20.  ,253.,18.2,254.,17.9,255.,18.4,  ...
              256.,19.1,257.,21.6,258.,24.1,259.,23.3,260.,25.  ,  ...
              261.,21.1,262.,17.6,263.,19.8,264.,19.9,265.,15.7,  ...
              266.,15.4,267.,15.2,268.,16.2,269.,17.1,270.,17.9,  ...
              271.,17.4,272.,12.5,273.,12.7
*         MAXIMUM TEMPERATURE
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*******      SECTION 2      ******************************

*        CALCULATIONS FOR PANONYCHUS ULMI

CONST SRP=.66
*        THE SEX RATIO IS A FIXED FACTOR

*        DIAPAUSE CONDITIONS

PROCED G=DAGLE(DAYL,DTEMD)
      IF (DAYL,GE,14,) GO TO 8
      IF (DTEMD,LT,14,) GO TO 1
      IF (DTEMD,LT,18,) GO TO 2
      IF (DTEMD,LT,21,) GO TO 3
      GO TO 4
    8 IF (DAYL,GE,15,) GO TO 9
      IF (DTEMD,LT,8,0) GO TO 1
      IF (DTEMD,LT,12,) GO TO 2
      IF (DTEMD,LT,18,) GO TO 3
      GO TO 4
    9 IF (DAYL,GE,17,) GO TO 6
      IF (DTEMD,LT,8,0) GO TO 3
      IF (DTEMD,LT,11,) GO TO 5
      GO TO 6
    1 G=1,00
      GO TO 7
    2 G=0,85
      GO TO 7
    3 G=0,50
      GO TO 7
    4 G=0,20
      GO TO 7
    5 G=0,35
      GO TO 7
    6 G=0,00
      GO TO 7
    7 CONTINUE
ENDPRO
      F=1,-G
*        F IS THE FRACTION OF JUVENILES FOR THE SUMMER FORMS AND
*        G IS THE FRACTION FOR THE WINTER FORMS

*     EGG STAGE PANONYCHUS ULMI

*        FOR THE SUMMER EGG OF PANONYCHUS ULMI
*        FOUR AGE CLASSES ARE DISTINGUISHED, THE METHOD OF
*        CONTROLLED DISPERSION IS APPLIED

PROCED DEJU=EGGPU(TEMP)
PARAM SL'1,10'=,19,,166,,17,,15,,132,,11,,096,,09,,084,,082
*        SLOPE OF LINEAR RELATION BETWEEN TEMPERATURE AND OVIPOSITION
*        RATE PER DAY, FOR EACH OF THE 10 AGE CLASSES
      FP'1,10'=AMAX1(0.,SL'1,10'*(TEMP-7,5) ) *SENA'1,10'
*        CALCULATION OF OVIPOSITION RATE PER AGE CLASS
      F1=SUMX(AFS'1,10',FP'1,10')
*        OVIPOSITION RATE
      LOLE=AFGEN(LOLET,TEMP) *SEN1
*        LONGEVITY EGGS
      EKO=(AFGEN(SDET,TEMP)/LOLE)**2 *SEN2
*        SQUARE OF THE RELATIVE DISPERSION
      RTE=LOLE/4.
*        RESIDENCE TIME PER AGE CLASS
      ZE=AMAX1(DELT/RTE,1.-4.*EKO)
*        FRACTION OF EGGS THAT IS SHIFTED
      PUSHE=INS*(GSE-1.,0.,1.)
*        TIME OF SHIFTING
      GSE=INTGRL(0.5,1./(ZE*RTE)-PUSHE*DELX)
*        DEVELOPMENT STAGE OF EGGS
      EMOR'1,4'=AFGEN(DMIB1,TEMP) *SEN3
```

```
*       RELATIVE RATE OF ABIOTIC MORTALITY
      FER1=2.*E0*(1.-EMOR1*DELT)/(RTE*2E)
      FER*2,5*=PUSHE*ZF*E*1,4*+(DELX-EMOR*1,4*)*INSW(E*1,4*-CHECK,0.,1.)
      ER0=F1-(FER1+E0*EMOR1)*INSW(E0-CHECK,0.,1.)
      ER*1,4*=(FER*1,4*-FER*2,5*-EMOR*1,4**E*1,4*)
*       RATES OF TRANSFER
      E0=INTGRL(0.,ER0)
      E*1,4*=INTGRL(0.,ER*1,4*)
*       NUMBER PER AGE CLASS
      DEJU=FERS
*       HATCHING RATE
ENDPRO

*       JUVENILE STAGE,LARVAE,PROTOCHRYSALIS,PROTONYMPAE,DEUTOCHRYSALIS
*       FOR THE JUVENILE PERIOD UP TO THE DEUTONYMPH STAGE
*       SIX AGE CLASSES ARE DISTINGUISHED
PROCED DEJUS=JUVPU(DEJU,PRED1,PRED2,PRED3,PRED4,PRED5,PRED9,F,TEMP)
      PRMO1=PRED1+PRED2+PRED3+PRED4
      PRMO2=PRMO1*.5
PARAM PRMO3=0.
      PRMO*4,5*=PRED5+PRED6+PRED7
*       RELATIVE PREDATION RATES, ALL PREDATORS INCLUDED
PARAM PRMO6=0.
      LOLJ=AFGEN(LOLJT,TEMP) *SEN4
*       LONGEVITY JUVENILES
      JK0=(AFGEN(SDJT,TEMP)/LOLJ)**2 *SEN5
*       SQUARE OF THE RELATIVE DISPERSION
      RTJ=LOLJ/6.
*       RESIDENCE TIME PER AGE CLASS
      ZJ=AMAX1(DELT/RTJ,1.-6.*JK0)
*       FRACTION THAT IS SHIFTED
      PUSHJ=INSW(GSJ-1.,0.,1.)
*       TIME OF SHIFTING
      GSJ=INTGRL(0.5,1./(ZJ*RTJ)-PUSHJ*DELX)
*       DEVELOPMENT STAGE
      JMOR*1,6*=(AFGEN(DMIB*2,7*,TEMP)+PRMO*1,5*7 *SEN6
*       RELATIVE MORTALITY RATE
      FJR1=2.*J0*(1.-JMOR1*DELT)/(RTJ*ZJ)
      FJR*2,7*=PUSHJ*ZJ*J*1,6*+(DELX-JMOR*1,6*)*INSW(J*1,6*-CHECK,0.,1.)
      JR0=DEJU-(FJR1+JMOR1*J0)+INSW(J0-CHECK,0.,1.)
      JR*1,6*=(FJR*1,6*-FJR*2,7*-JMOR*1,6**J*1,6*)
*       RATES OF TRANSFER
      J0=INTGRL(0.,JR0)
      J*1,6*=INTGRL(0.,JR*1,6*)
*       NUMBER OF ANIMALS PER AGE CLASS
      DEJUS=FJR7
*       RATE OF TRANSFER TO JUVENILES SUMMER
ENDPRO

*       JUVENILE STAGE SUMMER,DEUTONYMPH,TELEIOCHRYSALIS
*       THE CALCULATION FOR THE JUVENILES SUMMER ARE SIMILAR TO
*       THOSE FOR THE EGGS AND THE JUVENILES
PROCED DEANS=DEADP=JUSPU(PRED9,PRED8,DEJUS,TEMP)
PARAM PRMO9=0.,PRMO10=0.
      PRMO*7,8*=PRED8+PRED9
      LOLJS=AFGEN(LOLJST,TEMP) *SEN7
      JSK0=(AFGEN(SDJST,TEMP)/LOLJS)**2 *SEN8
      RTJS=LOLJS/4.
      ZJS=AMAX1(DELT/RTJS,1.-4.*JSK0)
      PUSHJS=INSW(GSJS-1.,0.,1.)
      GSJS=INTGRL(0.5,1./(ZJS*RTJS)-PUSHJS*DELX)
      JSMR*1,4*=(AFGEN(DMST1,TEMP)+PRMO*7,10*) *SEN9*1,4*
      FJSR1=Z.*JS0*(1.-JSMR1*DELT)/(RTJS*ZJS)
      FJSR*2,5*=PUSHJS*ZJS*JS*1,4*+(DELX-JSMR*1,4*)* ...
      INSW(JS*1,4*-CHECK,0.,1.)
      JSR0=DEJUS*F-(FJSR1+JSMR1*JS0)*INSW(JS0-CHECK,0.,1.)
      JSR*1,4*=(FJSR*1,4*-FJSR*2,5*-JSMR*1,4**JS*1,4*)
      JS0=INTGRL(0.,JSR0)
      JS*1,4*=INTGRL(0.,JSR*1,4*)
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      DEADP=SRP*FJSR5*INSW(JS4-CHECK,0.,1.)
      DEAMS=(1.-SRP)*FJSR5*INSW(JS1-CHECK,0.,1.)
ENDPRO

*        ADULT FEMALE STAGE SUMMER, PRE-OVIPOSITION

*        THE ADULT FEMALE PRE-OVIPOSITION IS SIMULATED WITH THE
*        MODEL OF 'CONTINUOUS' SIMULATION BECAUSE
*        OF THE CONSTANCY OF THE RELATIVE DISPERSION AT
*        VARIOUS TEMPERATURES

PROCED DEAFS,STPU=PAFPU(DEADP,PRED12,TEMP)
      PRMO'11,12'=PRED12
      LOPAFS=AFGEN(LOPAFT,TEMP) *SEN10
      RTPAFS=LOPAFS/2.
      FPFS1=DEADP
      AFPM'1,2'=PAFS'1,2'*(AFGEN(DMPFT,TEMP)+PRMO'11,12') *SEN11
      FPFS'2,3'=(PAFS'1,2'-AFPM'1,2'*DELT)/RTPAFS* ...
      INSW(PAFS'1,2'-CHECK,0.,1.)
      RPFS'1,2'=FPFS'1,2'-FPFS'2,3'-AFPM'1,2'
      STPU=IMPULS(SPU,FINTIM)
      PAFS1=INTGRL(0.,RPFS1+IPAFS*STPU*DELX)
      PAFS2=INTGRL(0.,RPFS2)
      DEAFS=FPFS3
ENDPRO

*        ADULT FEMALE STAGE, WINTER

*        WINTER FEMALES ARE ACCUMULATED,WINTER MALES ARE NOT CONSIDERED
      PAFW=INTGRL(0.,SRP*DEJUS*G-PAFW/LOPAFW)
PARAM LOPAFW=30.
      WEP=INTGRL(0.,AMAX1(0.,(TEMP-7.5)*.167)*PAFW)
*        NUMBER OF WINTER EGGS

*        ADULT MALE, SUMMER

PROCED AMSO=AMSPU(TEMP,DEAMS,PRED10,PRED11)
      LOAMS=AFGEN(LOAMST,TEMP) *SEN12
      AMSKO=(AFGEN(SDAMST,TEMP)/LOAMS)**2 *SEN13
      RTAMS=LOAMS/3.
      ZAMS=AMAX1(DELT/RTAMS,1.-3*AMSKO)
      PUAMS=INSW(GSAMS-1.,0.,1.)
      GSAMS=INTGRL(0.5,1./(ZAMS*RTAMS)-PUAMS*DELX)
      VM'1,3'=INSW(AMS'1,3'-CHECK,0.,1.)
      AMSMR=PRED10+PRED11
      FRMS1=2.*AMSO*(1.-AMSMR*DELT)/(RTAMS*ZAMS)
      FRMS'2,4'=PUAMS*ZAMS*AMS'1,3'*(DELX-AMSMR)* ...
      INSW(AMS'1,3'-CHECK,0.,1.)
      RAMSO=DEAMS-(FRMS1+AMSMR*AMSO)*INSW(AMSO-CHECK,0.,1.)
      RAMS'1,3'=(FRMS'1,3'-FRMS'2,4'-AMSMR*AMS'1,3')
      AMSO=INTGRL(0.,RAMSO)
      AMS'1,3'=INTGRL(0.,RAMS'1,3')
ENDPRO

*        ADULT FEMALE SUMMER, OVIPOSITION AND POST OVIPOSITION

*        THE AGEING OF THE ADULT FEMALES IS SIMULATED WITH THE
*        BOXCAR METHOD WITHOUT DISPERSION, ONLY THEN CAN THE AGE
*        DEPENDENCY OF OVIPOSITION BE CORRECTLY ACCOUNTED FOR

PROCED TOMOR=AGAFPU(TEMP,PRED12,DEAFS,TASF)
      LOAFS=AFGEN(LOAFST,TEMP) *SEN14
      RTAFS=LOAFS/10.
      PUAFS=INSW(GSAFS-1.,0.,1.)
      GSAFS=INTGRL(0.0,1./RTAFS-PUAFS*DELX)
      PRMO'13,17'=PRED12
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PARAM PRMO'10,22'=0,
      VV'8,17'=INSW(AFS'1,10'-CHECK,0.,1.)
      FMOR'1,9'=(AFGEN(DMFF'1,9',TEMP)+PRMO'13,21')*AFS'1,9'*SE15'1,9'
      FMOR10=PRMO22*AFS10
      TOMOR=SUM1(FMOR'1,10')
      TOMORT=INTGRL(0.,TOMOR)
      FAFS1=DEAFS
      FAFS'2,11'=PUAFS=(AFS'1,10'*DELX-FMOR'1,10')*VV'8,17'
      RAFS'1,10'=(FAFS'1,10'-FAFS'2,11'-FMOR'1,10')
      AFS'1,10'=INTGRL(0.,RAFS'1,10')
ENDPRO

*******      SECTION 3          **********************

*       AMBLYSEIUS POTENTILLAE
*       SEX RATIO IS A FIXED FACTOR
PARAM SRTS=.33,SRT=.67

*       THE CALCULATIONS OF DEVELOPMENT, AGEING AND REPRODUCTION
*       ARE SIMILAR TO THOSE FOR THE FRUIT-TREE RED SPIDER MITE
*       FURTHER COMMENTS ON THESE CALCULATIONS ARE THEREFORE OMITTED

*       THE NUMERICAL RESPONSE OF THE PREDATOR DEPENDS ON
*       THE COLOUR LEVEL OF THE VARIOUS STAGES

      NUMR1=AFGEN(NUMR1T,CAF) *SEN16
AFGEN NUMR1T=0.,.2,1.,.4,2.,.55,3.,.65,4.,.7,5.,.85,6.,1.,7.,1.3
*       COLOUR LEVEL DEPENDENCY OF OVIPOSITION RATE
AFGEN NUMR2T=0.,2.6,1.,2.1,2.,1.5,3.,1.2,4.,1.,7.,1.
*       DELAY OF DEVELOPMENT JUVENILES IN DEPENDENCE OF
*       THEIR COLOUR LEVEL
AFGEN NUMR3T=0.,2.6,1.,2.1,2.,1.5,3.,1.2,4.,1.,7.,1.
*       DELAY OF DEVELOPMENT JUVENILES SUMMER IN DEPENDENCE OF
*       THEIR COLOUR LEVEL
AFGEN NUMR4T=0.,6.,1.,2.6,2.,1.3,3.,1.2,4.,1.,7.,1.
*       DELAY OF MATURING IN DEPENCE OF COLOUR LEVEL

*       REPRODUCTION PREDATOR

      FT'1,10'=AFGEN(FETT'1,10',TEMP)*NUMR1 *SENB'1,10'
      FT=SUMX(FT'1,10',TASF'1,10')
*       THE SCALAR PRODUCT OF RELATIVE OVIPOSITION RATES AND THE
*       THE NUMBER OF FEMALES PER AGE CLASS TO CALCULATE THE
*       OVIPOSITION RATE
*       EGG STAGE

PROCED DETE=EGGTP(TEMP,FT)
      LOTTE=AFGEN(LOTTET,TEMP) *SEN18
      RTTE=LOTTE/3.
      TEKO=(AFGEN(SDTE,TEMP)/LOTTE)**2 *SEN19
      ZTE=AMAX1(DELT/RTTE,1.=3.=TEKO)
      PUTE=INSW(GTE-1.,0.,1.)
      GTE=INTGRL(0.5,1./(ZTE*RTTE)=PUTE*DELX)
      VVT'1,3'=INSW(TE'1,3'-CHECK,0.,1.)
      MRTE'1,3'=AFGEN(MTE1,TEMP) *SEN20
      FRTE1=2.*TE0*(1.-MRTE1*DELT)/(ZTE*RTTE)
      FRTE'2,4'=PUTE*ZTE*TE'1,3'*(DELX-MRTE'1,3')*VVT'1,3'
      RTE0=FT-(FRTE1+MRTE1*TE0)*INSW(TE0-CHECK,0.,1.)
      RTE'1,3'=(FRTE'1,3'-FRTE'2,4'*MRTE'1,3'*TE'1,3')
      TE0=INTGRL(0.,RTE0)
      TE'1,3'=INTGRL(0.,RTE'1,3')
      DETE=FRTE4
ENDPRO
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*         JUVENILE STAGE

PROCED DETJ=JUVTP(TEMP,DETE)
       NUMR2=AFGEN(NUMR2T,CPN) *SEN21
       LOTJ =AFGEN(LOTJT,TEMP)*NUMR2 *SEN22
       TJKO=(AFGEN(SDTJT,TEMP)/LOTJ)**2 *SEN23
       RTTJ =LOTJ/4.
       ZTJ  =AMAX1(DELT/RTTJ,1.-4.*TJKO)
       PUTJ =INSW(GTJ-1.,0.,1.)
       GTJ  =INTGRL(0.5,1./(ZTJ*RTTJ)-PUTJ*DELX)
       VVT*4,7*=INSW(TJ*1,4*-CHECK,0.,1.)
       MRTJ*1,4*=AFGEN(MTJ*1,4*,TEMP) *SEN24
       FRTJ1=2.*TJ0*(1.-MRTJ1*DELT)/(ZTJ*RTTJ)
       FRTJ*2,5*=PUTJ*ZTJ*TJ*1,4*-(DELX-MRTJ*1,4*)*VVT*4,7*
       RTJ0=DETE-(FRTJ1+MRTJ1+TJ0)*INSW(TJ0-CHECK,0.,1.)
       RTJ*1,4*=(FRTJ*1,4*-FRTJ*2,5*-MRTJ*1,4**TJ*1,4*)
       TJ0=INTGRL(0.,RTJ0)
       TJ*1,4*=INTGRL(0.,RTJ*1,4*)
       DETJ=FRTJ5
ENDPRO


*         JUVENILE STAGE, SUMMER

PROCED DETJS=JUSTP(TEMP,DETJ,F)
       NUMR3=AFGEN(NUMR3T,CDN) *SEN25
       LOTJS =AFGEN(LOTJST,TEMP)*NUMR3 *SEN26
       RTTJS =LOTJS/2.
       TJSKO=(AFGEN(SDTJST,TEMP)/LOTJS)**2
       ZTJS  =AMAX1(DELT/RTTJS,1.-2.*TJSKO)
       PUTJS =INSW(GTJS-1.,0.,1.)
       GTJS  =INTGRL(0.5,1./(ZTJS*RTTJS)-PUTJS*DELX)
       VVT*8,9*=INSW(TJS*1,2*-CHECK,0.,1.)
       MRJS*1,2*=AFGEN(MTJS1,TEMP)
       FTJS1=2.*TJS0*(1.-MRJS1*DELT)/(ZTJS*RTTJS)
       FTJS*2,3*=PUTJS*ZTJS*TJS*1,2**(DELX-MRJS*1,2*)*VVT*8,9*
       RTJS0=DETJ*F-(FTJS1+MRJS1*TJS0)*INSW(TJS0-CHECK,0.,1.)
       RTJS*1,2*=(FTJS*1,2*-FTJS*2,3*-MRJS*1,2**TJS*1,2*)
       TJS0=INTGRL(0.,RTJS0)
       TJS*1,2*=INTGRL(0.,RTJS*1,2*)
       DETJS=FTJS3
ENDPRO


*         ADULT FEMALE WINTER

       TAWF=INTGRL(0.,DETJ*G*SRT-TAWF/50.)
*           THE WINTER FEMALES ARE ACCUMULATED, WINTER JUVENILES ARE
*           NOT CONSIDERED


*         ADULT FEMALE STAGE SUMMER, PRE-OVIPOSITION

PROCED DEATFS=PROVTP(TEMP,DETJS,SRT,PUSH)
PARAM TASFI=1.
       NUMR4=AFGEN(NUMR4T,CAF) *SEN28
       LOTSF=AFGEN(LOTSFT,TEMP)*NUMR4 *SEN29
       TSFKO=(AFGEN(SDPSFT,TEMP)/LOTSF)**2 *SEN30
       RTTSF=LOTSF/2.
       PUTSF =INSW(GTSF-1.,0.,1.)
       GTSF  =INTGRL(0.5,1./(ZTSF*RTTSF)-PUTSF*DELX)
       ZTSF=AMAX1(DELT/RTTSF,1.-2.*TSFKO)
       VVT*10,11*=INSW(TPSF*1,2*-CHECK,0.,1.)
       MTPSF1=AFGEN(MTSF1,TEMP)
       MTPSF2=MTPSF1
       FTPSF1=2.*TPSF0*(1.-MTPSF1*DELT)/(RTTSF*ZTSF)
       FTPSF2=PUTSF*ZTSF*TPSF1*(DELX-MTPSF1)*VVT10
       FTPSF3=PUTSF*ZTSF*TPSF2*(DELX-MTPSF2)*VVT11
       RTPSF0=SRT*DETJS-(FTPSF1+MTPSF1*TPSF0)*INSW(TPSF0-CHECK,0.,1.)
       RTPSF1=(FTPSF1-FTPSF2-MTPSF1*TPSF1)
       RTPSF2=(FTPSF2-FTPSF3-MTPSF2*TPSF2)
       TPSF0=INTGRL(0.,RTPSF0+PUSH*TASFI*DELX)
       TPSF1=INTGRL(0.,RTPSF1)
       TPSF2=INTGRL(0.,RTPSF2)
       DEATSF=FTPSF3
ENDPRO
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*         ADULT MALE SUMMER
PROCED TASMO=AGTAMS(TEMP,SRTS,DETJS)
       LOTSM =AFGEN(LOTSMT,TEMP) *SEN31
       TSMKO=(AFGEN(SDTSMT,TEMP)/LOTSM)**2 *SEN32
       RTTSM =LOTSM/3.
       ZTSM  =AMAX1(DELT/RTTSM,1.-3.*TSMKO)
       PUTSM =INSW(GTSM-1.,0.,1.)
       GTSM  =INTGRL(0.5,1./(ZTSM*RTTSM)-PUTSM*DELX)
       FTSM1=2.*TASMO/(RTTSM*ZTSM)
       FTSM'2,4'=PUTSM*ZTSM*TASM'1,3'*DELX*INSW(TASM'1,3'-CHECK,0.,1.)
       RTSMO=SRTS*FTJS3-FTSM1*INSW(TASMO-CHECK,0.,1.)
       RTSM'1,3'=(FTSM'1,3'-FTSM'2,4')
       TASMO=INTGRL(0.,RTSMO)
       TASM'1,3'=INTGRL(0.,RTSM'1,3')
ENDPRO

*         ADULT FEMALE STAGE, 10 CLASSES SUFFICE TO DESCRIBE THE
*                             AGEING AND OVIPOSITION PROCESS CORRECTLY

*         THE AGEING OF FEMALES IS SIMULATED WITH THE BOXCAR METHOD
*         WITHOUT DISPERSION
PROCED TOMORF,TASF=AGTAFS(TEMP,DEATSF)
       LOTSFF=AFGEN(LOTFFT,TEMP) *SEN33
       RTTSFF=LOTSFF/10.
       GTSFF=INTGRL(0.,1./RTTSFF-PUTSFF*DELX)
       PUTSFF=INSW(GTSFF-1.,0.,1.)
       VVT'12,21'=INSW(TASF'1,10'-CHECK,0.,1.)
       MASF'1,10'=TASF'1,10'*AFGEN(MRFT'1,10',TEMP)*SE34'1,10'
       FTAS1=DEATSF
       FTAS'2,11'=PUTSFF*(TASF'1,10'*DELX-MASF'1,10')+VVT'12,21'
       RTAS'1,10'=(FTAS'1,10'-FTAS'2,11'-MASF'1,10')
       TOMOF=SUM1(MASF'1,10')
       TOMORF=INTGRL(0.,TOMOF)
       TASF'1,10'=INTGRL(0.,RTAS'1,10')
       TASF=SUM1(TASF'1,10')
ENDPRO

*******      SECTION 4      ****************************

*         PREDATION PROCESS

*         THE COLOUR LEVELS OF THE PREDATOR ARE LOWER BOUNDED
PARAM UL'1,4'=0.

*         CALCULATIONS FOR THE ADULT FEMALE PREDATOR

       INCAF=(PV1* PRED1 *TPL +PV2*PRED5 *TPPN ...
            +PV3*(PRED8 *TPDN+    PRED10*TPAMS) ...
            +PV4* PRED12*TPAFS)  *SENC1
       PV'1,4'=AFGEN(PVT'1,4',CAF)
*         CTAF,CAF,DECAF,RATE1,EQT1= ...
*         PRAEDA(UL1,TTAFS,RDCV1,SENC2,INCAF,EQTI1)
       CTAF=1./CAF
       CAF=LIMIT(UL1,7.,EQT1/(NOT(TTAFS)+TTAFS) )
       DECAF=AFGEN(RDCV1,TEMP)*INSW(EQT1-CHECK,0.,EQT1) *SENC2
       RATE1=INSW(EQT1+(INCAF-DECAF)*DELT,-EQT1*DELX,INCAF-DECAF)
       EQT1=INTGRL(0.,EQTI1*PUSH*DELX+RATE1)
PARAM EQTI'1,4'=5.

*         CALCULATIONS FOR THE DEUTONYMPHAE PREDATOR

       INCDN=(PV5*PRED2*TPL+PV6*PRED6*TPPN) *SENC3
       PV'5,6'=AFGEN(PVT'2,3',CDN)
*         CTDN,CDN,DECDN,RATE2,EQT2= ...
*         PRAEDA(UL2,TTDN,RDCV2,SENC4,INCDN,EQTI2)
       CTDN=1./CDN
       CDN=LIMIT(UL2,7.,EQT2/(NOT(TTDN)+TTDN) )
       DECDN=AFGEN(RDCV2,TEMP)*INSW(EQT2-CHECK,0.,EQT2) *SENC4
       RATE2=INSW(EQT2+(INCDN-DECDN)*DELT,-EQT2*DELX,INCDN-DECDN)
       EQT2=INTGRL(0.,EQTI2*PUSH*DELX+RATE2)
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*       CALCULATIONS FOR THE PROTONYMPHAL PREDATOR
      INCPN=PV7*PRED3*TPL *SENC5
      PV7=AFGEN(PVT3,CPN)
*        CTPN,CPN,DECPN,RATE3,EQT3= ...
*        PRAEDA(UL3,TTPN,RDCV3,SENC6,INCPN,EQTI3)
      CTPN=1./CPN
      CPN=LIMIT(UL3,7.,EQT3/(NOT(TTPN)+TTPN) )
      DECPN=AFGEN(RDCV3,TEMP)*INSW(EQT3-CHECK,0.,EQT3) *SENC6
      RATE3=INSW(EQT3+(INCPN-DECPN)*DELT,-EQT3*DELX,INCPN-DECPN)
      EQT3=INTGRL(0.,EQTI3*PUSH*DELX+RATE3)

*       CALCULATIONS FOR THE ADULT MALE PREDATOR

      INCAM=(PV8 *PRED4*TPL +PV9 *PRED7 *TPPN ...
          +PV10*PRED9*TPDN+PV11*PRED11*TPAMS) *SENC7
      PV8,10=AFGEN(PVT2,4,CAM)
      PV11=PV10
*        CTAM,CAM,DECAM,RATE4,EQT4= ...
*        PRAEDA(UL4,TTAMS,RDCV2,SENC8,INCAM,EQTI4)
      CTAM=1./CAM
      CAM=LIMIT(UL4,7.,EQT4/(NOT(TTAMS)+TTAMS) )
      DECAM=AFGEN(RDCV2,TEMP)*INSW(EQT4-CHECK,0.,EQT4) *SENC8
      RATE4=INSW(EQT4+(INCAM-DECAM)*DELT,-EQT4*DELX,INCAM-DECAM)
      EQT4=INTGRL(0.,EQTI4*PUSH*DELX+RATE4)

*       CALCULATION OF THE RELATIVE PREDATION RATES

      PRED1 =TWOVAR(RRL11,8,AY,XY1 ,CTAF,TEMP,I1 )*TTAFS*CFS*SENP1
      PRED2 =TWOVAR(RRL11,8,AY,XY2 ,CTDN,TEMP,I2 )*TTDN *CFS*SENP2 *RF1
      PRED3 =TWOVAR(RRL11,8,AY,XY3 ,CTPN,TEMP,I3 )*TTPN *CFS*SENP3 *RF2
      PRED4 =TWOVAR(RRL11,8,AY,XY4 ,CTAM,TEMP,I4 )*TTAMS*CFS*SENP4 *RF3
      PRED5 =TWOVAR(RRP11,8,AY,XY5 ,CTAF,TEMP,I5 )*TTAFS*CFS*SENP5
      PRED6 =TWOVAR(RRP11,8,AY,XY6 ,CTDN,TEMP,I6 )*TTDN *CFS*SENP6 *RF4
      PRED7 =TWOVAR(RRP11,8,AY,XY7 ,CTAM,TEMP,I7 )*TTAMS*CFS*SENP7 *RF5
      PRED8 =TWOVAR(RRD11,8,AY,XY8 ,CTAF,TEMP,I8 )*TTAFS*CFS*SENP8
      PRED9 =TWOVAR(RRD11,8,AY,XY9 ,CTAM,TEMP,I9 )*TTAMS*CFS*SENP9 *RF6
      PRED10=TWOVAR(RRD11,8,AY,XY10,CTAF,TEMP,I10)*TTAFS*CFS*SENP10*RF7
      PRED11=TWOVAR(RRAF1,8,AY,XY11,CTAM,TEMP,I11)*TTAMS*CFS*SENP11*RF8
      PRED12=TWOVAR(RRAF1,8,AY,XY12,CTAF,TEMP,I12)*TTAFS*CFS*SENP12

*       MULTIPLICATION FACTORS OF THE RELATIVE PREDATION RATES,
*       THE JUVENILE PREDATION ACTIVITY IS RELATED TO THE
*       EXPERIMENTALLY DETERMINED RELATIONS FOR THE ADULT FEMALE
*       PREDATOR. THESE FACTORS ARE THE VALUES OF THE QUOTIENT OF
*       PREDATOR SIZE TO PREY SIZE RELATED TO THOSE VALUES FOR THE
*       ADULT FEMALE PREDATOR. THESE FACTORS RANGE FROM 0.33 TO 1.00
*       AND ARE VERY REGULAR DUE TO THE ALLOMETRIC GROWTH OF
*       BOTH PREY AND PREDATOR

PARAM RF1=.66,RF2=.33,RF3=.66,RF4=.66,RF5=.66,RF6=.33,RF7=1.,RF8=1.

*******     SECTION 5     ********************************

*       QUANTITATIVE RELATIONS
*       DATA PREDATION

*       DATA RELATIVE RATE OF PREDATION DEPENDENT ON
*       TEMPERATURE AND DAYLENGTH

FUNCTION RRL11=0.,0.,7.5,0. ,10.,0. ,13.,.1 ,15.,.3 ,20.,1.  ,...
      25.,1.7 ,30.,2.  ,33.,1.7
FUNCTION RRL12=0.,0.,7.5,0. ,10.,.1 ,13.,.5 ,15.,1.2,20.,2.4 ,...
      25.,3.5 ,30.,4.  ,33.,3.5
FUNCTION RRL13=0.,0.,7.5,0. ,10.,.2 ,13.,.6 ,15.,2.1,20.,5.3 ,...
      25.,8.8 ,30.,10. ,33.,6.8
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FUNCTION RRL14=0.,0.,7.5,0. ,10.,.2 ,13.,.8 ,15.,.2.8,20.,7.9 ,...
      25.,12.1,30.,14. ,33.,12.1
FUNCTION RRL15=0.,0.,7.5,0. ,10.,.2 ,13.,.9 ,15.,.3.2,20.,9.8 ,...
      25.,16.4,30.,18. ,33.,16.4
FUNCTION RRL16=0.,0.,7.5,0. ,10.,.2 ,13.,1.2,15.,3.4,20.,10.8 ,...
      25.,18.4,30.,20. ,33.,18.4
FUNCTION RRL17=0.,0.,7.5,0. ,10.,.4 ,13.,1.6,15.,3.6,20.,12.2 ,...
      25.,20.8,30.,23. ,33.,20.8
FUNCTION RRL18=0.,0.,7.5,0. ,10.,.4 ,13.,1.6,15.,3.6,20.,12.6 ,...
      25.,22. ,30.,24. ,33.,22.
*       DATA LARVAE P.ULMI VERSUS ADULT FEMALE A.POTENTILLAE
FUNCTION RRP11=0.,0.,7.5,0. ,10.,.1 ,13.,.5 ,15.,.75,20.,1.4 ,...
      25.,2.  ,30.,2.5 ,33.,2.
FUNCTION RRP12=0.,0.,7.5,0. ,10.,.25,13.,.9 ,15.,1.4,20.,2.6 ,...
      25.,3.8 ,30.,4.5 ,33.,3.8
FUNCTION RRP13=0.,0.,7.5,0. ,10.,.4 ,13.,1.2,15.,2. ,20.,4.4 ,...
      25.,6.4 ,30.,7.5 ,33.,6.4
FUNCTION RRP14=0.,0.,7.5,0. ,10.,.6 ,13.,2.2,15.,3.3,20.,6.  ,...
      25.,8.7 ,30.,10. ,33.,8.7
FUNCTION RRP15=0.,0.,7.5,0. ,10.,1. ,13.,2.8,15.,4.1,20.,7.2 ,...
      25.,10.4,30.,11.5,33.,10.4
FUNCTION RRP16=0.,0.,7.5,0. ,10.,1.5,13.,3.5,15.,4.8,20.,8.2 ,...
      25.,11.5,30.,12.5,33.,11.5
FUNCTION RRP17=0.,0.,7.5,0. ,10.,1.7,13.,3.7,15.,5.2,20.,8.7 ,...
      25.,12.1,30.,13. ,33.,12.1
FUNCTION RRP18=0.,0.,7.5,0. ,10.,1.9,13.,4. ,15.,5.4,20.,8.4 ,...
      25.,12.4,30.,14.5,33.,12.4
*       DATA PROTONYMPHAE P.ULMI VERSUS ADULT FEMALE A.POTENTILLAE
FUNCTION RRD11=0.,0.,7.5,0. ,10.,.0. ,13.,.0. ,15.,.0. ,20.,.0.  ,...
      25.,0.  ,30.,.0.  ,33.,.0.
FUNCTION RRD12=0.,0.,7.5,0. ,10.,.3 ,13.,.4 ,15.,.6 ,20.,.9  ,...
      25.,1.2 ,30.,1.4 ,33.,1.0
FUNCTION RRD13=0.,0.,7.5,0. ,10.,.6 ,13.,1.1,15.,1.4,20.,2.1 ,...
      25.,2.9 ,30.,3.5 ,33.,3.
FUNCTION RRD14=0.,0.,7.5,.6 ,10.,1.4,13.,2.4,15.,3.1,20.,4.8 ,...
      25.,6.6 ,30.,7.  ,33.,6.5
FUNCTION RRD15=0.,0.,7.5,.8 ,10.,2. ,13.,3.5,15.,4.5,20.,7.1 ,...
      25.,9.5 ,30.,10.5,33.,9.5
FUNCTION RRD16=0.,0.,7.5,.9 ,10.,2.4,13.,4.2,15.,5.5,20.,8.5 ,...
      25.,11.5,30.,12.5,33.,11.5
FUNCTION RRD17=0.,0.,7.5,1. ,10.,2.6,13.,4.5,15.,5.7,20.,8.9 ,...
      25.,12. ,30.,13. ,33.,12.
FUNCTION RRD18=0.,0.,7.5,1.3,10.,2.8,13.,4.6,15.,6. ,20.,9.  ,...
      25.,12.2,30.,13.2,33.,12.
*       DATA DEUTONYMPHAE P.ULMI VERSUS ADULT FEMALE A.POTENTILLAE
FUNCTION RRAF1=0.,0.,7.5,0. ,10.,0. ,13.,0. ,15.,0. ,20.,0.  ,...
      25.,0.  ,30.,0.  ,33.,0.
FUNCTION RRAF2=0.,0.,7.5,.1 ,10.,.2 ,13.,.4 ,15.,.5 ,20.,.75 ,...
      25.,1.  ,30.,1.2 ,33.,1.
FUNCTION RRAF3=0.,0.,7.5,.15,10.,.35,13.,.55,15.,.7 ,20.,1.15 ,...
      25.,1.55,30.,1.75,33.,1.
FUNCTION RRAF4=0.,0.,7.5,.2 ,10.,.4 ,13.,.75,15.,1. ,20.,1.55 ,...
      25.,2.15,30.,2.5 ,33.,2.
FUNCTION RRAF5=0.,0.,7.5,.25,10.,.65,13.,1.1,15.,1.5,20.,2.35 ,...
      25.,3.2 ,30.,3.5 ,33.,3.
FUNCTION RRAF6=0.,0.,7.5,.35,10.,.85,13.,1.5,15.,1.9,20.,2.95 ,...
      25.,4.  ,30.,4.5 ,33.,4.
FUNCTION RRAF7=0.,0.,7.5,.35,10.,.9 ,13.,1.6,15.,1.9,20.,3.05 ,...
      25.,4.2 ,30.,4.6 ,33.,4.
FUNCTION RRAF8=0.,0.,7.5,.4 ,10.,.9 ,13.,1.5,15.,2. ,20.,3.1  ,...
      25.,4.2 ,30.,4.6 ,33.,4.
*       DATA ADULT FEMALE P.ULMI VERSUS ADULT FEMALE A.POTENTILLAE


*       DATA ON PREY UTILIZATION

AFGEN PVT1=0.,1.7,1.,1.2.2.,  ,88,3.,  ,6,4.,  ,43,5.,.34,6.,.29,7.,.23
AFGEN PVT2=0.,3. ,1.,2. ,2.,1.35,3.,  ,9,4.,  ,65,5.,.5 ,6.,.4 ,7.,.35
AFGEN PVT3=0.,4. ,1.,3. ,2.,2.2 ,3.,1.3,4.,1.  ,5.,.7 ,6.,.55,7.,.45
AFGEN PVT4=0.,4.5,1.,3. ,2.,2.4 ,3.,1.6,4.,1.2 ,5.,.9 ,6.,.7 ,7.,.6
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*       DATA ON RELATIVE RATE OF COLOUR DECREASE

AFGEN RDCV1=0.,0., 10.,.1 , 15.,.45, 20.,.78, 25.,1.10, 30.,1.43
AFGEN RDCV2=0.,0., 10.,.05, 15.,.22, 20.,.4 , 25., .5 , 30., .73
AFGEN RDCV3=0.,0., 10.,.05, 15.,.22, 20.,.4 , 25., .5 , 30., .73

*PARAM PVF*1,9*=1,


PARAM CFS=1.92E-3
*       CORRECTION FACTOR FOR SURFACE, BASED ON THE LEAF
*       SURFACE DETERMINATIONS OF THE SAMPLES.
*       THE VARIANCE OF THESE SAMPLES IS VERY SMALL


*       DATA FOR PANONYCHUS ULMI, 10 CLASSES.
*       MOST DATA ARE FROM EXPERIMENTS

AFGEN DMTB1=0.,.005,10.,.0021,15.,.0006,20.,.0012,25.,.0131,  ...
          30.,.0172,32.,.335,35.,1.1513
AFGEN DMTB2=0.,.24,10.,.1,15.,.05,20.,.04,25.,.04,30.,.05,33.,.19
AFGEN DMTB3=0.,.24,10.,.1,15.,.05,20.,.04,25.,.04,30.,.05,33.,.19
AFGEN DMTB4=0.,.24,10.,.1,15.,.05,20.,.04,25.,.04,30.,.05,33.,.19
AFGEN DMTB5=0.,.28,10.,.1,15.,.05,20.,.03,25.,.03,30.,.04,33.,.12
AFGEN DMTB6=0.,.28,10.,.1,15.,.05,20.,.03,25.,.03,30.,.04,33.,.12
AFGEN DMTB7=0.,.28,10.,.1,15.,.05,20.,.03,25.,.03,30.,.04,33.,.12
AFGEN DMST1=0.,.18,10.,.1,15.,.04,20.,.03,25.,.03,30.,.04,33.,.12
AFGEN DMWT1=0.,.18,10.,.1,15.,.04,20.,.03,25.,.03,30.,.05,33.,.14
AFGEN DMPF1=0.,.008,10.,.0051,15.,.0029,20.,.0044,25.,.0722,  ...
          30.,.1178,35.,.412
AFGEN LOLET=0.,100.,10.,50.,15.,17.40,20.,8.38,25.,5.53,30.,4.95,35.,4.8
AFGEN SDET=0.,20.,10.,20.,11.,8.,15.,.96,20.,.45,25.,.24,30.,.11,35.,.4
AFGEN LOLJT=0.,100.,10.,50.,11.,25.,15.,10.10,20.,4.76,25.,3.9,35.,2.29
AFGEN SDJT=0.,20.,10.,10.,11.,5.,15.,1.4,20.,.1.,25.,.82,30.,.57,35.,.7
AFGEN LOLJST=0.,100.,10.,20.,15.,5.55,20.,3.46,25.,2.16,30.,1.82,35.,2.
AFGEN LOLJWT=0.,100.,10.,20.,15.,5.71,20.,3.57,25.,1.96,30.,1.82,35.,2.
AFGEN SDJWT=0.,20.,10.,8.,11.,4.,15.,1.61,20.,1.64,25.,.72,30.,.78
AFGEN SDJST=0.,20.,10.,8.,11.,4.,15.,1.61,20.,1.64,25.,.72,30.,.78
AFGEN SDPAFS=0.,11.,5.,5.,10.,3.6,15.,1.7,20.,1.02,25.,.63,  ...
          30.,.55,33.,.35
AFGEN LOPAFT=0.,25.,5.,12.5,10.,8.,15.,3.43,20.,2.35,25.,1.71,  ...
          30.,1.51,35.,1.5
AFGEN LOAFST=0.,100.,10.,72.,15.,63.,20.,28.,25.,19.,30.,15.
AFGEN SDAFST=0.,50.,5.,33.8,10.,17.9,15.,10.6,20.,4.74,25.,2.9,  ...
          30.,1.7,33.,1.85
AFGEN LOAWST=0.,90.  ,10.,25.  ,15.,20.  ,20.,16.  ,25.,10.  ,35.,  4.
AFGEN SDAWST=0.,20.  ,10.,10.  ,15.,  5.  ,20.,  4.  ,25.,  3.  ,35.,  2.
AFGEN DMFF1 =0.,.0   ,10.,.01  ,15.,.0048,20.,.0   ,25.,.0   ,30.,.0
AFGEN DMFF2 =0.,.0   ,10.,.0157,15.,.0119,20.,.0   ,25.,.0   ,30.,.0
AFGEN DMFF3 =0.,.002,10.,.0277,15.,.0227,20.,.018,25.,.018,30.,.01
AFGEN DMFF4 =0.,.002,10.,.0484,15.,.0443,20.,.044,25.,.071,30.,.056
AFGEN DMFF5 =0.,.002,10.,.0699,15.,.0784,20.,.108,25.,.178,30.,.279
AFGEN DMFF6 =0.,.008,10.,.0916,15.,.110  ,20.,.194,25.,.152,30.,.413
AFGEN DMFF7 =0.,.013,10.,.127  ,15.,.129  ,20.,.313,25.,.396,30.,.71
AFGEN DMFF8 =0.,.041,10.,.152  ,15.,.156  ,20.,.472,25.,.6   ,30.,1.14
AFGEN DMFF9 =0.,.129,10.,1.    ,15.,1.    ,20.,1.   ,25.,.646,30.,1.46
AFGEN DMFF10=0.,1.   ,10.,1.   ,15.,1.    ,20.,1.   ,25.,1.09,30.,1.5


*       DATA FOR TYPHLODROMUS POTENTILLAE

AFGEN LOTTET=0.,100.,10.,7.29,15.,3.64,20.,2.3,25.,1.64,30.,1.4
AFGEN SDTE=0.,25.,10.,1.48,15.,.89,20.,.6,25.,.47,30.,.4
AFGEN MTJS1=0.,.001,10.,.010,15.,.005,20.,.005,25.,.005,30.,.010,33.,.02
AFGEN LOTSFT=0.,100.,5.,50.,10.,11.76,15.,7.38,20.,4.01,25.,3.73,  ...
          25.,3.51,30.,3.93,35.,2.35
AFGEN SDPSFT=0.,25.,5.,12.5,10.,2.94,15.,1.14,20.,.99,25.,.82,  ...
          25.,.88,30.,.78,35.,.59
AFGEN LOTJT=0.,100.,10.,6.57,15.,3.23,20.,2.3,25.,1.71,30.,1.4
AFGEN SDTJT=0.,25.,10.,1.37,15.,.99,20.,.6,25.,.29,30.,.4
AFGEN LOTJST=0.,100.,10.,5.07,15.,2.6,20.,1.5,25.,1.06,30.,.87
AFGEN SDTJST=0.,25.,10.,1.08,15.,.74,20.,.4,25.,.3,30.,.25
AFGEN LOTSMT=0.,18.  ,10.,10.  ,15.,  8.  ,20.,  6.3,25.,  4.  ,30.,  3.5
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AFGEN SDTSMT=0.,9. ,10.,5. ,15.,4. ,20.,3.3,25.,2. ,30.,1.8
AFGEN MTE1=0.,.0120,10.,.0701,15.,.0141,20.,.0044,25.,.0123,30.,.1594
AFGEN MTJ1=0.,.05,10.,.034,15.,.013,20.,.01,25.,.015,30.,.03,33.,.08
AFGEN MTJ2=0.,.05,10.,.034,15.,.013,20.,.01,25.,.015,30.,.03,33.,.08
AFGEN MTJ3=0.,.05,10.,.034,15.,.013,20.,.01,25.,.015,30.,.03,33.,.08
AFGEN MTJ4=0.,.05,10.,.034,15.,.013,20.,.01,25.,.015,30.,.03,33.,.08
AFGEN LOTFFT=0.,150,.10.,91.,15.,72.,20.,55.,25.,50.,30.,50.
AFGEN MRFT1 =0.,.0068,10.,.0068,15.,.0057,20.,.0009,25.,.002 ,30.,.006
AFGEN MRFT2 =0.,.0111,10.,.0111,15.,.0105,20.,.0009,25.,.007 ,30.,.015
AFGEN MRFT3 =0.,.0213,10.,.0213,15.,.0219,20.,.0075,25.,.0186,30.,.029
AFGEN MRFT4 =0.,.0327,10.,.0327,15.,.0375,20.,.022 ,25.,.043 ,30.,.052
AFGEN MRFT5 =0.,.0533,10.,.0533,15.,.0662,20.,.055 ,25.,.067 ,30.,.081
AFGEN MRFT6 =0.,.0632,10.,.0632,15.,.0816,20.,.079 ,25.,.109 ,30.,.119
AFGEN MRFT7 =0.,.089 ,10.,.089 ,15.,.127 ,20.,.156 ,25.,.160 ,30.,.158
AFGEN MRFT8 =0.,.108 ,10.,.108 ,15.,.136 ,20.,.222 ,25.,.212 ,30.,.241
AFGEN MRFT9 =0.,.145 ,10.,.145 ,15.,.186 ,20.,.293 ,25.,.301 ,30.,.22
AFGEN MRFT10=0.,.223 ,10.,.223 ,15.,.223 ,20.,.30  ,25.,.301 ,30.,.22
AFGEN FETT1 =0.,0.,  10.,.3, 15.,.8, 20.,1.3, 25.,1.8, 30.,1.6
AFGEN FETT2 =0.,0.,  10.,.3, 15.,.8, 20.,1.3, 25.,1.8, 30.,1.6
AFGEN FETT3 =0.,0.,  10.,.3, 15.,.7, 20.,1.1, 25.,1.3, 30.,1.0
AFGEN FETT4 =0.,0.,  10.,.2, 15.,.7, 20.,0.7, 25.,0.7, 30.,0.5
AFGEN FETT5 =0.,0.,  10.,.2, 15.,.4, 20.,0.6, 25.,0.5, 30.,0.2
AFGEN FETT6 =0.,0.,  10.,.2, 15.,.4, 20.,0.5, 25.,0.5, 30.,0.2
AFGEN FETT7 =0.,0.,  10.,.1, 15.,.3, 20.,0.4, 25.,0.3, 30.,0.1
AFGEN FETT8 =0.,0.,  10.,.1, 15.,.2, 20.,0.2, 25.,0.2, 30.,0.0
AFGEN FETT9 =0.,0.,  10.,.0, 15.,.2, 20.,0.2, 25.,0.2, 30.,0.0
AFGEN FETT10=0.,0.,  10.,.0, 15.,.0, 20.,0.0, 25.,0.0, 30.,0.0
AFGEN MTSF1=0.,.005 ,10.,.005 ,15.,.0101,20.,.0101,25.,.0201,30.,.0408


*       OUTPUT DATA ARE ONLY CALCULATED PERIODICALLY

NOSORT
      PRI=IMPULS(PRDEL,PRDEL)
      IF (PRI.NE.1.) GOTO 10
      LPE=ALOG10(TPE+1.)
      LPL=ALOG10(TPL+1.)
      LPPN=ALOG10(TPPN+1.)
      LPDN=ALOG10(TPDN+1.)
      LPAFS=ALOG10(TPAFS+1.)
      LPAMS=ALOG10(TPAMS+1.)
      LF1=ALOG10(F1+1.)
      LTE=ALOG10(TTE+1.)
      LTL=ALOG10(TTL+1.)
      LTPN=ALOG10(TTPN+1.)
      LTDN=ALOG10(TTDN+1.)
      LTAFS=ALOG10(TTAFS+1.)
      LTAMS=ALOG10(TTAMS+1.)
      LFT=ALOG10(FT+1.)
   10 CONTINUE

PRINT TPAFS,TPE,TPL,TPPC,TPPN,TPDC,TPDN,TPTC,PAFST,TPAMS, ...
      TTE,TTL,TTPN,TTDN,TTAFS,TTAMS,TOMORT,TOMORF,CAF,CAM,CPN,CDN, ...
      TEMP,LPE,LPL,LPPN,LPDN,LPAFS,LPAMS,LF1, ...
      LTE,LTL,LTPN,LTDN,LTAFS,LTAMS,LFT,PAFM,WEP,TAMF
PRTPLT TPAFS,TPE,TTAFS,TTE
METHOD RECT
TIMER FINTIM=40.,OUTDEL=1.,PRDEL=1.,DELT=.01
FINISH TPE=-1.E-10
END
STOP
ENDJOB
```

8.1.1. *Hatching of winter eggs*

The number of winter eggs laid in autumn was simulated, Section 8.1.3, but simulation of the complex phenomena of winter mortality has not been attempted as yet. However an analysis of literature showed that it may be feasible at this stage to simulate the time of emergence of the larvae of the prey, so that the population model may be initialized by counting the number of viable eggs at the beginning of April. A rudimentary submodel of the hatching process that is used at present is given in Fig. 62. In this model three development phases of winter eggs are considered. These are the blastoderm phase which starts shortly after the eggs are laid, a more advanced embryonic development phase in spring and the phase of emergence of the larvae. On the basis of Cranham's observations (1972), it is concluded that the threshold temperature for development is 5.6°C. It is assumed in the simulation program that development proceeds irreversibly as soon as the first order average of temperature with a time constant of two days after 1st march is 5.6°C.

The development stage is conserved in an integral of the development rate, which in its turn is a function of temperature, according to Cranham's data. This part of the simulation is presented in lines 1150 to 1270 of the submodel (Fig. 62). The internal development is completed when the development stage passes the value of 1.

Data of van de Vrie et al. (in prep.) summarized in Fig. 63, showed that the subsequent emergence of larvae may be simulated by transferring the eggs at the moment that the development equals 1, to a development series of two age classes. This part of the program is given in lines 1270 to 1410.

It is well known that the eggs need a cold period to hatch in spring. Since the number of viable eggs are supposed to be counted in April, it is not necessary to simulate this mortality aspect. However the data of Putman (1970) and Cranham (1972) show another effect of cold: the longer and the colder the eggs are stored during the blastoderm stage the shorter the time necessary for development (Fig. 64). This decrease in the developmental period is at present accounted for by assuming that its initial value is not necessarily zero, but increases with the increase in the number of days that the average temperature in winter is below 5°C. The number of days is counted from autumn in the previous year, until the 1st April. This part of the submodel is given in the lines 1090 to 1150.

Fig. 62 | Computer program for hatching process.

```
TITLE RABBINGE                                                          00000010
TITLE HATCHING WINTER EGGS                                              00000020
INITIAL                                                                 00000030
PARAM D=200.                                                            00000040
*       LENGTH OF COLD PERIOD                                           00000050
PARAM EI=100.                                                           00000060
*       INITIAL NUMBER OF WINTER EGGS COUNTED IN APRIL                  00000070
PARAM PI=3.141592                                                       00000080
PARAM LAT=52.                                                           00000090
*       LATITUDE SIDE                                                   00000100
PARAM RADL=0.01745329                                                   00000110
PARAM LONG=-5.                                                          00000120
      DLONG=AMOD((LONG+360.)/15.,1.)                                    00000130
*       DLONG IS DIFFERENCE IN HOURS WITH THE STANDARD SOLAR TIME       00000140
      CSLT=COS(RADL*LAT)                                                00000150
*       COSINE LATITUDE                                                 00000160
      SNLT=SIN(RADL*LAT)                                                00000170
*       SINE LATITUDE                                                   00000180
DYNAMIC                                                                 00000190
*                                                                       00000200
*                                                                       00000210
***     CALCULATIONS OF THE ABIOTIC FACTORS                             00000220
*                                                                       00000230
      DAY=TIME+STAR                                                     00000240
*       NUMBER OF THE DAY                                               00000250
      DELX=1./DELT                                                      00000260
PARAM STAR=60.                                                          00000270
*       THE MODEL IS STARTED AT DAY 60, 1 APRIL                         00000280
       HOUR=AMOD(TIME,1.)*24.                                           00000290
*       CALCULATION HOUR OF THE DAY                                     00000300
*                                                                       00000310
*                                                                       00000320
***     CALCULATION OF THE SINE ELEVATION OF SUN                        00000330
*                                                                       00000340
      DEC=-23.4*COS(6.2832/365.*(DAY+10.))                              00000350
*       DECLINATION OF THE SUN                                          00000360
      COSDEC=COS(RADL*DEC)                                              00000370
*       COSINE DECLINATION                                              00000380
      SINDEC=SIN(RADL*DEC)                                              00000390
*       SINE DECLINATION                                                00000400
      HA=2.*PI*(HOUR+12-DLONG)/24.                                      00000410
*       HOUR ANGLE IN DEGREES                                           00000420
      SNHSS=SNLT*SINDEC+CSLT*COSDEC*COS(HA)                             00000430
*       SINE ELEVATION OF SUN                                           00000440
      SNHS=AMAX1(0.,SNHSS)                                              00000450
*                                                                       00000460
*                                                                       00000470
***     CALCULATION OF AIR TEMPERATURE FROM MINIMUM AND MAXIMUM         00000480
*                                                                       00000490
PARAM RISEI = 6.5                                                       00000500
*       INITIAL TIME OF SUNRISE                                         00000510
      RISE=RISEI+ZHOLD(AND(SNHSS,-LSNHS)-0.5,HOUR-SNHSS/(SNHSS ...      00000520
          -LSNHS+NOT(SNHSS-LSNHS))-RISEI)                               00000530
*       MOMENT OF SUNRISE TODAY (HOURS)                                 00000540
      LSNHS=INTGRL(-0.5,(SNHSS-LSNHS)*DELX)                             00000550
*       SUN HEIGHT TODAY AT LAST TIMESTEP                               00000560
      VALAMP = (AFGEN(MXTT,DAY+HOUR/24.)-AFGEN(MNTT,DAY+HOUR/24.))/2.   00000570
*       DAILY AMPLITUDE TEMPERATURE                                     00000580
      VALAV =(AFGEN(MXTT,DAY+HOUR/24.)+AFGEN(MNTT,DAY+HOUR/24.))/2.     00000590
*       DAILY AVERAGE TEMPERATURE                                       00000600
      TIM = INSW(HOUR-14.,HOUR+10.,HOUR-14.)                            00000610
      VALSR = -COS(2.*PI*(HOUR-RISE)/(2.*(14.-RISE)))*VALAMP+VALAV      00000620
*       TEMPERATURE AT SUNRISE                                          00000630
      VALSS = COS(2.*PI*TIM/(2.*(10.+RISE)))*VALAMP+VALAV               00000640
*       TEMPERATURE AT SUNSET                                           00000650
      TEMP = INSW(AND(HOUR-RISE,14.-HOUR)-0.5,VALSS,VALSR)+SEN          00000660
*       ACTUAL TEMPERATURE                                              00000670
PARAM SEN=0.                                                            00000680
*       SENSITIVITY FACTOR TO INCREASE OR DECREASE TEMPERATURE          00000690
*       SYSTEMATICALLY                                                  00000700
*                                                                       00000710
*                                                                       00000720
*                                                                       00000730
```

```
***      TEMPERATURE DATA MEASURED IN A STEVENSON SCREEN                    00000740
***      AT 1,50 M AT THE SCHUYLENBURGH IN 1974, LIENDEN                    00000750
                                                                            00000760
*                                                                           00000770
AFGEN MXTT=60,..8,61..-.7,62,.-.7,63,.-2.2,64,.-3.5,65,.-3.7,66,.-.1....00000780
      67,..8,68,..5.7,69,..5.5,70,..5,6,71,..9.2,72,.8,9,73,..11.3, ...  00000790
      74,.9.8,75,..10,.76,.10,.77,.13,.78,.11.7,79,.9.6,80,.10.7, ...     00000800
      81,.7.7,82,..8.1,83,..8.6,84,.9,9,85,..8,..86,..7.7,87,..8,.88,.11,. ...00000810
      89,..9.4,90,..7,7,91,..9,3,92,.16.6,93,..11.8,94,..14.8,95,..11.5, ...00000820
      96,.8.5,97,..10.9,98,..13,.99,..14,.100,.13.1,101,..9.9,102,..13.4, ...00000830
      103,..12.3,104,.18.3,105,..20.9,106,..16.3,107,..9.5,108,.13.9, ...  00000840
      109,.14.7,110,..14.8,111,..18.4,112,..22.1,113,..24.4,114,..21.8, ...00000850
      115,..8.9,116,..9.2,117,..10,..118,.10,.119,..11.3,120,..11.9,...    00000860
      121,.13.6,122,..14.6,123,..17.3,124,..18.6,125,..20.1,126,..20.9,...00000870
      127,.24.2,128,..21.7,129,..19.7,130,..22.1,131,..24.2, ...           00000880
      132,.27,.133,..22,.134,..18.7,135,..20.8,136,..21.2, ...             00000890
      137,.21.3,138,..19.3,139,..20.3,140,..19.7,141,..19.4, ...           00000900
      142,..19,.143,..22.4,144,..16.9,145,..13.1,146,..17.6,147,..20.9,... 00000910
      148,..16,.149,..17,..150,..20.5                                       00000920
*        MAXIMUM TEMPERATURE                                                00000930
AFGEN MNTT=60,.-2.6,61,.-3.7,62,.-6,.63,.-15.1,64,.-17.6, ...               00000940
      65,.-15.3,66,.-18.7,67,.-3.7,68,..3.69,.-2.4,70,..3,71,.-.3, ...     00000950
      72,.3.4,73,..2.1,74,.5.2,75,.-.2,76,.3.6,77,.5.4,78,.7.3, ...        00000960
      79,.5.1,80,..3.4,81,..2.7,82,.3.5,83,..3.5,84,.5.7,85,.2.2, ...      00000970
      86,.-2.6,87,.-1.3,88,..-2.4,89,...6,90,..1.2,91,.2.5,92,.-.9,...     00000980
      93,.4.2,94,.6.1,95,.1.6,96,.4.6,97,.5.3,98,..6,99,.2.5, ...          00000990
      100,.3.7,101,.3.1,102,.-1.3,103,.4.8,104,.4,.105,.6.2, ...           00001000
      106,.4.6,107,.3,.108,.2,.109,.2.2,110,.4.7,111,.2.1, ...             00001010
      112,.9,.113,.13.1,114,.8.4,115,.3.7,116,.-4,.117,.1.7, ...           00001020
      118,.-2.4,119,.-.1,120,.-5,7,121,..6,122,.1.7,123,.-2,. ...          00001030
      124,..4,125,.2,.126,.8,9,127,.11.2,128,.12.8,129,.10.4, ...          00001040
      130,.4.7,131,.7.7,132,.9.2,133,.10.2,134,.11.9,135,.10,. ...         00001050
      136,.12.5,137,.12,.138,.11,.139,.9.6,140,.6.5,141,.2.7, ...          00001060
      142,.9.2,143,.11,.144,.10.5,145,.7.5,146,.9.6,147,.10,. ...          00001070
      148,.10.8,149,.7.2,150,.9.1,151,.9.1                                  00001080
*        MINIMUM TEMPERATURE                                                00001090
*                                                                           00001100
AFGEN INPER=136,.0,.170,.,5,200,..66,231,.,84,255,..92                      00001110
*        THE INITIAL DEVELOPMENT STAGE OF WINTER EGGS DEPENDS ON            00001120
*        THE NUMBER OF DAYS WITH AVERAGE TEMPERATURE BELOW                  00001130
*        5 DEGREE CELSIUS, UNTIL  1 APRIL                                   00001140
      COLDP=0                                                               00001150
*        COLD PERIOD                                                        00001160
      ININ=AFGEN(INPER,COLDP)                                               00001170
*        CALCULATION OF INITIAL DEVELOPMENT STAGE                           00001180
      TEMI=INTGRL(0,,(TEMP-TEMI)/2,)                                        00001190
*        FIRST ORDER TEMPERATURE AVERAGE WITH A TIME CONSTANT OF 2 DAYS     00001200
      DEWE=AMAX1(0,,.0044*(TEMI-5.6))                                       00001210
*        DEVELOPMENT RATE OF WINTER EGGS                                    00001220
      PUS=IMPULS(0,,FINTIM)                                                 00001230
*        START PROGRAM AT TIME ZERO                                         00001240
      GSH=INTGRL(0,,DEWE+PUS*(ININ/DELT)-PUWE/DELT)                         00001250
*        DEVELOPMENT STAGE OF WINTER EGGS                                   00001260
      PUWE=INSW(GSH-1,,0,,1,)                                               00001270
*        END DIAPAUSE AND START EMERGENCE PROCESS                           00001280
      LOLEW=AFGEN(LOLEWT,TEMP)                                              00001290
AFGEN LOLEWT=-10,,200,,0,,200,,5,,100,,10,,25,,15,,10,,20,,5,5,25,,4,8     00001300
*        LENGTH OF HATCHING PERIOD                                          00001310
      RTEW=LOLEW/2,                                                         00001320
*        RESIDENCE TIME OF EGGS PER AGE CLASS                               00001330
      EW1=INTGRL(0,,PUWE*EI/DELT-EW1/RTEW)                                  00001340
*        FIRST AGE CLASS                                                    00001350
      DEEW=INSW(EW2-1,E-2,0,,EW2)/RTEW                                      00001360
*        HATCHING RATE                                                      00001370
      EW2=INTGRL(0,,EW1/RTEW-DEEW)                                          00001380
*        SECOND AGE CLASS                                                   00001390
      TPEW=EW1+EW2                                                          00001400
*        ACCUMULATED NUMBER OF WINTER EGGS                                  00001410
      PL=INTGRL(0,,DEEW)                                                    00001420
*        ACCUMULATED NUMBER OF LARVAE                                       00001430
TIMER FINTIM=10,,OUTDEL=1,,DELT=.1,PRDEL=1,                                 00001440
METHOD RECT                                                                 00001450
PRINT TPEW,EW1,EW2,PL,TEMP                                                  00001460
PRTPLT TPEW,PL                                                              00001470
END                                                                         00001480
STOP                                                                        00001490
ENDJOB
```

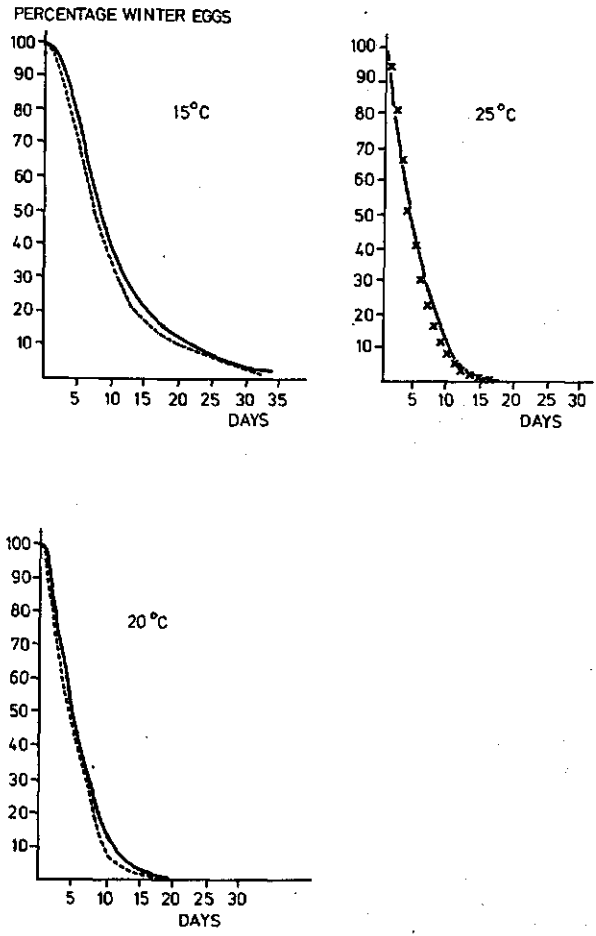

Fig. 63 | Emergence curves of winter eggs at different temperatures (data from van de Vrie – drawn lines; simulated curves – broken lines).

As an illustration of the whole hatching process, the simulated internal development stage and the emergence of the eggs is presented in Fig. 65 and Table 33 for a year with a warm winter and cold spring and a year with a cold winter and warm spring. Simulated emergence dates of larvae are in reasonable agreement with experimental records of acarologists. To improve the model a thorough analysis of the overwintering processes in winter and spring is required.

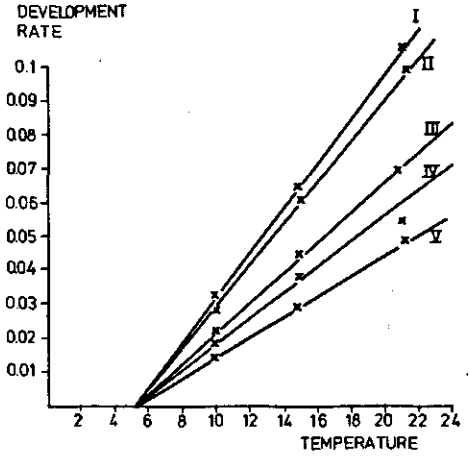

Fig. 64 | Development rate of winter eggs against temperature in °C for various cold periods. I=255 days; II=231 days; III=200 days; IV=170 days; V=136 days.

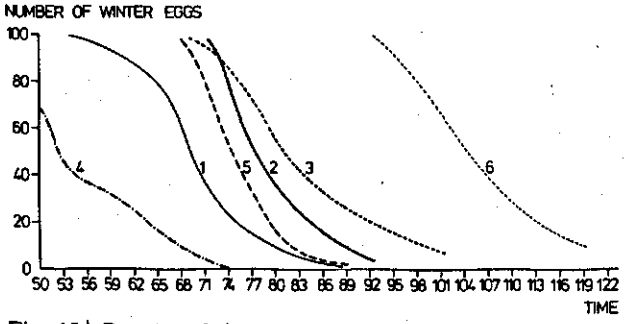

Fig. 65 | Results of simulations with the preliminary program on hatching of winter eggs. 1. cold period = 200 days; 2. cold period = 160 days; 3. cold period = 200 days, springtemperatures systematically 2°C lowered. 4. cold period = 200 days, springtemperatures systematically 2°C highered; 5. cold period = 136 days, springtemperatures systematically 2°C highered; 6. cold period = 136 days, springtemperatures systematically 2°C lowered; Day 50 = 20 April.

Table 33 Simulated start of emergence of winter eggs for various combinations of spring and winter. Spring 1971 was taken as normal.

	Date of start of emergence
Cold winter (D=200) normal spring (SEN=0)	14 April
Warm winter (D=160) normal spring	1 May
Cold winter (D=200) cold spring (SEN=−2)	2 May
Cold winter (D=200) warm spring (SEN=+2)	1 April
Warm winter (D=136) warm spring (SEN=+2)	28 April
Warm winter (D=136) cold spring (SEN=−2)	29 May

8.1.2 Population fluctuations during the season and under controlled conditions

The main program for population growth comprises a section where the physical factors are calculated, sections on the development and ageing of the fruit-tree red spider mite and the predatory mites, and a section in which the predation process is described.
Although the listing of the program in Fig. 61 is provided with comprehensive comments some additional remarks should be made.

1. The INITIAL comprises all parameters and initial values and the DYNAMIC concerns the actual simulation.
2. To reduce the computer time required for translation and to prevent a too large number of input variables for the CSMP compiler, the successive stages are given in PROCEDURES.
3. The predation process is given in Section 4 of the program. The colour of the adult female predator, CAF, is found by dividing the total amount of colour units per unit of surface, EQTI, by the number of the adult female predators, TTAFS. An upper limit of 7 and a lower limit of 1 are introduced by the LIMIT function. The temperature, TEMP, and the inverse of the colour value, CTAF = 1/CAF, are used as input variables for the functions that determine the relative predation rate. The rate of increase of the colour is found as the sum of the products of the total number of prey of each stage with their prey utilization and relative predation rates, both read from tabulated functions.
The same calculations are done for the other predator stages.
The effects of the colour value of the predator on its rates of development and oviposition are introduced with multiplication factors read

from tabulated functions.
4. The sections that concern development, ageing and oviposition of predator and prey were treated in Chapters 3 and 4 and do not need further explanation here.

8.1.3 Diapause

The relational diagrams for the reversible transfer of juveniles and adults between summer and winter forms, Fig. 10, are discussed in Section 4.1. The program itself is presented in Fig. 66. The quantitative information is mainly derived from detailed experiments of Lees (1953). He showed that temperature, daylength and food condition are the important driving variables.
The effect of food is only important when very high densities of the mites are reached, or when the quality of the leaves in terms of photosynthesis rate or nitrogen content is very poor. Field observations in 1974, in orchards with different mite densities showed that there is a significant influence on diapause when the adult female density becomes higher than 10 per leaf (van de Vrie et al., in prep.) Section 9.4.2. In these situations the model does not anticipate because these densities are much higher than the accepted threshold level.
The results of the experiments of Lees are given in Table 34, in the form of relative transfer rates of summer and winter forms dependent on temperature and daylength. Lees' experiments showed that the minimum light intensity for diapause induction is at 0.1 $J m^{-2}$ $sec.^{-1}$. This light intensity is already reached during twilight so that daylength, DAYL, is calculated as the time between sunrise and sunset increased by one hour for the twilight.
No data on diapause induction in predatory mites are available, so that it is impossible to construct a simulation program for this process. However field observations in 1973, 1974 and 1975 showed that some overwintering females are at their winter sites when the first winter eggs of the prey are laid. Therefore and for reasons of simplicity in the population models, the induction of diapause in the predator is assumed to be similar to that for the prey. This simplification may cause erroneous results but since the population models are used until the beginning of September, this assumption seems justified.

8.2 Predation in replacement series of prey

It was shown in Section 4.3 that the presence of more than one prey stage is easily accounted for by the colour of the predator that

Table 34 Sensitivity of different developmental stages of *P. ulmi* to combinations of temperature and photoperiod. Treatment A: mites transferred from a diapause-neutral temperature (15 °C) to a diapause-preventing temperature (25 °C) with a photoperiod of 8h throughout; Treatment B: mites transferred from 25 °C to 15 °C with a photoperiod of 8h throughout; Treatment C: mites transferred from an 8-h photoperiod at 15 °C to a 16-h photoperiod at 25 °C; Treatment D: mites transferred from a 16-h photoperiod at 25 °C to an 8-h photoperiod at 15 °C (data from Lees, 1953).

Treatment	Winter eggs only	Winter then summer eggs	Summer eggs only	Summer then winter eggs	Mean time interval to switch over (in days)
A protonymph	0	0	1.0	0	< 6
deutonymph	0	0.4	0.6	0	< 5
teleiochrysalid ♀	0	0.8	0.2	0	4
egg laying ♀	0.2	0.8	0	0	8
B protonymph	1.0	0	0	0	< 12
deutonymph	1.0	0	0	0	< 8
teleiochrysalid ♀	0.5	0	0.2	0.3	12
egg laying ♀	0	0	0.5	0.5	11
C protonymph	0	0	1.0	0	< 6
deutonymph	0	0.1	0.9	0	< 5
teleiochrysalid ♀	0	0.9	0.1	0	3
egg laying ♀	0	1.0	0	0	6
D protonymph	1.	0	0	0	< 12
deutonymph	0.9	0	0	0.1	< 8
teleiochrysalid ♀	0	0	0	1.0	11
egg laying ♀	0	0	0.8	0.2	15

determines the relative predation rate and the prey utilization of each prey. It is implicitly assumed that the presence of more than one prey stage does not affect the relations between colour value and relative rate of predation for each of the prey stages.
This assumption is verified by measuring the predation rate of different prey species in a replacement series in which the total number of prey is kept constant (at 10) and the relative frequency of each prey is changed from 0–1. The experimental results are compared with the results of a simulation model for this replacement experiment.

The results and the comparison is discussed in Section 9.2. In essence the model is a submodel of the predation process in the population model. Fig. 67 presents a listing of the program. The predation rate per day is calculated by multiplying the relative rates of predation by the prey densities. The prey densities are given as parameters and are thus constant. The relative predation rates are read from the tabulated functions with colour value and temperature as independent variables. The temperature during the experiments is constant, Section 9.1, and the colour value is expressed in the state variable CAF.
It was found in Section 6.2.3 that there was some effect of temperature on prey utilization, but this effect is not incorporated in the main population model. The possible effect of this simplification is analysed with the present program. For this purpose the rate of increase of the colour of the adult females, INCAF, is multiplied by a factor MUFAI that depends on temperature and colour and is estimated from the figures of Section 6.2.3. Comparison of simulated results at various prey densities and at two temperatures with the results of the model for MUFAI = 1.0 showed no important differences, Table 35, so that this temperature effect could be neglected.

8.3 Microweather model

The model for the evaluation of the influence of the microclimate on the population dynamics includes calculations for sun inclination, temperature and air humidity in the orchard and leaf temperature in each of the 12 classes distinguished in Section 7.3.1. It also includes calculations for the weighted average of the relative rate of development, oviposition and ageing.
Fig. 68 presents a listing of the model. Here the microclimate simulator is coupled to a population model of the prey, in which the proper dispersion is achieved by the introduction of a large number of age classes. This procedure is less cumbersome than the averaging of the transfer in a model with a few age classes and controlled dispersion. The results of some runs for the prey have been given in Fig. 60.
Fig. 69 presents the same runs but for the predatory mite under the assumption that abundant food is available.
For both predator and prey the systematic effect of the small change in oviposition rate is larger than the systematic effect of a detailed account of the micro-weather. Hence it may be safely assumed that all leaves in the orchard are at air temperature.

Table 35 Effect of temperature on prey utilization. Simulation results of a replacement series of prey stages, with and without an effect of temperature on the relation between colour value and prey utilization. Predation rate and colour value of the predator are given.

Temperature (°C)	Combination		Predation rate (number/day)				Colour value	
	larva	adult female	larva		adult female		with temperature effect	average of all temperatures
			with temperature effect	average of all temperatures	with temperature effect	average of all temperatures		
15	10	0	10.31	10.31			6.27	6.27
15	8	2	8.97	9.2	0.21	0.21	6.15	6.11
15	5	5	6.47	6.89	0.59	0.61	5.86	5.71
15	2	8	3.14	3.58	1.09	1.20	5.38	5.01
15	0	10			1.64	2.2	4.96	4.78
25	10	0	22.94	22.93			6.02	6.02
25	8	2	20.76	20.49	0.81	0.80	5.95	5.96
25	5	5	16.52	15.89	2.28	2.23	5.79	5.82
25	2	8	9.52	8.78	4.49	4.28	5.48	5.56
25	0	10			7.36	6.69	5.05	5.21

Fig. 66 | Computer program on diapause induction.

```
TITLE PANONYCHUS ULMI  SUBMODEL INDUCTION DIAPAUSE                              00000010
*                                                                               00000020
*                                                                               00000030
*       THE ABIOTIC FACTOR CALCULATIONS EQUAL THOSE FOR THE                     00000040
*       OTHER PROGRAMS FURTHER COMMENT IS THEREFORE OMITTED                     00000050
*                                                                               00000060
INITIAL                                                                         00000070
PARAM PI=3,141592                                                               00000080
PARAM LAT=52,                                                                   00000090
PARAM RADL=0,01745329                                                           00000100
PARAM LONG=-5,                                                                  00000110
      DLONG=AMOD((LONG+360,)/15,,1,)                                            00000120
      CSLT=COS(RADL*LAT)                                                        00000130
      SNLT=SIN(RADL*LAT)                                                        00000140
      DTEMI=(AFGEN(MXTT,START)+AFGEN(MNTT,START))*0,5                           00000150
      TELLER=0,                                                                 00000160
      DELX=1,/DELT                                                              00000170
PARAM SRP=,66                                                                   00000180
PARAM PRED1=0,,PRED2=0,                                                         00000190
DYNAMIC                                                                         00000200
*                                                                               00000210
*                                                                               00000220
***      CALCULATIONS OF THE ABIOTIC FACTORS                                    00000230
*                                                                               00000240
       DAY=TIME+START                                                           00000250
PARAM START=232,                                                                00000260
*        START OF THE PROGRAM ON 20 AUGUST                                      00000270
       HOUR=AMOD(TIME,1,)*24,                                                   00000280
*                                                                               00000290
*                                                                               00000300
***      CALCULATION SINE ELEVATION OF SUN                                      00000310
*                                                                               00000320
      DEC=-23,4*COS(6,2832/365,*(DAY+10,))                                      00000330
      COSDEC=COS(RADL*DEC)                                                      00000340
      SINDEC=SIN(RADL*DEC)                                                      00000350
      HA=2,*PI*(HOUR+12-DLONG)/24,                                              00000360
      SNHSS=SNLT*SINDEC+CSLT*COSDEC*COS(HA)                                     00000370
      SNHS=AMAX1(0,,SNHSS)                                                      00000380
*                                                                               00000390
*                                                                               00000400
***      CALCULATION OF AIR TEMPERATURE FROM MINIMUM AND MAXIMUM                00000410
*                                                                               00000420
PARAM RISEI = 6,5                                                               00000430
      RISE=RISEI+ZHOLD(AND(SNHSS,-LSNHS)-0,5,HOUR-SNHSS/(SNHSS-LSNHS+...       00000440
                NOT(SNHSS-LSNHS))-RISEI)                                        00000450
      LSNHS=INTGRL(-0,5,(SNHSS-LSNHS)*DELX)                                     00000460
      VALAMP = (AFGEN(MXTT,DAY+HOUR/24,)-AFGEN(MNTT,DAY+HOUR/24,))/2,           00000470
      VALAV =(AFGEN(MXTT,DAY+HOUR/24,)+AFGEN(MNTT,DAY+HOUR/24,))/2,             00000480
      TIM = INSW(HOUR-14,,HOUR+10,,HOUR-14,)                                    00000490
      VALSR = -COS(2,*PI*(HOUR-RISE)/(2,*(14,-RISE)))*VALAMP+VALAV              00000500
      VALSS = COS(2,*PI*TIM/(2,*(10,+RISE)))*VALAMP+VALAV                       00000510
      TEMP = INSW(AND(HOUR-RISE,14,-HOUR)-0,5,VALSS,VALSR)+SEN                  00000520
PARAM SEN=0,                                                                    00000530
PARAM DL=1,                                                                     00000540
*        THE DAYLENGTH IS INCREASED BY ONE HOUR TO INCLUDE THE TWILIGHT         00000550
      DAYL=(12+DLONG-RISE)*2+DL                                                 00000560
*        CALCULATION DAYLENGTH                                                  00000570
      TEMS=INTGRL(0,,TEMP)                                                      00000580
*        TEMPERATURE SUM                                                        00000590
      DTEMD=INTGRL(0,,(TEMP-DTEMD)/2,)                                          00000600
*        FIRST ORDER AVERAGE TEMPERATURE WITH A TIME CONSTANT OF 2 DAYS         00000610
*                                                                               00000620
*                                                                               00000630
***      MACRO-METEOROLOGICAL DATA, 1974, LIENDEN                               00000640
*                                                                               00000650
FUNCTION MNTT=136.,,3,137.,5,5,138.,7,5,139.,8,4,140.,12,4,  ...                00000660
             141.,11,2,142.,10,2,143.,11,4,144.,10,4,145.,7,4,  ...             00000670
             146.,5,3,147.,9,8,148.,10,1,149.,10,5,150.,11,3,  ...              00000680
             151.,11,5,152.,10,4,153.,6,1,154.,7,4,155.,6,....                  00000690
             156.,4,3,157.,5,2,158.,7,4,159.,9,3,160.,9,3,...                   00000700
             161.,12,,162.,7,2,163.,4,5,164.,5,4,165.,1,6,...                   00000710
             166.,2,7,167.,6,5,168.,10.,169.,11,4,170.,7,3,...                  00000720
             171.,14,1,172.,14,8,173.,11,9,174.,11,9,175.,13,2,...              00000730
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                176.,11.8,177.,13.3,178.,17.6,179.,15.4,180.,12.4,...     00000740
                181.,10.,182.,11.6,183.,16.5,184.,12.8,185.,11.2,...      00000750
                186.,13.8,187.,15.5,188.,15.4,189.,10.9,190.,6.6,...      00000760
                191.,7.5,192.,14.4,193.,14.1,194.,13.3,195.,12.1,...      00000770
                196.,13.7,197.,13.7,198.,10.7,199.,10.7,200.,13.1,...     00000780
                201.,13.4,202.,12.5,203.,11.7,204.,8.6,205.,7.4,...       00000790
                206.,6.5,207.,12.4,208.,12.4,209.,14.3,210.,14.7,...      00000800
                211.,11.8,212.,11.8,213.,12.1,214.,13.4,215.,10.4,...     00000810
                216.,14.2,217.,12.5,218.,14.2,219.,12.5,220.,11.4,...     00000820
                221.,6.9,222.,8.2,223.,13.6,224.,12.5,225.,12.4,...       00000830
                226.,13.6,227.,14.4,228.,14.4,229.,12.3,230.,16.5,...     00000840
                231.,14.4,232.,11.8,233.,6.8,234.,2.9,235.,8.7,...        00000850
                236.,8.2,237.,8.,238.,8.9,239.,8.5,240.,13.4,...          00000860
                241.,9.8,242.,11.4,243.,5.6,244.,13.7,245.,15.2,...       00000870
                246.,12.6,247.,10.3,248.,11.7,249.,13.7,250.,12.4,...     00000880
                251.,9.5,252.,13.7,253.,11.4,254.,5.5,255.,3.,...         00000890
                256.,6.7,257.,3.8,258.,8.3,259.,12.3,260.,11.,...         00000900
                261.,13.5,262.,12.5,263.,11.5,264.,11.1,265.,11.3,...     00000910
                266.,5.2,267.,3.8,268.,6.8,269.,4.4,270.,8.6,...          00000920
                271.,11.2,272.,7.7,273.,7.7                               00000930
*       MINIMUM TEMPERATURE                                               00000940
FUNCTION MXTT=136.,14.4,137.,17.8,138.,19.3,139.,20.2,140.,22.3,...       00000950
                141.,23.2,142.,20.7,143.,19.8,144.,15.2,145.,19.2,...     00000960
                146.,21.1,147.,22.5,148.,24.2,149.,18.7,150.,16.2,...     00000970
                151.,20.,152.,15.1,153.,13.5,154.,18.2,155.,17.6,...      00000980
                156.,17.7,157.,20.1,158.,19.,159.,20.2,160.,23.1,...      00000990
                161.,18.6,162.,18.8,163.,23.7,164.,19.5,165.,17.9,...     00001000
                166.,21.7,167.,23.1,168.,24.7,169.,23.3,170.,26.,...      00001010
                171.,26.4,172.,23.6,173.,23.7,174.,24.3,175.,26.,...      00001020
                176.,27.2,177.,29.2,178.,29.6,179.,23.5,180.,22.4,...     00001030
                181.,25.4,182.,29.2,183.,30.0,184.,24.2,185.,27.8,...     00001040
                186.,29.9,187.,26.6,188.,21.,189.,20.5,190.,21.3,...      00001050
                191.,23.9,192.,19.8,193.,20.6,194.,21.8,195.,23.9,...     00001060
                196.,19.3,197.,22.2,198.,19.8,199.,19.4,200.,20.3,...     00001070
                201.,19.6,202.,18.5,203.,18.8,204.,17.8,205.,19.7,...     00001080
                206.,19.1,207.,16.3,208.,15.3,209.,23.7,210.,19.5,...     00001090
                211.,18.,212.,21.7,213.,26.8,214.,26.2,215.,20.1,...      00001100
                216.,20.7,217.,19.4,218.,28.8,219.,19.7,220.,19.3,...     00001110
                221.,22.1,222.,26.6,223.,27.2,224.,25.6,225.,26.7,...     00001120
                226.,27.8,227.,27.9,228.,29.7,229.,28.8,230.,23.7,...     00001130
                231.,23.9,232.,23.2,233.,20.6,234.,20.3,235.,24.2,...     00001140
                236.,22.3,237.,22.9,238.,23.8,239.,26.2,240.,22.2,...     00001150
                241.,21.7,242.,18.1,243.,18.2,244.,20.3,245.,19.7,...     00001160
                246.,23.1,247.,26.2,248.,28.7,249.,20.3,250.,23.9,...     00001170
                251.,25.8,252.,20.,253.,18.2,254.,17.9,255.,18.4,...      00001180
                256.,19.1,257.,21.6,258.,24.1,259.,23.3,260.,25.,...      00001190
                261.,21.1,262.,17.6,263.,19.8,264.,19.9,265.,15.7,...     00001200
                266.,15.4,267.,15.2,268.,16.2,269.,17.1,270.,17.9,...     00001210
                271.,17.4,272.,12.5,273.,12.7                             00001220
*       MAXIMUM TEMPERATURE                                               00001230
*                                                                         00001240
*                                                                         00001250
***     INDUCTION DIAPAUSE ACCORDING TO DATA OF LEES 1953                 00001260
*                                                                         00001270
PROCED G=DAGLE(DAYL,DTEMD)                                                00001280
      IF(DAYL.LT.14.,AND.DTEMD.LT.14.) GO TO 1                            00001290
      IF(DAYL.LT.14.,AND.DTEMD.GE.14.,AND.DTEMD.LT.18.) GO TO 2           00001300
      IF(DAYL.LT.14.,AND.DTEMD.GE.18.,AND.DTEMD.LT.21.) GO TO 3           00001310
      IF(DAYL.LT.14.,AND.DTEMD.GE.21.) GO TO 4                            00001320
      IF(DAYL.GE.14.,AND.DAYL.LT.15.,AND.DTEMD.LT.8.0) GO TO 1            00001330
      IF(DAYL.GE.14.,AND.DAYL.LT.15.,AND.DTEMD.GE.8.00 ...                00001340
     ,AND.DTEMD.LT.12.) GO TO 2                                           00001350
      IF(DAYL.GE.14.,AND.DAYL.LT.15.,AND.DTEMD.GE.12.0 ...                00001360
     ,AND.DTEMD.LT.18.) GO TO 3                                           00001370
      IF(DAYL.GE.14.,AND.DAYL.LT.15.,AND.DTEMD.GE.18.) GO TO 4            00001380
      IF(DAYL.GE.15.,AND.DAYL.LT.17.,AND.DTEMD.LT.8.0) GO TO 3            00001390
      IF(DAYL.GE.15.,AND.DAYL.LT.17.,AND.DTEMD.GE.8.0  ...                00001400
     ,AND.DTEMD.LT.11.) GO TO 5                                           00001410
      IF(DAYL.GE.15.,AND.DAYL.LT.17.,AND.DTEMD.GE.11.) GO TO 6            00001420
      IF(DAYL.GE.17.) GO TO 6                                             00001430
    1 G=1.                                                                00001440
      GO TO 7                                                             00001450
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    2 G=.85                                                                 00001460
      GO TO 7                                                               00001470
    3 G=.5                                                                  00001480
      GO TO 7                                                               00001490
    4 G=.2                                                                  00001500
      GO TO 7                                                               00001510
    5 G=.35                                                                 00001520
      GO TO 7                                                               00001530
    6 G=0.                                                                  00001540
      GO TO 7                                                               00001550
    7 CONTINUE                                                              00001560
ENDPRO                                                                      00001570
      F=1.-G                                                                00001580
*       F IS THE FRACTION OF JUVENILES FOR THE SUMMER FORMS AND             00001590
*       G IS THE FRACTION FOR THE WINTER FORMS                              00001600
*                                                                           00001610
*                                                                           00001620
***     CALCULATION  OF PERCENTAGES OF WINTER AND SUMMER FORMS              00001630
*                                                                           00001640
      TPJU=TPJS+TPJW                                                        00001650
      PERCJW=TPJW/TPJU                                                      00001660
*       PERCENTAGE WINTER JUVENILES                                         00001670
      TPAF=AFW+AFS                                                          00001680
      PERCAF=AFW/TPAF                                                       00001690
*       PERCENTAGE WINTER FEMALES                                           00001700
*                                                                           00001710
*                                                                           00001720
***     JUVENILES                                                           00001730
*                                                                           00001740
*       THE MODEL IS STARTED WITH JUVENILES INSENSITIVE TO                  00001750
*       DIAPAUSE CONDITIONS, THIS IS A PART OF THE POPULATION MODEL         00001760
      PUSHJ=INSW(GSJ-1.,0.,1.)                                              00001770
      GSJ=INTGRL(.5,1./(ZJ*RTJ)-PUSHJ*DELX)                                 00001780
      RTJ=LOLJ/5.                                                           00001790
      ZJ=AMAX1(DELT/RTJ,1.-5.*JKO)                                          00001800
      LOLJ=AFGEN(LOLJT,TEMP)                                                00001810
      JKO=(AFGEN(SDJT,TEMP)/LOLJ)**2                                        00001820
      JS=INTGRL(0.,IJS*PUIJ/DELT+JR5)                                       00001830
PARAM IJS=100.                                                              00001840
      PUIJ=IMPULS(0.,FINTIM)                                                00001850
*       AT THE START OF THE PROGRAM 100 ANIMALS ARE INTRODUCED              00001860
*       IN THE LAST BOXCAR OF THE JUVENILES                                 00001870
      JR5=-PUSHJ*ZJ*INSW(JS-1.E-2,0.,JS)*DELX                               00001880
*       RATE OF DEVELOPMENT JUVENILES                                       00001890
*                                                                           00001900
*                                                                           00001910
***     JUVENILES SENSITIVE TO DIAPAUSE CONDITIONS , SUMMER FORMS           00001920
*                                                                           00001930
*       4 AGE CLASSES AND 1 PRECLASS ARE USED TO MIMICK THE                 00001940
*       DISPERSION, THE METHOD OF CONTROLLED DISPERSION IS USED             00001950
*                                                                           00001960
*       THE SIMULATION OF THE DIFFERENT DEVELOPMENTAL STAGES IS             00001970
*       SIMILAR TO THE POPULATION MODEL, THEREFORE FURTHER COMMENTS         00001980
*       ARE OMITTED                                                         00001990
*       THE REVERSIBILITY OF THE DIAPAUSING PROCESS IS SIMULATED            00002000
*       IN A SIMILAR WAY TO THE FIRST BIFURCATION , THE SIZE OF THE         00002010
*       FRACTIONS IS SMALLER AND DEPENDS ON THE AGE OF JUVENILES            00002020
*       AND ADULTS; THE OLDER THE STAGE THE SMALLER THE REVERSING           00002030
*       FRACTION                                                            00002031
*                                                                           00002040
      PUSHJS=INSW(GSJS-1.,0.,1.)                                            00002050
      GSJS=INTGRL(.5,1./(ZJS*RTJS)-PUSHJS*DELX)                             00002060
      RTJS=LOLJS/5.                                                         00002070
      LOLJS=AFGEN(LOLJST,TEMP)                                              00002080
      ZJS=AMAX1(DELT/RTJS,1.-4*JSKO)                                        00002090
      JSKO=(AFGEN(SDJST,TEMP)/LOLJS)**2                                     00002100
      JR50=PUSHJ*J5*ZJ*DELX*F-(2./(RTJS*ZJS))*JS0                           00002110
      JR51=2.*JS0/(RTJS*ZJS)-(PUSHJS*ZJS*JS1*(DELX-AFGEN(DMST1,TEMP)...     00002120
           )+JS1*AFGEN(DMST1,TEMP))+INSW(JS1-1.E-5,0.,1.)                   00002130
      QJS02,40=1. *F*JW01,30*PUSHJW*ZJW*(DELX-AFGEN(DMWT01,30,TEMP))        00002140
      RJS02,40=(PUSHJS*ZJS*JS02,40*(DELX-AFGEN(DMST02,40,TEMP))+    ...     00002150
               JS02,40*AFGEN(DMST02,40,TEMP))*YS02,40                       00002160
      YS02,40=INSW(JS02,40-1.E-5,0.,1.)                                     00002170
      JS0=INTGRL(0.,JR50)                                                   00002180
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      JRS@2,40=PUSHJS*ZJS*JS@1,30*F*(DELX*AFGEN(DMST@1,30,TEMP))+ ...   00002190
             QJS@2,40-RJS@2,40                                          00002200
      JS@1,40=INTGRL(0.,JRS@1,40)                                       00002210
*                                                                       00002220
*                                                                       00002230
***      ADULT FEMALES , SUMMER FORMS                                   00002240
*                                                                       00002250
*        ONLY 5 AGE CLASSES ARE DISTINGUISHED  SO THAT AGEING AND       00002260
*        OVIPOSITION MAY BE SIMULATED WRONGLY.     THE LIMITED          00002270
*        PURPOSE OF THIS SIMULATION MODEL ALLOWS SUCH A SIMPLIFICATION  00002280
*        THE REVERSIBILITY FOR DIAPAUSE IS LESS STRONG AND THIS IS      00002290
*        ACCOUNTED FOR BY USING .8 OF THE FRACTIONS.                    00002300
*        OLD FEMALES ARE LESS SENSITIVE THAN YOUNGER FEMALES.           00002310
*        THEREFORE THE MULTIPLICATION FACTOR .5 IS USED                 00002320
*                                                                       00002330
      GSAFS=INTGRL(.5,1./(ZAFS*RTAFS)-PUAFS)                            00002340
      PUAFS=INSW(GSAFS-1.,0.,DELX)                                      00002350
      RTAFS=LOAFS/5.                                                    00002360
      LOAFS=AFGEN(LOAFST,TEMP)                                          00002370
      ZAFS=AMAX1(DELT/RTAFS,1.-5.*AFSKO)                                00002380
      AFSKO=(AFGEN(SDAFST,TEMP)/LOAFS)**2                               00002390
      RAFS0=SRP*PUSHJS*JS4*ZJS*DELX*AFS0*2./(RTAFS*ZAFS)                00002400
      AFS0=INTGRL(0.,RAFS0)                                             00002410
      RAFS1=2.*AFS0/(RTAFS*ZAFS)-PUAFS*ZAFS*AFS1                        00002420
      RAFS2=PUAFS*ZAFS*AFS1*(1.-.8*G)+PUAFW*ZAFW*AFW1*1.*F*PUAFS* ...   00002430
            ZAFS*AFS2                                                   00002440
      RAFS@3,50=PUAFS*ZAFS*AFS@2,40*(1.-.5*G)+PUAFW*ZAFW*AFW@2,40*...   00002450
              .8*F*PUAFS*ZAFS*AFS@3,50                                  00002460
      AFS@1,50=INTGRL(0.,RAFS@1,50)                                     00002470
*                                                                       00002480
*                                                                       00002490
***      JUVENILES SENSITIVE TO DIAPAUSE CONDITIONS, WINTER FORMS       00002500
*                                                                       00002510
*        THESE ANIMALS ARE SIMULATED IN THE SAME WAY                    00002520
*        AS THE SUMMER JUVENILES                                        00002530
*                                                                       00002540
      GSJW=INTGRL(.5,1./(ZJW*RTJW)-PUSHJW*DELX)                         00002550
      PUSHJW=INSW(GSJW-1.,0.,1.)                                        00002560
      RTJW=LOLJW/5.                                                     00002570
      LOLJW=AFGEN(LOLJWT,TEMP)                                          00002580
      ZJW=AMAX1(DELT/RTJW,1.-4*JWKO)                                    00002590
      JWKO=(AFGEN(SDJWT,TEMP)/LOLJW)**2                                 00002600
      JRW0=PUSHJ*J5*ZJ*DELX*G-(2./(RTJW*ZJW))*JW0                       00002610
      JW0=INTGRL(0.,JRW0)                                               00002620
      JRW1=2.*JW0/(RTJW*ZJW)-(PUSHJW*ZJW*JW1*(DELX-AFGEN(DMWT1,TEMP) ...00002630
           )+JW1*AFGEN(DMWT1,TEMP))*INSW(JW1-1.E-5,0.,1.)               00002640
      QJW@2,40=G*JS@1,30*PUSHJS*ZJS*(DELX-AFGEN(DMST@1,30,TEMP))       00002650
      RJW@2,40=(PUSHJW*ZJW*JW@2,40*(DELX-AFGEN(DMWT@2,40,TEMP))+ ...    00002660
              JW@2,40*AFGEN(DMWT@2,40,TEMP))*YW@2,40                    00002670
      YW@2,40=INSW(JW@2,40-1.E-5,0.,1.)                                 00002680
      JRW@2,40=PUSHJW*ZJW*JW@1,30*(1.-1. *F)*(DELX- ...                 00002690
              AFGEN(DMWT@1,30,TEMP))+QJW@2,40-RJW@2,40                  00002700
      JW@1,40=INTGRL(0.,JRW@1,40)                                       00002710
*                                                                       00002720
*                                                                       00002730
***      ADULT FEMALES , WINTER FORMS                                   00002740
*                                                                       00002750
*        THESE ANIMALS ARE SIMULATED IN THE SAME                        00002760
*        WAY AS SUMMER FEMALES                                          00002770
*                                                                       00002780
      GSAFW=INTGRL(.5,1./(ZAFW*RTAFW)-PUAFW)                            00002790
      PUAFW=INSW(GSAFW-1.,0.,DELX)                                      00002800
      ZAFW=AMAX1(DELT/RTAFW,1.-5.*AFWKO)                                00002810
      RTAFW=LOAFW/5.                                                    00002820
      LOAFW=AFGEN(LOAFWT,TEMP)                                          00002830
      AFWKO=(AFGEN(SDAFWT,TEMP)/LOAFW)**2                               00002840
      RAFW0=SRP*PUSHJW*JW4*ZJW*DELX-(2./(RTAFW*ZAFW))*AFW0              00002850
      AFW0=INTGRL(0.,RAFW0)                                             00002860
      RAFW1=2.*AFW0/(RTAFW*ZAFW)-PUAFW*ZAFW*AFW1                        00002870
      RAFW2=PUAFW*ZAFW*AFW1*(1.-1.*F)+PUAFS*ZAFS*AFS1*.8*G- ...         00002880
            PUAFW*ZAFW*AFW2                                             00002890
      RAFW@3,50=PUAFW*ZAFW*AFW@2,40*(1.-.8*F)+PUAFS*ZAFS*AFS@2,40* ...  00002900
              .5*G-PUAFW*ZAFW*AFW@3,50                                  00002910
      AFW@1,50=INTGRL(0.,RAFW@1,50)                                     00002920
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*                                                                       00002930
*                                                                       00002940
***      TOTALS OF THE DIFFERENT STAGES                                 00002950
*                                                                       00002960
      AFS=AFS1+AFS2+AFS3+AFS4+AFS5+AFS0                                 00002970
*        ADULT FEMALES SUMMER                                           00002980
      SE=INTGRL(0.,AFS*AFGEN(FE2T,TEMP))                                00002990
*        SUMMER EGGS, ACCUMULATED                                       00003000
      AFW=AFW1+AFW2+AFW3+AFW4+AFW5+AFW0                                 00003010
*        ADULT FEMALES WINTER                                           00003020
      WE=INTGRL(0.,AFW*AFGEN(FE1T,TEMP))                                00003030
*        WINTER EGGS, ACCUMULATED                                       00003040
      TPJW=JW1+JW2+JW3+JW4+JW0                                          00003050
*        WINTER JUVENILES, ACCUMULATED                                  00003060
      TPJS=JS1+JS2+JS3+JS4+JS0                                          00003070
*        SUMMER JUVENILES                                               00003080
*                                                                       00003090
*                                                                       00003100
***      DATA FOR PANONYCHUS ULMI                                       00003110
*                                                                       00003120
*                                                                       00003130
*        THE LIMITED PURPOSE ALLOWS SIMPLIFICATION OF THE RELATIONS,    00003140
*        FOR THE ADULT FEMALE OVIPOSITION IS CONSIDERED AGE INDEPENDENT 00003150
*        THE OTHER RELATIONS EQUAL THOSE OF THE POPULATION MODEL        00003160
*                                                                       00003170
FUNCTION LOLJT=0.,100.,10.,50.,11.,25.,15.,10.09,17.,6.83,25.,4.43,...  00003180
          30.,2.38                                                      00003190
AFGEN SDJT=-1.,0.,0.,0.,10.,1.,15.,1.,20.,1.,25.,.9,30.,.6,31.,.6       00003200
AFGEN DMST1=-1.,.0005,0.,.0005,10.,.0003,15.,.0001,20.,.0001,...        00003210
      25.,.0005,30.,.001,31.,.001                                       00003220
AFGEN DMST2=-1.,.0005,0.,.0005,10.,.0003,15.,.0001,20.,.0001,...        00003230
      25.,.0005,30.,.001,31.,.001                                       00003240
AFGEN DMST3=-1.,.0004,0.,.0004,10.,.0002,15.,.0001,20.,.0001,...        00003250
      25.,.0005,30.,.002,31.,.002                                       00003260
AFGEN DMST4=-1.,.0004,0.,.0004,10.,.0002,15.,.0001,20.,.0001,...        00003270
      25.,.0005,30.,.002,31.,.002                                       00003280
FUNCTION LOLJST=0.,100.,10.,20.,15.,5.55,17.,4.26,25.,1.96,30.,1.82     00003290
AFGEN SDJST=-1.,0.,0.,0.,10.,1.,15.,.5,20.,.5,25.,.5,30.,.5,31.,.5      00003300
AFGEN LOAFST=5.,.85,.10.,24,1.15.,25.5,20.,12.0,25.,8.95,30.,7.52       00003310
AFGEN LOAFWT=5.,.85,.10.,24,1.15.,25.5,20.,12.0,25.,8.95,30.,7.52       00003320
AFGEN SDAFST=5.,33.8,10.,17.9,15.,10.6,20.,4.74,25.,2.9,30.,1.7,33.,1.85000003330
AFGEN SDAFWT=5.,33.8,10.,17.9,15.,10.6,20.,4.74,25.,2.9,30.,1.7,33.,1.85000003340
AFGEN DMWT1 =-1.,.0004,0.,.0004,10.,.0002,15.,.0001,20.,.0001,...      00003350
      25.,.0005,30.,.001,31.,.001                                       00003360
AFGEN DMWT2 =-1.,.0004,0.,.0004,10.,.0002,15.,.0001,20.,.0001,...      00003370
      25.,.005 ,30.,.002,31.,.002                                       00003380
AFGEN DMWT3 =-1.,.0004,0.,.0004,10.,.0002,15.,.0001,20.,.0001,...      00003390
      25.,.005 ,30.,.002,31.,.002                                       00003400
AFGEN DMWT4 =-1.,.0004,0.,.0004,10.,.0002,15.,.0001,20.,.0001,...      00003410
      25.,.005 ,30.,.002,31.,.002                                       00003420
FUNCTION LOLJWT=0.,100.,10.,20.,15.,5.55,17.,4.26,25.,1.96,30.,1.82     00003430
AFGEN SDJWT=-1.,0.,0.,0.,10.,1.,15.,.5,20.,.5,25.,.5,30.,.5,31.,.5      00003440
AFGEN FE1T=0.,0.,10.,.53,15.,1.13,20.,1.86,25.,2.93,30.,3.99            00003450
AFGEN FE2T=0.,0.,10.,.53,15.,1.13,20.,1.86,25.,2.93,30.,3.99            00003460
AFGEN FE3T=0.,0.,10.,.53,15.,1.13,20.,1.86,25.,2.93,30.,3.99            00003470
*                                                                       00003480
PRINT TPJS,TPJW,AFS,AFW,WE,G,AFS01,40,AFW01,40,JS01,40,....             00003490
      JW01,40 ,DTEND,TEMP,DAYL,SE,PERCJW,PERCAF                         00003500
PRTPLT WE,SE                                                            00003510
TIMER FINTIM= 10.,DELT=.0416,PRDEL=1.,OUTDEL=.5                         00003520
METHOD RECT                                                             00003530
END                                                                     00003540
STOP                                                                    00003550
ENDJOB                                                                  00003560
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Fig. 67| Computer program for predation in replacement series.

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TITLE RABBINGE                                                          00000010
TITLE REPLACEMENT SERIES OF LARVAE AND ADULT FEMALES                    00000020
*         FUNCTIONAL RESPONSE OF AMBLYSEIUS POTENTILLAE                 00000030
FIXED ITAG1,ITAG2,ITAG3,ITAG4,ITAG5,ITAG6,ITAG7,ITAG8,ITAG9             00000040
FIXED ITAG10,ITAG11,ITAG12,ITAG13,ITAG14,ITAG15,ITAG16                  00000050
STORAGE AY(8),XY1(8),XY2(8),XY3(8),XY4(8),XY5(8),XY6(8),XY7(8)          00000060
STORAGE XY8(8),XY9(8),XY10(8),XY11(8),XY12(8),XY13(4),XY14(4),XY15(4)   00000070
STORAGE XY16(4),BY(4)                                                   00000080
*         RELATIVE RATES OF PREDATION DEPEND ON TEMPERATURE AND         00000090
*         COLOUR LEVEL , THESE VALUES ARE READ FROM THREE DIMENSIONAL   00000100
*         TABULATED FUNCTIONS,                                          00000110
*         TEMPERATURE IS GIVEN ALONG THE X-AXIS AND THE RELATIVE RATES  00000120
*         OF PREDATION ALONG THE Y-AXIS                                 00000130
*         THE POINTS ON THE Z-AXIS ARE GIVEN BY                         00000140
TABLE AY(1-8)=.142,.166,.2,.25,.333,.5,1.,100.                          00000150
*         THE INVERSES OF THE DISTINGUISHED COLOUR LEVELS ON THE Z-AXIS 00000160
TABLE BY(1-4)=0.,3.,5.,7.                                               00000170
*         THE COLOUR LEVELS ON THE Z-AXIS FOR THE THREE-DIMENSIONAL     00000180
*         TABULATED FUNCTION FOR PREY UTILIZATION DEPENDENT ON          00000190
*         TEMPERATURE AND COLOUR LEVEL                                  00000200
*                                                                       00000210
INITIAL                                                                 00000220
*                                                                       00000230
***       INITIALIZING THE TWOVAR FUNCTIONS                             00000240
INCON ITAG1=0.,ITAG2=0.,ITAG3=0.,ITAG4=0.,ITAG5=0.,ITAG6=0.             00000250
INCON ITAG7=0.,ITAG8=0.,ITAG9=0.,ITAG10=0.,ITAG11=0.,ITAG12=0.          00000260
INCON ITAG13=0.,ITAG14=0.,ITAG15=0.,ITAG16=0.                           00000270
*                                                                       00000280
***       INITIAL COLOUR LEVELS                                         00000290
INCON EQT1I=5.                                                          00000300
INCON EQT2I=5.                                                          00000310
INCON EQT3I=5.                                                          00000320
INCON EQT4I=5.                                                          00000330
DYNAMIC                                                                 00000340
      DELX=1./DELT                                                      00000350
      TPL=PPLI*(PRED1+PRED2+PRED3+PRED4)                                00000360
*        NUMBER OF PREDATED LARVAE                                      00000370
      TPPN=PPNI*(PRED5+PRED6+PRED7)                                     00000380
*        NUMBER OF PREDATED PROTONYMPHAE                                00000390
      TPDN=PDNI*(PRED8+PRED9)                                           00000400
*        NUMBER OF PREDATED DEUTONYMPHAE                                00000410
      TPAFS=PAFI*(PRED11+PRED12)                                        00000420
*        NUMBER OF PREDATED ADULT FEMALES                               00000430
      TPAMS=PAMSI*(PRED10+PRED11)                                       00000440
*        NUMBER OF PREDATED ADULT MALES                                 00000450
*                                                                       00000460
*                                                                       00000470
*                                                                       00000480
*                                                                       00000490
*******  PREDATION PROCESS                                              00000500
*                                                                       00000510
***       CALCULATIONS FOR ADULT FEMALE PREDATOR                        00000520
      CTAF=1./CAF                                                       00000530
*        INVERSE COLOUR PER PREDATOR                                    00000540
      CAF=AMIN1(7.,EQT1/(TTAFS+NOT(TTAFS)))                             00000550
*        COLOUR PER PREDATOR,ADULT FEMALE                               00000560
      INCAF=(AFGEN(PV1T,CAF)*PRED1+PPLI*MUF1+AFGEN(PV2T,CAF)*PRED5* ... 00000570
            PPNI*MUF2+AFGEN(PV3T,CAF)*PRED8+PDNI*MUF3+AFGEN(PV3T,CAF),,,00000580
            +PRED10*PAMSI*MUF3+AFGEN(PV4T,CAF)*PRED12*PAFI*MUF4)        00000590
*        INCREASE COLOUR                                                00000600
      DECAF=AFGEN(RDCV1,TEMP)*IN3W(EQT1-1.E-2,0.,EQT1)                  00000610
*        DECREASE COLOUR                                                00000620
      EQT1=INTGRL(EQT1I,INCAF-DECAF)                                    00000630
*        NUMBER OF COLOUR UNITS FEMALES PER UNIT OF SURFACE             00000640
*                                                                       00000650
***       CALCULATIONS FOR DEUTONYMPHAE PREDATOR                        00000660
      CTDN=1./CDN                                                       00000670
*        INVERSE COLOUR PER PREDATOR                                    00000680
      CDN=AMIN1(7.,EQT2/(TTDN+NOT(TTDN)))                               00000690
*        COLOUR PER PREDATOR                                            00000700
      INCDN=PV5*PRED2*PPLI+PV6*PRED5*PPNI                               00000710
*        INCREASE COLOUR                                                00000720
      DECDN=AFGEN(RDCV2,TEMP)*IN3W(EQT2,0.,EQT2)                        00000730
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*       DECREASE COLOUR                                                 00000740
      EQT2=INTGRL(EQT2I,INCDN-DECDN)                                    00000750
*       NUMBER OF COLOUR UNITS DEUTONYMPHS PER UNIT OF SURFACE          00000760
*                                                                       00000770
***     CALCULATIONS FOR PROTONYMPHAE PREDATOR                          00000780
      CTPN=1./CPN                                                       00000790
*       INVERSE COLOUR PER PREDATOR                                     00000800
      CPN=AMIN1(7.,EQT3/(TTPN+NOT(TTPN)))                               00000810
*       COLOUR PER PREDATOR                                             00000820
      INCPN=PV7*PRED3*PPLI                                              00000830
*       INCREASE COLOUR                                                 00000840
      DECPN=AFGEN(RDCV3,TEMP)*INSW(EQT3,0.,EQT3)                        00000850
*       DECREASE COLOUR                                                 00000860
      EQT3=INTGRL(EQT3I,INCPN-DECPN)                                    00000870
*       NUMBER OF COLOUR UNITS PROTONYMPHAE PER UNIT OF SURFACE         00000880
*                                                                       00000890
***     CALCULATIONS FOR ADULT MALE PREDATOR                            00000900
      CTAM=1./CAM                                                       00000910
*       INVERSE COLOUR PER PREDATOR                                     00000920
      CAM=AMIN1(7.,EQT4/(TTAMS+NOT(TTAMS)))                             00000930
*       COLOUR PER PREDATOR                                             00000940
      INCAM=PV6*PRED4*PPLI*PV9*PRED7*PPNI*PV10*PRED9*PDNI*PV11*  ...    00000950
          PRED11*PAMSI                                                  00000960
*       INCREASE COLOUR                                                 00000970
      DECAM=AFGEN(RDCV2,TEMP)*INSW(EQT4-1.E-5,0.,EQT4)                  00000980
*       DECREASE COLOUR                                                 00000990
      EQT4=INTGRL(EQT4I,INCAM-DECAM)                                    00001000
*       NUMBER OF COLOUR UNITS ADULT MALES PER UNIT OF SURFACE          00001010
*                                                                       00001020
*                                                                       00001030
***     CALCULATIONS FOR ADULT MALES RELATIVE PREDATION RATES           00001040
      PRED1=TWOVAR(RRL11, 8,AY,XY1,CTAF,TEMP,ITAG1)*TTAFS*CFS*SENP1     00001050
*       LARVAE PREY VERSUS ADULT FEMALE PREDATOR                        00001060
      PRED2=TWOVAR(RRL11, 8,AY,XY2,CTDN,TEMP,ITAG2)*TTDN*CFS*SENP2*RF1  00001070
*       LARVAE PREY VERSUS DEUTONYMPH PREDATOR                          00001080
      PRED3=TWOVAR(RRL11, 8,AY,XY3,CTPN,TEMP,ITAG3)*TTPN*CFS*SENP3*RF2  00001090
*       LARVAE PREY VERSUS PROTONYMPH PREDATOR                          00001110
      PRED4=TWOVAR(RRL11, 8,AY,XY4,CTAM,TEMP,ITAG4)*TTAMS*  ...         00001120
          CFS*SENP4*RF3                                                 00001130
*       LARVAE PREY VERSUS ADULT MALE PREDATOR                          00001140
      PRED5=TWOVAR(RRP11, 8,AY,XY5,CTAF,TEMP,ITAG5)*TTAFS*CFS*SENP5     00001150
*       PROTONYMPH PREY VERSUS ADULT FEMALE PREDATOR                    00001160
      PRED6=TWOVAR(RRP11, 8,AY,XY6,CTDN,TEMP,ITAG6)*TTDN*CFS*SENP6*RF4  00001170
*       PROTONYMPH PREY VERSUS DEUTONYMPH PREDATOR                      00001180
      PRED7=TWOVAR(RRP11, 8,AY,XY7,CTAM,TEMP,ITAG7)*TTAMS*CFS*SENP7*RF5 00001190
*       PROTONYMPH PREY VERSUS ADULT MALE PREDATOR                      00001200
      PRED8=TWOVAR(RRD11, 8,AY,XY8,CTAF,TEMP,ITAG8)*TTAFS*CFS*SENP8     00001210
*       DEUTONYMPH PREY VERSUS ADULT FEMALE PREDATOR                    00001220
      PRED9=TWOVAR(RRD11, 8,AY,XY9,CTAM,TEMP,ITAG9)*TTAMS*CFS*SENP9*RF6 00001230
*       DEUTONYMPH PREY VERSUS ADULT MALE PREDATOR                      00001240
      PRED10=TWOVAR(RRD11, 8,AY,XY10,CTAF,TEMP,ITAG10)*TTAFS*  ...      00001250
          CFS*SENP10*RF7                                                00001260
*       ADULT MALE PREY VERSUS ADULT FEMALE PREDATOR                    00001270
      PRED11=TWOVAR(RRAF1, 8,AY,XY11,CTAM,TEMP,ITAG11)*TTAMS*  ...      00001280
          CFS*SENP11*RF8                                                00001290
*       ADULT MALE PREY VERSUS ADULT MALE PREDATOR                      00001300
      PRED12=TWOVAR(RRAF1, 8,AY,XY12,CTAF,TEMP,ITAG12)*TTAFS*  ...      00001310
          CFS*SENP12                                                    00001320
*       ADULT FEMALE PREY VERSUS ADULT FEMALE PREDATOR                  00001330
PARAM RF1=.66,RF2=.33,RF3=.66,RF4=.66,RF5=.66,RF6=.33,RF7=1.,RF8=1.     00001340
*       MULTIPLICATION FACTORS FOR THE RELATIVE PREDATION RATES         00001350
*       THE JUVENILE PREDATION ACTIVITY IS RELATED TO THE               00001360
*       EXPERIMENTALLY DETERMINED ADULT FEMALE PREDATION RATE           00001370
*       THE FACTORS ARE THE VALUES OF THE QUOTIENT PREDATOR STAGE SIZE  00001380
*       TO PREY STAGE SIZE, RELATED TO THESE VALUES FOR THE ADULT       00001390
*       FEMALE PREDATOR  THE FACTORS ARE .33 , .66 OR 1.                00001400
*       THE REGULARITY BEING DUE TO THE ALLOMETRIC GROWTH               00001410
*       OF BOTH, PREY AND PREDATOR.                                     00001420
*       IN A SMALL SCALE EXPERIMENT THESE FACTORS WERE VERIFIED         00001430
*       ADULT MALE PREDATION ACTIVITY PROVED TO EQUAL THE               00001440
*       DEUTONYMPH PREDATION ACTIVITY                                   00001450
*                                                                       00001460
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***      SENSITIVITY FACTORS FOR THE PREDATION RATES                    00001470
PARAM SENP1=1.,SENP2=1.,SENP3=1.,SENP4=1.,SENP5=1.,SENP6=1.,SENP7=1.    00001480
PARAM SENP8=1.,SENP9=1.,SENP10=1.,SENP11=1.,SENP12=1.                   00001490
*                                                                       00001500
*                                                                       00001510
***      DATA PREDATION                                                 00001520
*                                                                       00001530
***      RELATIONS BETWEEN TEMPERATURE AND RELATIVE RATE OF             00001540
***      PREDATION AT A CERTAIN COLOUR LEVEL, SEE TABLE A4              00001550
*                                                                       00001560
***      LARVAE                                                         00001570
*                                                                       00001580
FUNCTION RRL11=0.,0.,7.5,0.,10.,0.,13.,.1,15.,.7,20.,.9,   ...         00001590
      25.,1.3,30.,1.7,33.,1.7                                           00001600
FUNCTION RRL12=0.,0.,7.5,0. ,10.,.1 ,13.,.5 ,15.,1.6 ,20.,2.2,  ...    00001610
      25.,3.0,30.,3.8,33.,3.8                                           00001620
FUNCTION RRL13=0.,0.,7.5,0. ,10.,.2 ,13.,.6 ,15.,2.4,20.,6.0,  ...     00001630
      25.,9.8,30.,13.5,33.,13.5                                         00001640
FUNCTION RRL14=0.,0.,7.5,0. ,10.,.2 ,13.,.8 ,15.,2.9,20.,8.5,  ...     00001650
      25.,14.,30.,16.,33.,16                                            00001660
FUNCTION RRL15=0.,0.,7.5,0. ,10.,.2 ,13.,.9 ,15.,3.4,20.,10.5,  ...    00001670
      25.,18.,30.,20.,33.,20.                                           00001680
FUNCTION RRL16=0.,0.,7.5,0. ,10.,.2 ,13.,1.2,15.,3.6,20.,11.8,  ...    00001690
      25.,20.,30.,27.,33.,27.                                           00001700
FUNCTION RRL17=0.,0.,7.5,0. ,10.,.4 ,13.,1.6,15.,3.7,20.,14.,  ...     00001710
      25.,21.8,30.,30.,33.,30.                                          00001720
FUNCTION RRL18=0.,0.,7.5,0. ,10.,.4 ,13.,1.6,15.,3.8,20.,14.,  ...     00001730
      25.,22.2,30.,34.,33.,34.                                          00001740
*                                                                       00001750
***      PROTONYMPHAE                                                   00001760
*                                                                       00001770
FUNCTION RRP11=0.,0.,7.5,0.,10.,.15,13.,.5,15.,.4,20.,1.3,   ...        00001780
      25.,2.5,30.,3. ,33.,3.                                            00001790
FUNCTION RRP12=0.,0.,7.5,0. ,10.,.5,13.,.8,15.,1. ,20.,3.0,   ...       00001800
      25.,4.9,30.,6.8,33.,6.8                                           00001810
FUNCTION RRP13=0.,0.,7.5,0. ,10.,.6,13.,2.2,15.,3.0,20.,5.4,   ...      00001820
      25.,7.8,30.,10.3,33.,10.3                                         00001830
FUNCTION RRP14=0.,0.,7.5,0. ,10.,.75,13.,2.7,15.,4. ,20.,7.4,   ...     00001840
      25.,10.8,30.,14.2,33.,14.2                                        00001850
FUNCTION RRP15=0.,0.,7.5,0. ,10.,1.4,13.,3.6,15.,5. ,20.,8.6,   ...     00001860
      25.,12.1,30.,15.7,33.,15.7                                        00001870
FUNCTION RRP16=0.,0.,7.5,0. ,10.,1.8,13.,4.4,15.,6. ,20.,10.2,   ...    00001880
      25.,14.6,30.,18. ,33.,18.                                         00001890
FUNCTION RRP17=0.,0.,7.5,0. ,10.,1.9,13.,4.7,15.,6.4,20.,11.2,   ...    00001900
      25.,15.7,30.,19.,33.,19.                                          00001910
FUNCTION RRP18=0.,0.,7.5,0. ,10.,2. ,13.,5.,15.,6.5,20.,11.5,   ...     00001920
      25.,15.5,30.,19.2,33.,19.2                                        00001930
*                                                                       00001940
***      DEUTONYMPHAE                                                   00001950
*                                                                       00001960
FUNCTION RRD11=0.,0.,7.5,0.,13.,0.,15.,0.,20.,0.,25.,0.,30.,0.,33.,0.  00001970
FUNCTION RRD12=0.,0.,7.5,0.,10.,0.,13.,.1,15.,.15,20.,.35,25.,.4,   ... 00001980
      30.,.5,33.,.5                                                     00001990
FUNCTION RRD13=0.,0.,7.5,0.,10.,.15,13.,.3,15.,.4,20.,.7,25.,1.,   ...  00002000
      30.,1.2,33.,1.2                                                   00002010
FUNCTION RRD14=0.,0.,7.5,0.,10.,.8,13.,1.8,15.,2.5,20.,4.2,25.,5.9, ... 00002020
      30.,7.6,33.,7.6                                                   00002030
FUNCTION RRD15=0.,0.,7.5,0.,10.,1.2,13.,2.8,15.,3.9,20.,6.7,25.,9.4,... 00002040
      30.,12.1,33.,12.1                                                 00002050
FUNCTION RRD16=0.,0.,7.5,0.,10.,1.6,13.,3.5,15.,4.8,20.,8.,25.,11.2,... 00002060
      30.,14.3,33.,14.3                                                 00002070
FUNCTION RRD17=0.,0.,7.5,0.,10.,2.,13.,4.1,15.,5.5,20.,8.9,25.,12.3,... 00002080
      30.,15.8,33.,15.8                                                 00002081
FUNCTION RRD18=0.,0.,7.5,0.,10.,2.1,13.,4.4,15.,6.,20.,9.6,25.,13.3,... 00002090
      30.,17.2,33.,17.2                                                 00002100
*                                                                       00002110
***      ADULT FEMALE                                                   00002120
*                                                                       00002130
FUNCTION RRAF1=0.,0.,7.5,0. ,10.,0. ,13.,0.2,15.,.05,20.,.15,   ...     00002140
      25.,.2,30.,.3 ,33.,.3                                             00002150
FUNCTION RRAF2=0.,0.,7.5,0.,10.,0.,13.,.1 ,15.,.15,20.,.3 ,   ...      00002160
      25.,.5,30.,.7,33.,.7                                              00002170
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FUNCTION RRAF3=0.,0.,7.5,0.,10.,0.,13.,.15,15.,.2 ,20.,.6 ,   ...
     25.,1. ,30.,1.3 ,33.,1.3
FUNCTION RRAF4=0.,0.,7.5,0.,10.,.2 ,13.,.5 ,15.,.7 ,20.,1.1 ,   ...
     25.,1.5,30.,2.,33.,2.
FUNCTION RRAF5=0.,0.,7.5,0.,10.,.3 ,13.,.85,15.,1.25,20.,2.15,   ...
     25.,3.2 ,30.,4. ,33.,4.
FUNCTION RRAF6=0.,0.,7.5,.3 ,10.,.75,13.,1.3,15.,1.7 ,20.,2.7 ,   ...
     25.,3.75,30.,4.75,33.,4.75
FUNCTION RRAF7=0.,0.,7.5,.35,10.,.9 ,13.,1.6,15.,1.9,20.,3.05 ,...
     25.,4.2 ,30.,4.6 ,33.,4.
FUNCTION RRAF8=0.,0.,7.5,.4 ,10.,.9 ,13.,1.5,15.,2. ,20.,3.1  ,...
     25.,4.2 ,30.,4.6 ,33.,4.
*
*
***      MULTIPLICATION FACTOR FOR TEMPERATURE
***      DEPENDENCY OF PREY UTILIZATION
*
      MUF1=TWOVAR(MUF11,4,BY,XY13,CAF,TEMP,ITAG13)
      MUF2=TWOVAR(MUF21,4,BY,XY14,CAF,TEMP,ITAG14)
      MUF3=TWOVAR(MUF31,4,BY,XY15,CAF,TEMP,ITAG15)
      MUF4=TWOVAR(MUF41,4,BY,XY16,CAF,TEMP,ITAG16)
*
*
***      RELATION BETWEEN TEMPERATURE AND MULTIPLICATION FACTOR
***      AT A CERTAIN COLOUR LEVEL , SEE TABLE BY
*
FUNCTION MUF11=0.,1.,35.,1.
FUNCTION MUF12=0.,1.,35.,1.
FUNCTION MUF13=0.,1.,35.,1.
FUNCTION MUF14=0.,1.,35.,1.
FUNCTION MUF21=0.,1.,7.5,1.,15.,1.,25.,1.
FUNCTION MUF22=0.,1.,7.5,1.,15.,1.1,25.,.92
FUNCTION MUF23=0.,1.,7.5,1.,15.,1.4,25.,.9
FUNCTION MUF24=0.,1.,7.5,1.,15.,1.6,25.,.85
FUNCTION MUF31=0.,1.,7.5,1.,15.,1.,25.,1.
FUNCTION MUF32=0.,1.,7.5,1.,15.,1.2,25.,.9
FUNCTION MUF33=0.,1.,7.5,1.,15.,1.4,25.,.8
FUNCTION MUF34=0.,1.,7.5,1.,15.,1.8,25.,.7
FUNCTION MUF41=0.,1.,7.5,1.,15.,1.,25.,1.
FUNCTION MUF42=0.,1.,7.5,1.,15.,1.2,25.,.9
FUNCTION MUF43=0.,1.,7.5,1.,15.,1.5,25.,.85
FUNCTION MUF44=0.,1.,7.5,1.,15.,1.9,25.,.8
*
***      RELATION BETWEEN COLOUR LEVEL AND PREY UTILIZATION
*
AFGEN PV1T=0.,1.7,1.,1.2,2.,.88,3.,.6,4.,.43,5.,.34,6.,.29,7.,.23
*        PREY LARVAE OPPOSITE ADULT FEMALE PREDATOR
AFGEN PV2T=0.,.3.,1.,2.,2.,1.35,3.,.9,4.,.65,5.,.5,6.,.4,7.,.35
*        PREY PROTONYMPHAE OPPOSITE ADULT FEMALE PREDATOR
AFGEN PV3T=0.,.4.,1.,3.,2.,2.2,3.,1.3,4.,1.,5.,.7,6.,.55,7.,.45
*        PREY DEUTONYMPHE OPPOSITE ADULT FEMALE PREDATOR
AFGEN PV4T=0.,.4.5,1.,3.,2.,2.4,3.,1.6,4.,1.2,5.,.9,6.,.7,7.,.6
*        PREY ADULT FEMALE OPPOSITE ADULT FEMALE PREDATOR
*
*
***      PREY UTILIZATION OF THE OTHER PREY STAGE AND PREDATOR STAGE
***      COMBINATIONS ARE CALCULATED WITH THE RELATIONS
***      DETERMINED FOR THE ADULT FEMALE PREDATOR
***      IN THESE CALCULATIONS THE SIZE OF THE PREY SPECIES
***      IS TAKEN INTO ACCOUNT
*
      PV5=AFGEN(PV2T,CDN)
*        LARVAE OF THE PREY VERSUS DEUTONYMPHAE OF THE PREDATOR
*        EQUALS PROTONYMPHAE OF THE PREY VERSUS ADULT FEMALE
*        OF THE PREDATOR
      PV6=AFGEN(PV3T,CDN)
*        PROTONYMPHAE OF THE PREY VERSUS DEUTONYMPHAE OF THE
*        PREDATOR EQUALS DEUTONYMPHAE OF THE PREY VERSUS
*        ADULT FEMALE OF THE PREDATOR
      PV7=AFGEN(PV3T,CPN)
*        LARVAE OF THE PREY VERSUS PROTONYMPHAE OF THE PREDATOR
*        EQUALS DEUTONYMPHAE OF THE PREY VERSUS ADULT FEMALE PREDATORS
      PV8=AFGEN(PV2T,CAM)
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*       THE PREY UTILIZATION OF THE ADULT MALE PREDATOR IS SET          00002910
*       EQUAL TO THAT OF THE DEUTONYMPHAE                               00002920
      PV9=AFGEN(PV3T,CAN)                                               00002930
      PV10=AFGEN(PV4T,CAN)                                              00002940
      PV11=AFGEN(PV4T,CAN)                                              00002950
*                                                                       00002960
***     RELATIVE RATES OF DECREASE COLOUR LEVEL                         00002970
*                                                                       00002980
AFGEN RDCV1=0.,0.,10.,.01,15.,.45,20.,.78,25.,1.10,30.,1.43             00002990
*       ADULT FEMALE PREDATOR                                           00003000
AFGEN RDCV2=0.,0.,10.,.01,15.,.22,20.,.4,25.,.5,30.,.73                 00003010
*       DEUTONYMPHAE PREDATOR                                           00003020
AFGEN RDCV3=0.,0.,10.,.01,15.,.22,20.,.4,25.,.5,30.,.73                 00003030
*       PROTONYMPHAE PREDATOR                                           00003040
PARAM CFS=.76                                                           00003050
*       MULTIPLICATION FACTOR SURFACE, THE REPLACEMENT EXPERIMENT       00003060
*       IS DONE ON A LARGER SURFACE THAN THE PROCESS EXPERIMENTS        00003070
PARAM TEMP=15.                                                          00003080
*       TEMPERATURE                                                     00003090
*                                                                       00003100
***     NUMBER OF PREYS AND PREDATORS IN THE EXPERIMENT                 00003110
PARAM TTAFS=1.,TTDN=0.,TTPN=0.,TTAMS=0.                                 00003120
PARAM PPNI=0.,PDNI=0.,PAFI=0.,PAMSI=0.,PPLI=10.                         00003130
*                                                                       00003140
*                                                                       00003150
PRINT TPL,TPPN,TPDN,TPAFS,CAF,CTAF                                      00003160
METHOD RECT                                                             00003170
TIMER FINTIM=10.,OUTDEL=.2,DELT=.0417,PRDEL=.2                          00003180
END                                                                     00003190
STOP                                                                    00003200
ENDJOB                                                                  00003210
```

Fig. 68 | Computer program for micro-weather in a hedgerowed orchard coupled to a population model of *Panonychus ulmi* or *Amblyseius potentillae.*

```
TITLE MICROCLIMATE

*       DAILY TOTAL OF RADIATION
MACRO DTOT=DLYTOT(DTOTI,RATE)
      DTOTI=INTGRL(DTOTI,RATE)
      DTOT=DTOTI-ZHOLD(IMPULS(DELT,1.)*KEEP,DTOTI)
*       THE ACCUMULATOR IS EMPTIED AFTER MIDNIGHT,
*       SO CONTENTS ARE AVAILABLE FOR PRINTING
ENDMAC

*       LEAF TEMPERATURE
MACRO TLF=PENMAN(RAD)
      RS=AFGEN(RSLTB,0.7*RAD)
      TLF=TEMP+(PSCH*(RA+RS)*(RAD-LWR)/RHOCP-VPD)/XXX
      XXX=PSCH*(RA+RS)/RA+SLOPE
ENDMAC
CONST PSCH=0.67,RHOCP=1250.
*       PSYCHROMETRIC CONSTANT AND VOLUMETRIC HEAT CAPACITY OF AIR

*       TOTAL RELATIVE RATE OF TRANSFER IN POPULATION MODEL
MACRO RR=SUMTLF(LONGEV,N)
      R'1,12'=CFSR'1,12'/AFGEN(LONGEV,TLF'1,12')
      RR=N*(SUM1(R'1,12') )
ENDMAC


*******          SECTION 1          **********************************

*       CALCULATION EXPOSITION OF LEAVES TO SUN

*       CALCULATION PROJECTION OF LEAF CLASSES
INITIAL
STORAGE F(9),OPGA(11)
TABLE F(1-9)=0.222,0.193,0.164,0.125,0.097,0.085,0.057,0.034,0.023
*       LEAF ANGLE DISTRIBUTION FUNCTION
      RAD=PI/180.
CONST PI=3.1415927
NOSORT
/     DIMENSION S(9,10),Z(9,10)
FIXED IS,IL,SN
        DO 8 IS=1,9
        FS=(10*IS-5)*RAD
        SI=SIN(FS)
        CO=COS(FS)
        D=0.
          DO 5 IL=1,9
          FL=(10*IL-5)*RAD
          A=SI*COS(FL)
          B=CO*SIN(FL)
          C=A
          IF (IS.GE.IL) GO TO 1
          SQ=SQRT(B*B-A*A)
          C=2.*(A*ATAN(A/SQ)+SQ)/PI
    1     D=D+C*F(IL)
            DO 4 SN=1,9
            FN=SN/10.
            FA=FN-A
            C=1.
            IF (IS.LT.IL) GO TO 3
            IF (FN-B.GE.A) GO TO 4
            IF (FN+B.GT.A) GO TO 2
            C=0.
            GO TO 4
    2       SQ=SQRT(B*B-FA*FA)
            C=ATAN(FA/SQ)/PI+0.5
            GO TO 4
    3       IF (FN-A.GE.B) GO TO 4
            IF (FN+A.GE.B) GO TO 2
            SQ=SQRT(B*B-FA*FA)
            C=ATAN(FA/SQ)
            FA=FN+A
```

```
            SQ=SQRT(B*B-FA*FA)
            C=(ATAN(FA/SQ)+C)/PI
    4       S(IL,SN)=C
    5     S(IL,10)=1.
        E=0.
          DO 7 SN=1,10
          C=0.
            DO 6 IL=1,9
    6       C=C+F(IL)*S(IL,SN)
          Z(IS,SN)=C-E
    7     E=C
    8   OPGA(IS+1)=D
      OPGA( 1)=OPGA( 2)
      OPGA(11)=OPGA(10)

SORT
*       LOCATION PARAMETERS
PARAM LAT=52.
*       LATITUDE SITE
      CO=COS(RAD*LAT)
*       COSINE LATITUDE
      SI=SIN(RAD*LAT)
*       SINE LATITUDE
PARAM LONG=-5.
      DLONG=AMOD( (LONG+360.)/15.,1.)
*       DIFFERENCE IN HOURS WITH THE STANDARD SOLAR TIME


DYNAMIC

*       PROJECTION OF THE LEAVES IN THE DIRECTION OF THE SUN

      IS=FS/10.+1.
**      TEMPERATE ZONE
      FL=FS/10.+1.5
      SN=FL
      FN=FL-SN
      OPG=OPGA(SN)*(1.-FN)+FN*OPGA(SN+1)


*******           SECTION 2          **********************************

*       CALCULATION WEATHER CONDITIONS

*       THIS SECTION CONCERNS THE CALCULATION OF VARIABLES
*       USED IN THE PENMAN FORMULA

PARAM START=136.
*       START OF THE MODEL IN DAYS
      DAY=TIME+START
INCON SOLST=10.173
      DEC=-23.45*COS(PI*(DAY+SOLST)/182.621)
*       DECLINATION
      COSDEC=COS(RAD*DEC)
*       COSINE DECLINATION
      SINDEC=SIN(RAD*DEC)
*       SINE DECLINATION
      HOUR=AMOD(TIME,1.)*24.
*       HOUR OF THE DAY
      HA=PI*(HOUR+12.-DLONG)/12.
*       HOUR ANGLE
      SINSS=SI*SINDEC+CO*COSDEC*COS(HA)
*        SINE ELEVATION OF SUN
```

```
*        CALCULATION OF AIR TEMPERATURE FROM MINIMUM AND MAXIMUM

PARAM HEAT  = 14.
      TEMP  = INSW(AND(HOUR-RISE,HEAT-HOUR)-0.5,VALSS,VALSR)
*        AIR TEMPERATURE
INCON RISEI = 5.
      RISE  = RISEI+ZHOLD(AND(SNHSS,-LSNHS)-0.5, ...
              HOUR-SNHSS/(NOT(SNHSS-LSNHS)+SNHSS-LSNHS)-RISEI)
*        INTERPOLATION AFTER OCCURRENCE
      LSNHS = INTGRL(-0.5,(SNHSS-LSNHS)/DELT)
*        ELEVATION OF SUN AT LAST TIME STEP
      VALSR = VALAV-COS(PI*(HOUR-RISE)/(HEAT-RISE) )*VALAMP
      VALSS = VALAV+COS(PI*TIM/(24.-HEAT+RISE) )*VALAMP
*        COURSE OF AIR TEMPERATURE BEFORE AND AFTER HEAT OF THE DAY,
*        PROFILED IN SINE WAVE
      TIM   = INSW(HOUR-HEAT,HOUR+24.-HEAT,HOUR-HEAT)
      VALAV = 0.5*(MAXT+MINT)
*        AVERAGE AIR TEMPERATURE
      VALAMP= 0.5*(MAXT-MINT)
*        AMPLITUDE OF AIR TEMPERATURE
      MAXT  = AFGEN(MXTT,DAY)
      MINT  = AFGEN(MNTT,DAY)

      TA239=TEMP+239.
      EA=AFGEN(EATB,DAY)
*        VAPOUR PRESSURE AIR
      ES=6.11*EXP(17.4*TEMP/TA239)
*        VAPOUR PRESSURE SATURATED
      VPD=ES-EA
*        VAPOUR PRESSURE DEFICIT
      SLOPE=4158.6*ES/(TA239*TA239)
*        SLOPE OF THE SATURATION CURVE
      LWR=(0.56-0.079*SQRT(.75*EA) )*(1.-0.9*FOV)* ...
          5.6696E-8*(TEMP+273.15)**4
*        LONG WAVE RADIATION, CALCULATED WITH BRUNT FORMULA


*        RADIATION

      COSHS=SQRT(1.-SNHS*SNHS)
*        COSINE ELEVATION OF SUN
      SNHS=AMAX1(0.,SNHSS)
      FS=ATAN(SNHS/COSHS)/RAD
*        INCLINATION OF THE SUN IN DEGREES
PARAM CCL=2.
      SUNDCL=CCL*AFGEN(SUNDT,FS)
*        INCIDENT DIRECT RADIATION WITH CLEAR SKY
      DIFCL=CCL*AFGEN(DIFCLT,FS)
*        INCIDENT DIFFUSE RADIATION WITH CLEAR SKY
      CRC=SUNDCL+DIFCL
*        CURRENT RADIATION CLEAR
PARAM COV=1.7
      DIFOV=COV*AFGEN(DIFOVT,FS)
*        INCIDENT DIFFUSE RADIATION WITH OVERCAST SKY
      CRO=DIFOV
*        CURRENT RADIATION OVERCAST
      DRC=DLITOT(DRCI,CRC*86400.)
*        DAILY RADIATION CLEAR
INCON DROI=6.6E6,DRCI=3.3E7
      DRO=DLITOT(DROI,CRO*86400.)
*        DAILY RADIATION OVERCAST
      DRCP=ZHOLD(IMPULS(0.,1.),DRC)
*        DAILY RADIATION CLEAR, YESTERDAY
      DROP=ZHOLD(IMPULS(0.,1.),DRO)
*        DAILY RADIATION OVERCAST, YESTERDAY
      DTR=AFGEN(DTRT,DAY)*10000.
*        DAILY TOTAL RADIATION
      A=(DTR-DROP)/(NOT(DRCP-DROP)+DRCP-DROP)
      FCL=LIMIT(0.,1.,A)
*        FRACTION CLEAR
      FOV=1.-FCL
*        FRACTION OVERCAST

      WIND=AFGEN(WINDTB,DAY)*FRACT
PARAM FRACT=.2
```

```
*        WIND INSIDE ORCHARD IS 20 PER CENT, OF THAT ABOVE
PARAM WIDTH=0.07
*        WIDTH OF THE LEAF
      RA=92.5*SQRT(COEFF*WIDTH/WIND)
*        LAMINAR RESISTANCE TO TRANSPORT OF HEAT, WATER VAPOUR AND CO2,
*        AFTER PARLANGE, 1971
      COEFF=(NOT(SNHS)+1.)*0.75


*******            SECTION 3            ********************************

*        CALCULATION RELATIVE RATES AT NIGHT

NOSORT
      IF (SNHS.GT.0.) GO TO 9
      TLF=PENMAN(RAD0)
PARAM RAD0=0.
      RFE=AFGEN(FEC,TLF)
      RRE=30./AFGEN(LOLET,TLF)
      RRJ=15./AFGEN(LOLJT,TLF)
      RRJS=10./AFGEN(LOLJST,TLF)
      RRFS=10./AFGEN(LOLFST,TLF)
      RRF=10./AFGEN(LOLAFT.TLF)
      GO TO 10
    9 CONTINUE
SORT


*******            SECTION 4            ********************************

*        CALCULATION LEAF TEMPERATURES

PARAM SCAT=0.4
*        SCATTERING COEFFICIENT
      RAD1=(1.-SCAT)*(DIFCL*FCL+DIFOV*FOV)
*        DIFFUSE RADIATION
PARAM SNIN'2,11'=0.05,0.15,0.25,0.35,0.45,0.55,0.65,0.75,0.85,0.95
*        SINE OF INCIDENCE
      RAD'2,11'=RAD1+SNIN'2,11'*SUNPER*(1.-SCAT)
      SUNPER=SUNDCL/(NOT(SNHS)+SNHS)
*        LIGHT INTENSITY OF THE SUN ON A PLANE PERPENDICULAR
*        TO THE SUN BEAMS
      TLF'1,11'=PENMAN(RAD'1,11')
*        TEMPERATURE OF LEAVES RECEIVING ONLY DIFFUSE LIGHT, AND
*        10 TEMPERATURES OF LEAVES RECEIVING ALSO DIRECT RADIATION,
*        IN DEPENDENCE OF THEIR POSITION WITH RESPECT TO THE SUN
      TLF12=TEMP
*        TEMPERATURE OF COMPLETELY SHADED LEAVES EQUALS AIR TEMPERATURE


*******            SECTION 5            ********************************

*        CALCULATION OF THE FRACTION OF LEAVES IN EACH
*        OF THE TEMPERATURE CLASSES

*        CALCULATION OF THE DIFFERENCE IN AZIMUTH BETWEEN
*        THE SUN AND THE ROWS
      B=SIN(HA)*COSDEC/COSHS
      AZ=ATAN(B/SQRT(1.-B*B) )
*        AZIMUTH
PARAM RICHT=45.
*        RICHT IS THE AZIMUTH OF THE ROWS
      RAZ=ABS(AZ-RAD*RICHT)
*        DIFFERENCE BETWEEN DIRECTION OF THE ROWS AND THE SUN
      SHH=HROW*COSHS*SIN(RAZ)/(NOT(SNHS)+SNHS)
      SH=AMIN1(WPATH,SHH)
*        CALCULATION OF THE SHADOW CAST BY THE ROW ONTO THE PATH
```

```
PARAM HROW=2.,WROW=2.,WPATH=2.,LAIM=4.
*       HEIGHT ROW, WIDTH ROW, WIDTH PATH, LEAF AREA INDEX ROWS
      LAISH=LAIM*WROW/(WROW+SH)
*       CALCULATION OF THE LAI RELATIVE TO THE AREA OF THE ROW AND SH
      PROJ=SNHS*(WROW+SH)/WROW
*       PROJECTION OF THE SECTION RADIATED BY THE SUN


*       CALCULATION OF THE LAI OF THE DIFFERENT CLASSES

      SLLAI=SNHS*(1.-EXP(-OPG*LAIM/PROJ) )/OPG
*       SUNLIT LEAF AREA INDEX, LEAVES RECEIVING DIFFUSE AND
*       DIRECT RADIATION
      FSR=SLLAI*FCL/LAISH
      DIFABS=DIFCL*AMIN1(WROW+WPATH,WROW+HROW)* ...
            (1.-EXP(-.7*LAIM*WROW/(WROW+HROW) ) )/(WROW+SH)
      DIFL=(1.-SCAT)*DIFCL
      TLLAI=DIFABS/DIFL
      SLLAI1=SNHS*(1.-EXP(-OPG*TLLAI/SNHS) )/OPG
      DLLAI=TLLAI-SLLAI1
*       DIFFUSELY LIT LEAF AREA INDEX
      DARKLI=AMAX1(0.,LAISH-SLLAI-DLLAI)
*       DARK LEAF AREA INDEX
      CFSR1=(DLLAI*FCL+(LAISH-DARKLI)*FDV)/LAISH
      CFSR'2,11'=FSR*Z(IS,'1,10')
      CFSR12=DARKLI/LAISH


*       CALCULATION OF THE WEIGHTED MEAN OF LEAF TEMPERATURES

      LTAV=SUMX(CFSR'1,12',TLF'1,12')
      DIFT=LTAV-TEMP
*       MEAN DIFFERENCE BETWEEN LEAF AND AIR TEMPERATURES


*******           SECTION 6           ********************************


*       CALCULATION OF RELATIVE RATES DURING THE DAY

      RFE'1,12'=AFGEN(FEC,TLF'1,12')*CFSR'1,12'
      RFE=SUM1(RFE'1,12')
      RRE=SUMTLF(LOLET,30.)
      RRJ=SUMTLF(LOLJT,15.)
      RRJS=SUMTLF(LOLJST,10.)
      RRFS=SUMTLF(LOLFST,10.)
      RRF=SUMTLF(LOLAFT,10.)
NOSORT
   10 CONTINUE
SORT


*******           SECTION 7           ********************************


*       CALCULATION OF NUMBERS OF MITES

*       EGGS
      E=SUM1(E'1,30')
      E'1,30'=INTGRL(0.,RE'1,30')
      RE1=RFE*AF*RRE*E1
      RE'2,30'=RRE*(E'1,29'-E'2,30')

*       JUVENILES, LARVAE, PROTOCHRYSALIS, PROTONYMPHAE, DEUTOCHRYSALIS
      J=SUM1(J'1,15')
      J'1,15'=INTGRL(0.,RJ'1,15')
      RJ1=RRE*E30-RRJ*J1
      RJ'2,15'=RRJ*(J'1,14'-J'2,15')
```

```
*        JUVENILES, DEUTONYMPHAE, TELEIOCHRYSALIS
      JS=SUM1(JS'1,10')
      JS'1,10'=INTGRL(0.,RJS'1,10')
      RJS1=RRJ*J15*RRJS*JS1
      RJS'2,10'=RRJS*(JS'1,9'-JS'2,10')

*        ADULT FEMALE, PRE-OVIPOSITION
      AFS=SUM1(AFS'1,10')
      AFS'1,10'=INTGRL(0.,RFS'1,10')
      RFS1=RRJS*JS10-RRFS*AFS1
      RFS'2,10'=RRFS*(AFS'1,9'-AFS'2,10')

*        ADULT FEMALE, OVIPOSITION AND POST OVIPOSITION
      AF=SUM1(AF'1,10')
      AF'1,10'=INTGRL(IAF'1,10',RAF'1,10')
INCON IAF1=1.,IAF'2,12'=0.
*        INITIAL NUMBERS OF FEMALES
      RAF1=RRFS*AFS10-RRF*AF1
      RAF'2,10'=RRF*(AF'1,9'-AF'2,10')

*        ALL MITES, BOTH JUVENILE AND ADULT
      N=J+JS+AFS+AF


*******            SECTION 8            ********************************

*        DATA PANONYCHUS ULMI

FUNCTION LOLAFT=5.,85., 10.,27.8, 15.,25.5, 20.,12.0, 25.,8.95, 30.,7.52
FUNCTION LOLFST=5.,12.5, 10.,5.0, 15.,3.43, 20.,2.38, 25.,1.62, ...
                30.,1.51, 33.,.52
FUNCTION LOLJST=0.,100., 10.,20., 15.,5.55, 20.,3.56, 25.,1.96, 30.,1.62
FUNCTION LOLJT =0.,100., 10.,50., 11.,25., 15.,10.04, 20.,6.66, ...
                25.,4.45, 30.,2.29
FUNCTION LOLET =0.,100., 10.,50., 15.,17.04, 20.,8.38, 25.,5.53, ...
                30.,4.85, 35.,.40,
FUNCTION FEC   =0.,0., 10.,.53, 15.,1.13, 20.,1.86, 25.,2.93, 30.,3.99


*******            SECTION 9            ********************************

***      DATA FOR TEMPERATURE, WIND, HUMIDITY AND RADIATION

*        DAILY MINIMUM TEMPERATURE
FUNCTION MNTT= ...
      136.,0.3, 137.,5.5, 138.,7.5, 139.,8.4, 140.,12.4, ...
      141.,11.2, 142.,10.2, 143.,11.4, 144.,10.4, 145.,7.4, ...
      146.,5.3, 147.,9.8, 148.,10.1, 149.,10.5, 150.,11.3, ...
      151.,11.5, 152.,10.4, 153.,6.1, 154.,7.4, 155.,6. , ...
      156.,4.3, 157.,5.2, 158.,7.4, 159.,9.3, 160.,9.3, ...
      161.,12. , 162.,7.2, 163.,4.5, 164.,5.4, 165.,1.6, ...
      166.,2.7, 167.,6.5, 168.,10. , 169.,11.4, 170.,7.3, ...
      171.,14.1, 172.,14.8, 173.,11.9, 174.,11.9, 175.,13.2, ...
      176.,11.8, 177.,13.3, 178.,17.6, 179.,15.4, 180.,12.4, ...
      181.,10. , 182.,11.6, 183.,16.5, 184.,12.8, 185.,11.2, ...
      186.,13.8, 187.,15.5, 188.,15.4, 189.,10.9, 190.,6.6, ...
      191.,7.5, 192.,14.4, 193.,14.1, 194.,13.3, 195.,12.1, ...
      196.,13.7, 197.,13.7, 198.,10.7, 199.,10.7, 200.,13.1, ...
      201.,13.4, 202.,12.5, 203.,11.7, 204.,8.6, 205.,7.4, ...
      206.,6.5, 207.,12.4, 208.,12.4, 209.,14.3, 210.,14.7, ...
      211.,11.8, 212.,11.8, 213.,12.1, 214.,13.4, 215.,10.4, ...
      216.,14.2, 217.,12.5, 218.,14.2, 219.,12.5, 220.,11.4, ...
      221.,6.9, 222.,8.2, 223.,13.6, 224.,12.5, 225.,12.4, ...
      226.,13.6, 227.,14.4, 228.,14.4, 229.,12.3, 230.,16.5, ...
      231.,14.4, 232.,11.8, 233.,6.8, 234.,2.9, 235.,9.7, ...
      236.,8.2, 237.,8. , 238.,8.9, 239.,8.5, 240.,13.4, ...
      241.,9.8, 242.,11.4, 243.,5.6, 244.,13.7, 245.,15.2, ...
      246.,12.6, 247.,10.3, 248.,11.7, 249.,13.7, 250.,12.4, ...
      251.,9.5, 252.,13.7, 253.,11.4, 254.,5.5, 255.,3. , ...
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      256.,  6.7,  257.,  3.8,  258.,  8.3,  259.,12.3,  260.,11. , ...
      261.,13.5,  262.,12.5,  263.,11.5,  264.,11.1,  265.,11.3, ...
      266.,  5.2,  267.,  3.8,  268.,  6.8,  269.,  4.4,  270.,  8.6, ...
      271.,11.2,  272.,  7.7,  273.,  7.7

*        DAILY MAXIMUM TEMPERATURE
FUNCTION MXTT= ...
      136.,14.4,  137.,17.8,  138.,19.3,  139.,20.2,  140.,22.3, ...
      141.,23.2,  142.,20.7,  143.,19.8,  144.,15.2,  145.,19.2, ...
      146.,21.1,  147.,22.5,  148.,24.2,  149.,18.7,  150.,16.2, ...
      151.,20. ,  152.,15.1,  153.,13.5,  154.,18.2,  155.,17.6, ...
      156.,17.7,  157.,20.1,  158.,19. ,  159.,20.2,  160.,23.1, ...
      161.,18.6,  162.,18.8,  163.,23.7,  164.,19.5,  165.,17.9, ...
      166.,21.7,  167.,23.1,  168.,24.7,  169.,23.3,  170.,26. , ...
      171.,26.4,  172.,23.6,  173.,23.7,  174.,24.3,  175.,26. , ...
      176.,27.2,  177.,29.2,  178.,29.6,  179.,23.5,  180.,22.4, ...
      181.,25.4,  182.,29.2,  183.,30.9,  184.,24.2,  185.,27.8, ...
      186.,29.9,  187.,26.6,  188.,21. ,  189.,20.5,  190.,21.3, ...
      191.,23.9,  192.,19.8,  193.,20.6,  194.,21.8,  195.,23.9, ...
      196.,19.3,  197.,22.2,  198.,19.8,  199.,19.4,  200.,20.3, ...
      201.,19.6,  202.,18.5,  203.,18.8,  204.,17.8,  205.,19.7, ...
      206.,19.1,  207.,16.3,  208.,15.3,  209.,23.7,  210.,19.5, ...
      211.,18. ,  212.,21.7,  213.,26.8,  214.,26.2,  215.,20.1, ...
      216.,20.7,  217.,19.4,  218.,28.8,  219.,19.7,  220.,19.3, ...
      221.,22.1,  222.,26.6,  223.,27.2,  224.,25.6,  225.,26.7, ...
      226.,27.8,  227.,27.9,  228.,29.7,  229.,28.8,  230.,23.7, ...
      231.,23.9,  232.,23.2,  233.,20.6,  234.,20.3,  235.,24.2, ...
      236.,22.3,  237.,22.9,  238.,23.8,  239.,26.2,  240.,22.2, ...
      241.,21.7,  242.,18.1,  243.,18.2,  244.,20.3,  245.,19.7, ...
      246.,23.1,  247.,26.2,  248.,28.7,  249.,20.3,  250.,23.9, ...
      251.,25.8,  252.,20. ,  253.,18.2,  254.,17.9,  255.,18.4, ...
      256.,19.1,  257.,21.6,  258.,24.1,  259.,23.3,  260.,25. , ...
      261.,21.1,  262.,17.6,  263.,19.8,  264.,19.9,  265.,15.7, ...
      266.,15.4,  267.,15.2,  268.,16.2,  269.,17.1,  270.,17.9, ...
      271.,17.4,  272.,12.5,  273.,12.7

*        WINDSPEED
FUNCTION WINDTB= ...
      136.,4.5,  137.,.8. ,  138.,.4. ,  139.,.4.5,  140.,2.5, ...
      141.,2.5,  142.,3.5,  143.,.5. ,  144.,.6. ,  145.,1. , ...
      146.,2.5,  147.,.4. ,  148.,.5. ,  149.,.3. ,  150.,.4. , ...
      151.,2.5,  152.,3.5,  153.,.5.5,  154.,3.5,  155.,.3. , ...
      156.,.4. ,  157.,.4. ,  158.,.4.5,  159.,2.5,  160.,.3.5, ...
      161.,4.5,  162.,2.5,  163.,.2.5,  164.,.5. ,  165.,.3.5, ...
      166.,2. ,  167.,.2.5,  168.,.3. ,  169.,.2.5,  170.,.2. , ...
      171.,.4. ,  172.,.2.5,  173.,.5.5,  174.,.6. ,  175.,.5.5, ...
      176.,1.5,  177.,.1.5,  178.,.1.5,  179.,.6.5,  180.,.5.5, ...
      181.,1.5,  182.,.2. ,  183.,.3. ,  184.,.3.5,  185.,.1.5, ...
      186.,.3. ,  187.,.3. ,  188.,.5. ,  189.,.4. ,  190.,.2.5, ...
      191.,.1.5,  192.,.3.5,  193.,.3.5,  194.,.1.5,  195.,.3.5, ...
      196.,.4.5,  197.,.4. ,  198.,.5. ,  199.,.4.5,  200.,.6.5, ...
      201.,.6.5,  202.,.6. ,  203.,.6.5,  204.,.5. ,  205.,.3.5, ...
      206.,.5. ,  207.,.7.5,  208.,.6.5,  209.,.4 .,  210.,.4.5, ...
      211.,.2.5,  212.,.3. ,  213.,.2.5,  214.,.1.5,  215.,.3.5, ...
      216.,.3.5,  217. ,.7.,  218.,.8.0,  219.,.8.5,  220.,.5. , ...
      221.,.2.5,  222.,.2.5,  223.,.2. ,  224.,.4. ,  225.,.4. , ...
      226.,.4. ,  227.,.4. ,  228.,.2.5,  229.,.1.5,  230.,.2.5, ...
      231.,.1.5,  232.,.2.5,  233.,.4.5,  234.,.3. ,  235.,.3. , ...
      236.,.2.5,  237.,.3. ,  238.,.3. ,  239.,.2. ,  240.,.2. , ...
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      251.,.2. ,  252.,.2.5,  253.,.3.5,  254.,.1. ,  255.,.1.5, ...
      256.,.2.5,  257.,.3.5,  258.,.4. ,  259.,.3. ,  260.,.2. , ...
      261.,.2. ,  262.,.8. ,  263.,.2.5,  264.,.7. ,  265.,.4. , ...
      266.,.2. ,  267.,.1.5,  268.,.3. ,  269.,.1.5,  270.,.3. , ...
      271.,.8.5,  272.,.7. ,  273.,.7,

*        DAILY MAXIMUM AND MINIMUM AIR HUMIDITY
FUNCTION EATB= ...
      136.0, 6.9, 136.7, 6.3, 137.2, 7.9, 137.6, 5.4, 138.2, 7.6, ...
      138.7, 7.8, 139.3,10.9, 139.5,11.7, 140.2,14.3, 140.7, 8.6, ...
      141.1,13.3, 141.6,13.6, 141.8,15.8, 142.3,15.3, 142.7,11.8, ...
      143.1,15.3, 143.6,11.4, 143.7,13.1, 144.5,16.3, 144.6,11.8, ...
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271.2,11.8, 271.5,17.6, 271.6,11.7, 272. ,13.4, 272.5,12.6, ...
272.55,8.4, 272.6,11. , 272.7, 8.7 ,273.3,11. , 273.4,11.2, ...
273.5,11.8 ,274.,9.9
```
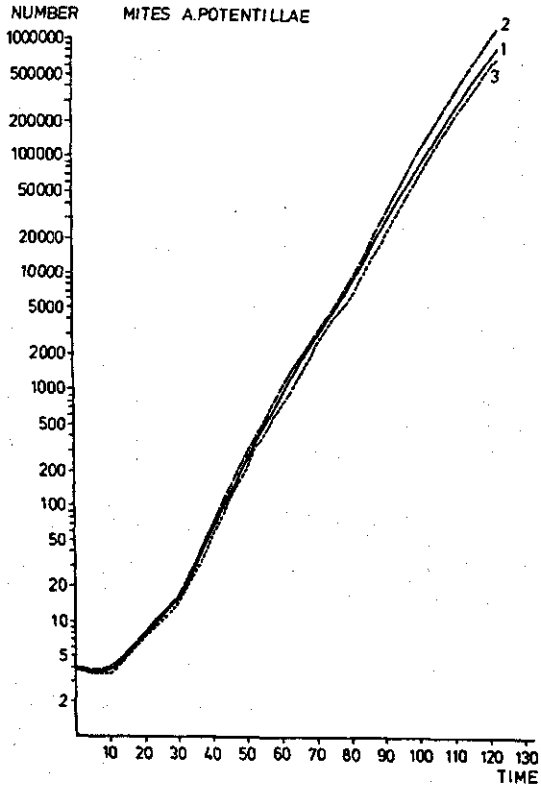

```
*       DAILY TOTAL GLOBAL RADIATION
FUNCTION DTRT= ...
      136.,2748.,  137.,2616.,  138.,1937.,  139.,1389.,  140.,1305., ...
      141.,1998.,  142.,2268.,  143.,1018.,  144.,  666.,  145.,1786., ...
      146.,2732.,  147.,2645.,  148.,2537.,  149.,  985.,  150.,  781., ...
      151.,  751.,  152.,  517.,  153.,  615.,  154.,1555.,  155.,2383., ...
      156.,2850.,  157.,2924.,  158.,1904.,  159.,1548.,  160.,1931., ...
      161.,  894.,  162.,1898.,  163.,2653.,  164.,1702.,  165.,2604., ...
      166.,2817.,  167.,2725.,  168.,1575.,  169.,2443.,  170.,2448., ...
      171.,1785.,  172.,1691.,  173.,2805.,  174.,2503.,  175.,2508., ...
      176.,2661.,  177.,2333.,  178.,2200.,  179.,1860.,  180.,2098., ...
      181.,2809.,  182.,2455.,  183.,2555.,  184.,2728.,  185.,2364., ...
      186.,2237.,  187.,1622.,  188.,  801.,  189.,2154.,  190.,2642., ...
      191.,2527.,  192.,  613.,  193.,1343.,  194.,1564.,  195.,1912., ...
      196.,  679.,  197.,1976.,  198.,1706.,  199.,1487.,  200.,1065., ...
      201.,1324.,  202.,  914.,  203.,1575.,  204.,1949.,  205.,2361., ...
      206.,1729.,  207.,  744.,  208.,  667.,  209.,1844.,  210.,1585., ...
      211.,  914.,  212.,2028.,  213.,1758.,  214.,2102.,  215.,1265., ...
      216.,1014.,  217.,  353.,  218.,2119.,  219.,1968.,  220.,2171., ...
      221.,2127.,  222.,2462.,  223.,1923.,  224.,2403.,  225.,2381., ...
      226.,2340.,  227.,2234.,  228.,2141.,  229.,1397.,  230.,1346., ...
      231.,  977.,  232.,1100.,  233.,1490.,  234.,2264.,  235.,2064., ...
      236.,1599.,  237.,1914.,  238.,2087.,  239.,1635.,  240.,  757., ...
      241.,1270.,  242.,  440.,  243.,1450.,  244.,1262.,  245.,  465., ...
      246.,1048.,  247.,1578.,  248.,1391.,  249.,  537.,  250.,1363., ...
      251.,1690.,  252.,  773.,  253.,1747.,  254.,  946.,  255.,1327., ...
      256.,1225.,  257.,1791.,  258.,1685.,  259.,1205.,  260.,1460., ...
      261.,1687.,  262.,  399.,  263.,1224.,  264.,  277.,  265.,  880., ...
      266.,  715.,  267.,1050.,  268.,  656.,  269.,  949.,  270.,  998., ...
      271.,  709.,  272.,  548.,  273.,  389.

FUNCTION DIFOVT=0.,0.,  5.,6.,  15.,26.,  25.,45.,  35.,64.,  45.,80., ...
                55.,94.,  65.,105.,  75.,112.,  90.,116.
FUNCTION SUNDT =0.,0.,  5.,0.,  15.,88.,  25.,175.,  35.,262.,  45.,336., ...
                55.,402.,  65.,452.,  75.,483.,  90.,504.
FUNCTION DIFCLT=0.,0.,  5.,59.,  15.,42.,  25.,49.,  35.,56.,  45.,64., ...
                55.,68.,  65.,71.,  75.,75.,  90.,77.

FUNCTION RSLTB =0.,1276.,  42.,1276.,  61.6,927.,  84.,307.,  140.,134., ...
                210.,135.,  280.,124.
*       RELATION BETWEEN STOMATAL RESISTANCE AND TOTAL INCIDENT
*       RADIATION MEASURED IN THE PHOTOSYNTHESIS ROOM OF THE IBS (CABO)
PRINT TLF*1,12*,AF,E,J,M,DARKLI,SLLAI,DLLAI,TLLAI,LTAV,DIFT
PRTPLT E,M
TIMER FINTIM=120.,DELT=0.0416,OUTDEL=0.1,PRDEL=0.1
METHOD RECT
END
STOP
ENDJOB
```



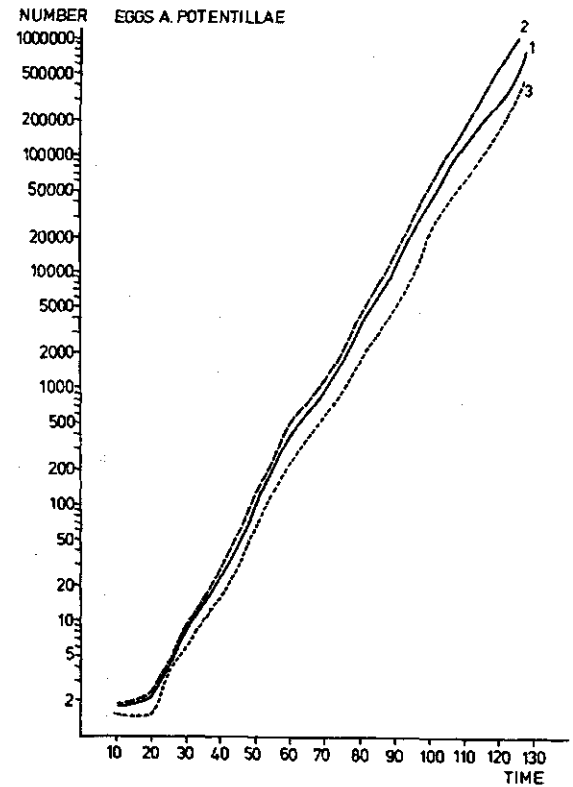


Fig. 69 | Population growth of *Amblyseius potentillae*. 1. population model with air temperature; 2. population model with leaf temperatures; 3. population model with air temperature and oviposition rate x 0.9.

9 Verification

9.1 Introduction

Section 5.1 described how the models are used iteratively in the phase of model development and experimentation to determine the required accuracy of measurement of the input relations. It was shown that the accuracy of the experiments on the population level determines the required accuracy of the lower order experiments on the different rates. At the end of model development and experimentation, the results of the population models are once more compared with independent experimental data. This comparison is done for ecosystems at two levels of complexity. The low level of complexity consist of small single apple trees in which the population growth of the fruit-tree red spider mite is accurately followed under controlled conditions with or without predatory mites. These experiments and the comparison with the model output is given in Section 9.3.
The higher level of complexity concerns the field situation. Two models were developed for this situation and require verification: the diapausing proces and the population growth of prey and predator throughout the season. The experiments, their results and the comparison with the results of simulation are given in Section 9.4. However, not only the final results of the population model should be verified, but also the important assumptions underlying the predation process. Thus the results of a submodel on the predatory activity in a replacement series, given in Section 8.2, were compared with experimental results in Section 9.2

9.2 Replacement series

Predation in two or more prey species systems was determined with the same technique as described in Section 6.1.
The experiments were carried out with standardized adult female predatory mites, and with larvae and adult females of the prey, kept on leaf disks of 5.0 cm^2. In replacement series with the combinations: 10–0, 8–2, 5–5, 2–8, 0–10 the predatory rate and the colour value of

the predatory mite were continuously observed at constant temperatures of 15° C and 25° C. Every prey eaten, otherwise killed or moulted was replaced within one hour. The predation rate per day and the colour value of the predator are given in terms of confidence intervals in Figs. 70 and 71.

The same experiment was simulated (Section 8.2), the results being represented by the drawn lines in Figs. 70 and 71, which also show the measured and simulated colour value of the predator. All simulated results, except one, are well within the confidence intervals, and consequently it can be concluded that the predation rate of each stage of the prey is affected only by the other stages through the gut content of the predator.

The deviating observation concerns the highest prey density of the

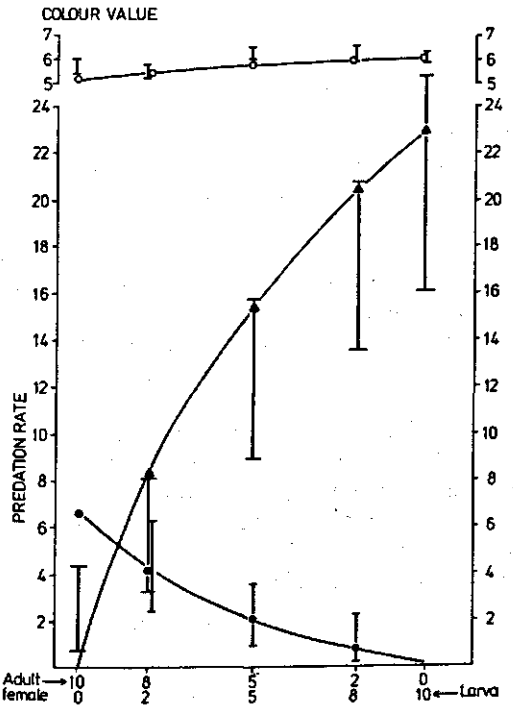


Fig. 70 | Simulated and experimental results of a replacement series of larvae and adult females of *Panonychus ulmi* with one adult female of *Amblyseius potentillae* at 25°C, in terms of simulated values and confidence intervals.

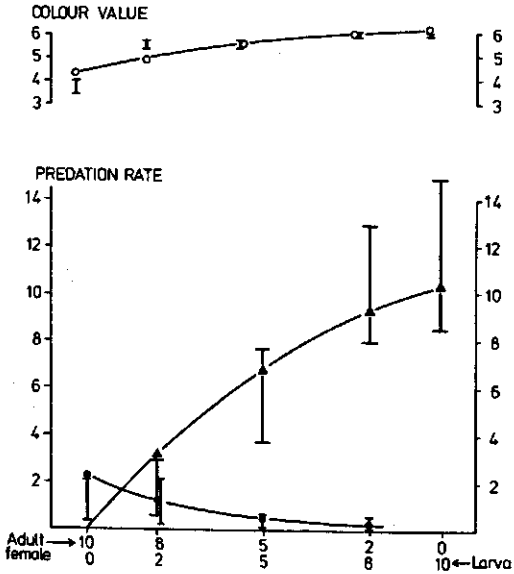


Fig. 71 | Simulated and experimental results of a replacement series of larvae and adult females of *Panonychus ulmi* with one adult female of *Amblyseius potentillae* at 15°C, in terms of simulated values and conficence intervals.

females and may be attributed to response waning, Section 4.3. In retrospect it would have been better to carry out the experiments with a lower density of prey. However this would have taken an excessive amount of experimenting time because more time is required for equilibration of the system.

With the colour approach the predation process in 'mixed cultures' of prey stages can be explained by the results in 'monocultures' of prey stages. However there are many predator-prey systems where the satiation level is not visually determinable and for these another method was developed.

In section 6.2.3 the rate of predation was calculated from the functional response curve with

$$MORT = \frac{E \times D}{E \times D + M} = \frac{\frac{E}{M} \times D}{\frac{E}{M} \times D + 1} M$$

in which E is the predation efficiency in time^{-1}, D is the prey density in preys cm^{-2} and M is the maximum predation rate in prey cm^{-2} time^{-1}. In analogy to de Wit's treatment of plant competition, the following equations may be given for the calculation of rate of predation in mixed cultures:

$$MORT_1 = \frac{\frac{E_1}{M_1} \times D_1}{\frac{E_1}{M_1} \times D_1 + \frac{E_2}{M_2} \times D_2 + 1} M_1$$

$$MORT_2 = \frac{\frac{E_2}{M_2} \times D_2}{\frac{E_1}{M_1} \times D_1 + \frac{E_2}{M_2} \times D_2 + 1} M_2$$

It was, however, shown by de Wit (1960) that these formulas only hold when plants are competing for the same space and develop in a similar way in course of time. Although it may be visualized that prey individuals 'compete' for the same space in the gut of the predator, it is necessary to evaluate whether these generalizations hold for mixed prey species. This is indeed so as is shown in Figs. 72 and 73 in which the measured confidence interval and the predation, calculated according to this approach is given.

The relative gut content is now defined by

$$RGC = \frac{MORT_1}{M_1} + \frac{MORT_2}{M_2} = \frac{\frac{E_1}{M_1} \times D_1 + \frac{E_2}{M_2} \times D_2}{\frac{E_1}{M_1} \times D_1 + \frac{E_2}{M_2} \times D_2 + 1}$$

and has a value between 0 and 1.

This variable may now be related to the oviposition rate and the development rate in the same way as the colour value in the former approach.

Figs 72 and 73 also give the corresponding colour values calculated with

$CAF = RGC \times MCAF$ in which MCAF is the maximum colour value (7).

As the colour value so calculated is within the confidence intervals of nearly all experiments, this approach is generally applicable in prey-predator systems.

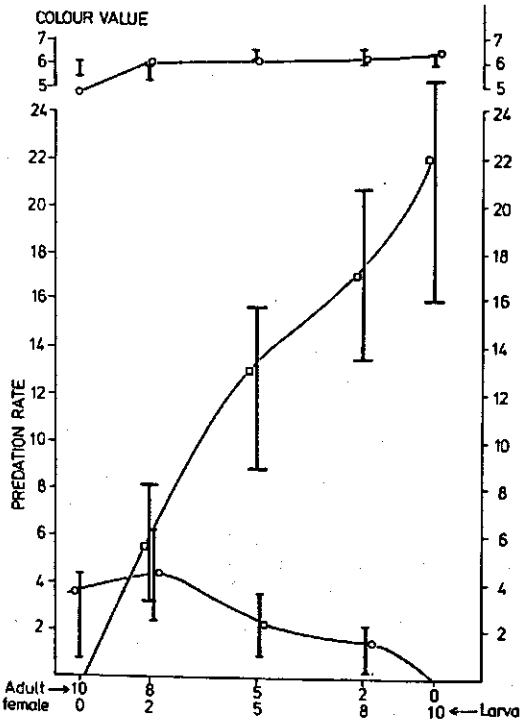


Fig. 72 | Calculated and experimental results of a replacement series of larvae and adult females of *Panonychus ulmi* with one adult female of *Amblyseius potentillae* at 25°C, in terms of calculated values and confidence intervals.

9.3 Greenhouse experiments

The population model is first verified in rather simple ecosystems according to methods described by Mc Murtry & van de Vrie (1973). Small Golden Delicious trees on rootstock M9, reared under controlled conditions, 16 h light, 18° C, 70% relative humidity, were placed in greenhouses with temperatures varying between 19 and 22° C, and a constant relative humidity of 70%.
The trees were severely pruned so that only one shoot with sixteen leaves remained. They were optimally supplied with nitrogen and sprayed once with a fungicide before the experiment was started. Further spraying against insects or fungi was unnecessary. In these

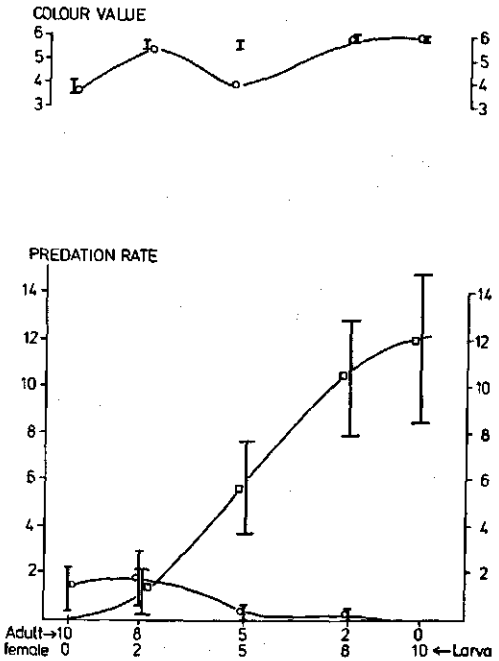


Fig. 73 | Calculated and experimental results of a replacement series of larvae and adult females of *Panonychus ulmi* with one adult female of *Amblyseius potentillae* at 15°C, in terms of calculated values and confidence intervals.

small ecosystems, leaf area $\bar{x} = 903$ cm² (S $(\bar{x}) = 29.4$) and twig length $\bar{x} = 91$ cm and (S $(\bar{x}) = 3.6$), the population growth of fruit-tree red spider mite was determined. Two experiments were done one with and the other without predatory mites, both in nine replicates and with an observation frequency of once per three days.

Both experiments were started with four female teleiochrysalids and four males of the prey isolated from the mass cultures and transferred on small leaf disks to one of the leaves of the tree. In the second experiment one female predator that had just moulted and had been fertilized was transferred to the trees 14 days after the start of the experiment. To prevent the escape of preys and predator an elastic band covered with Tangle Foot was attached to the base of the shoot. Since in both experiments no animals were found on the 18 barriers, emigration and immigration of prey or predators was absent.

A higher number of replicates and more frequent observation would improve the accuracy of the experiments but requires an excessive amount of labour since one population assessment for one replicate requires at least 4 hours, 20 days after the start of the experiment. The assessments were made by direct countings on the trees. This method was chosen to limit the number of trees in the experiments and to prevent additional assumptions on the distribution of the mites.
The population growth was followed up to a level at which density could possibly have an effect on the fruit-tree red spider mite. This level, corresponding with a density of 200 adult females on 100 July leaf equivalents, is reached in the experiments without predatory mites in 30 days and with predators in 36–39 days.
In Figs 74–76 the results of the experiments are given in terms of confidence intervals for the various stages at different moments:

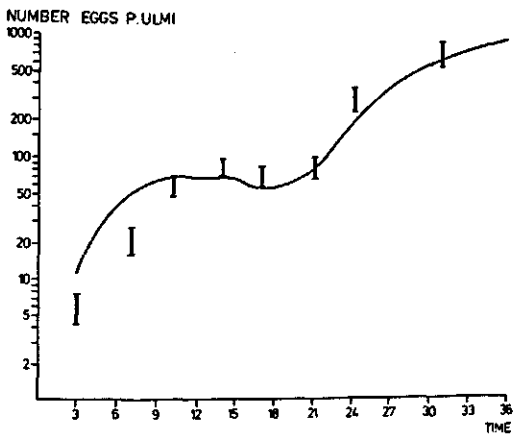
$$\bar{x} - \frac{Sn}{\sqrt{n}} t^{0.025}_{n-1} < x < \bar{x} + \frac{Sn}{\sqrt{n}} t^{0.025}_{n-1}$$

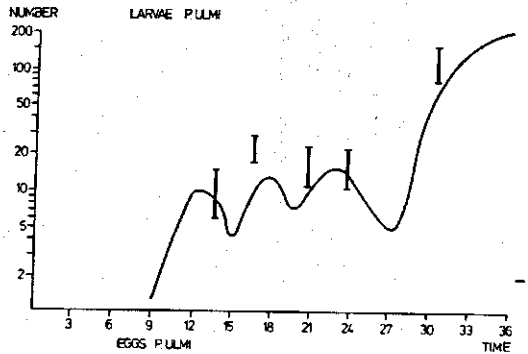
$\alpha \leftrightharpoons 0.005$

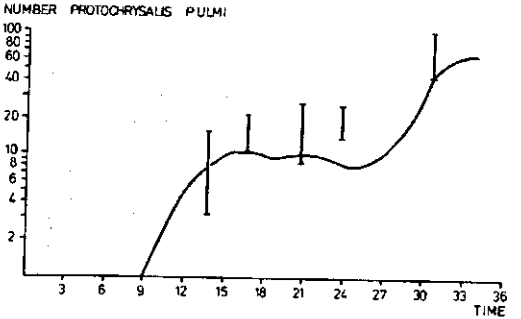
In the same figures the simulated results of the population models are given by solid (prey) and broken (predators) lines. These simulation results were reached with an unadapted population model except for the mean length of the adult female period of the prey and the numerical response of the predator. These were multiplied by factors within the 90% confidence interval. The assumption was made that the predatory mites are searching at random over the whole surface of the tree. At the start the simulated curves for egg and juvenile stages of the prey are systematically higher than the experimental values. Experimental and simulated results show that the prey population is not regulated by the predator within the observation period. The only effects of the predator are a delay of 6–10 days on the population growth and a change in the relative contribution of the different developmental stages.
In similar experiments with 1 or 8 leaf systems, Mc Murtry & van de Vrie, (1973), showed that the prey in the mono leaf systems was regulated in all 8 replicates within 30 days even when initial prey-predator ratios of 8:1 were used. In the 8 leaf systems the prey was regulated in seven of the 8 replicates when the initial prey-predator ratio was 1:1, in five of the 8 replicates with a ratio of 4:1 and in seven out of 8 replicates with a ratio of 8:1. From their experiments Mc Murtry & van de Vrie concluded that regulation is possible in both systems within the considered observation period of 50 days and that

the large scatter in the data makes lumping or averaging of data inadvisable as details of varying interactions among subunits will then be obscured. Therefore they presented all replicates separately. For the same reasons average values are omitted here but replaced by confidence intervals for the dates of measurement.
This processing of the data is required because of the limited aim of the experiment: comparison with simulation. Because the systems studied were more than twice as large as the 8 leaf systems of Mc Murtry & van de Vrie, regulation of the prey population within 40 days was impossible. This was mainly because of the delayed numerical response of the predator, induced by the low colour value of the predator when it is first present and does not find prey. Unfortunately temperature measurements and accurate determinations of the surface of the system were not done by Mc Murtry & van de Vrie so that comparison of simulation with experimental results can only be done by estimating surface and temperature fluctuations during the experiments. These simulations show the general tendency of fluctuations in prey and predator populations as described by Mc Murtry & van de Vrie. These are given in the sensitivity analysis of Chapter 10.

Fig. 74 | Simulated and experimental numbers of *Panonychus ulmi* in a population experiment in a greenhouse without predators. The experimental results are given in terms of confidence intervals for egg, larva, protochrysalis, protonymph, deutochrysalis, deutonymph, teleiochrysalis, adult male and adult female of *Panonychus ulmi*. The solid line represents the simulated numbers.




NUMBER
LARVAE P.ULMI
200
100
50
20
10
5
2
3 6 9 12 15 18 21 24 27 30 33 36
EGGS P.ULMI
TIME


NUMBER PROTOCHRYSALIS P.ULMI
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80
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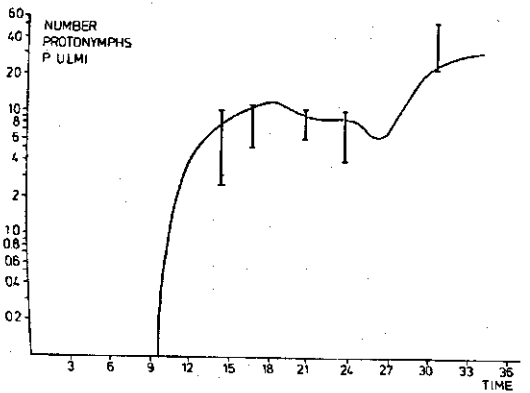
40
20
10
8
6
4
2
3 6 9 12 15 18 21 24 27 30 33 36
TIME


NUMBER
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P.ULMI
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40
20
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2
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0.6
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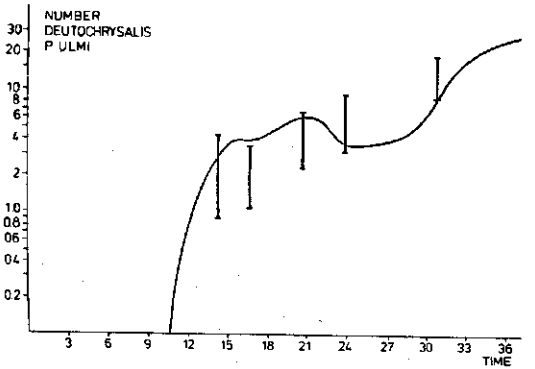
0.2
3 6 9 12 15 18 21 24 27 30 33 36
TIME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P.ULMI
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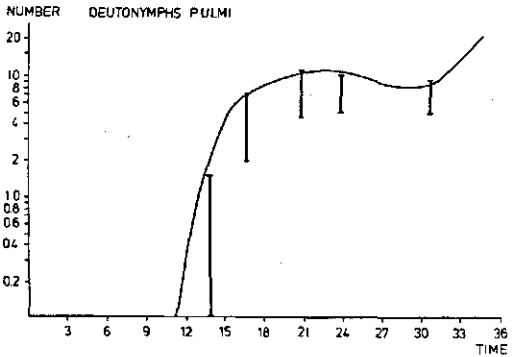
0.2
3 6 9 12 15 18 21 24 27 30 33 36
TIME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0.2
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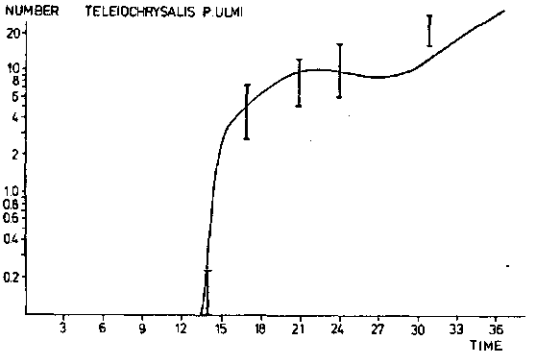
TIME


NUMBER TELEIOCHRYSALIS P.ULMI
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0.4
0.2
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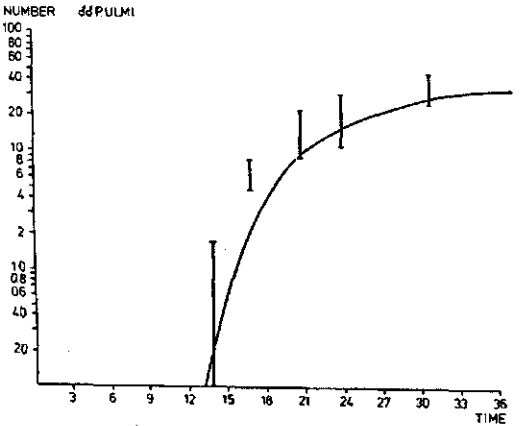
TIME


NUMBER ♂♂P.ULMI
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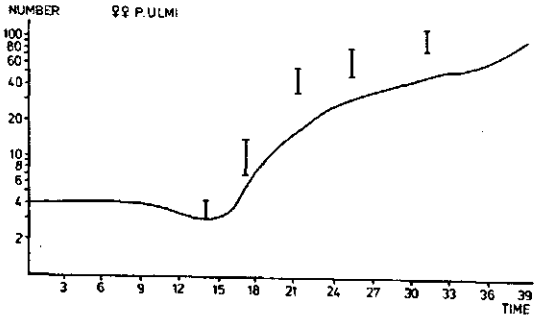
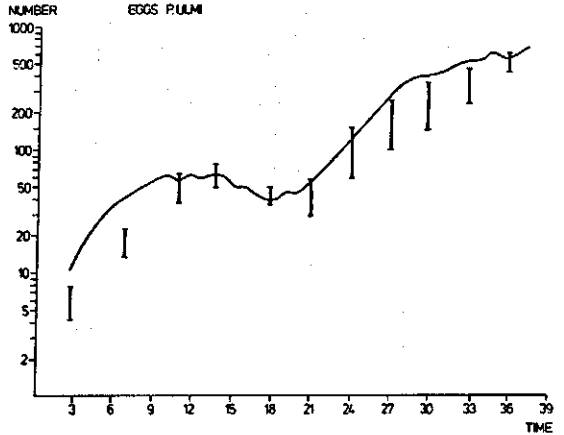
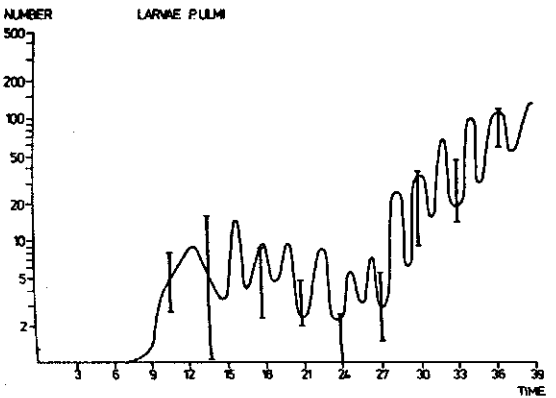
80
60
40
20
10
8
6
4
2
1.0
0.8
0.6
0.4
0.2
3 6 9 12 15 18 21 24 27 30 33 36
TIME


NUMBER ♀♀ P.ULMI
100
80
60
40
20
10
8
6
4
2
3 6 9 12 15 18 21 24 27 30 33 36 39
TIME





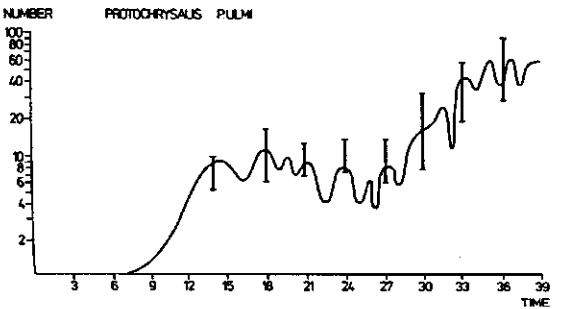
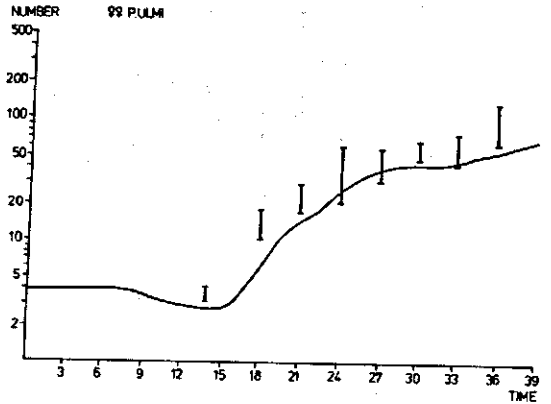


Fig. 75 | Simulated and experimental numbers of *Panonychus ulmi* in a population experiment in a greenhouse with predators. The experimental results are given in terms of confidence intervals for egg, larva, protochrysalis, protonymph, deutochrysalis, deutonymph, teleiochrysalis, adult male and adult female of *Panonychus ulmi*. The solid line represents the simulated numbers.

NUMBER
PROTONYMPHS PULMI
DEUTOCHRYSALIS PULMI
TELEOCHRYSALIS PULMI
DEUTONYMPHS PULMI
TIME


NUMBER
♀♀ P.ULMI
500
200
100
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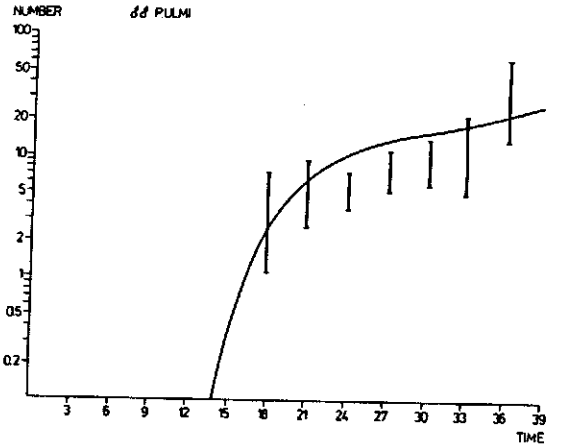
10
5
2
3
6
9
12
15
18
21
24
27
30
33
36
39
TIME


NUMBER
♂♂ P.ULMI
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50
20
10
5
2
1
0.5
0.2
3
6
9
12
15
18
21
24
27
30
33
36
39
TIME

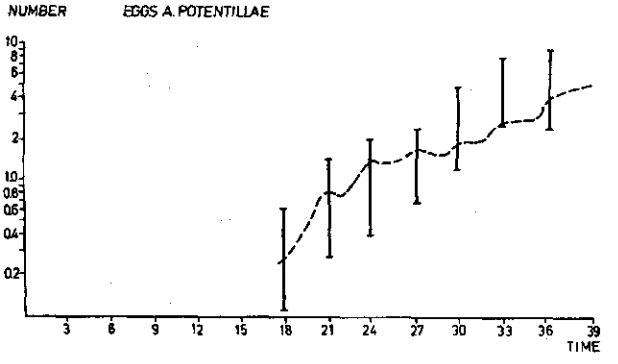
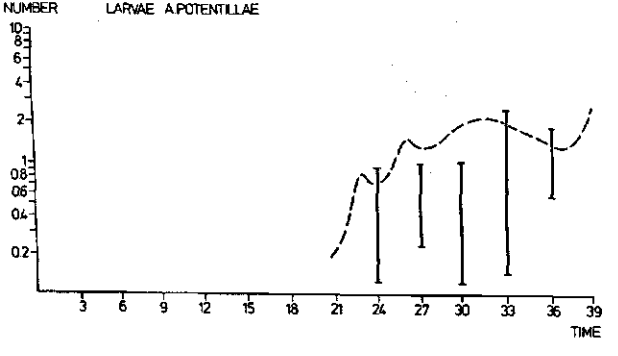
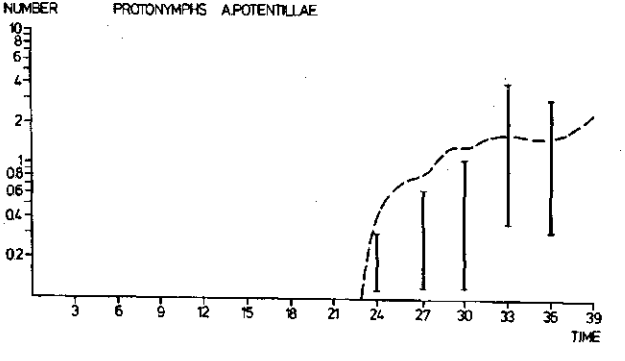
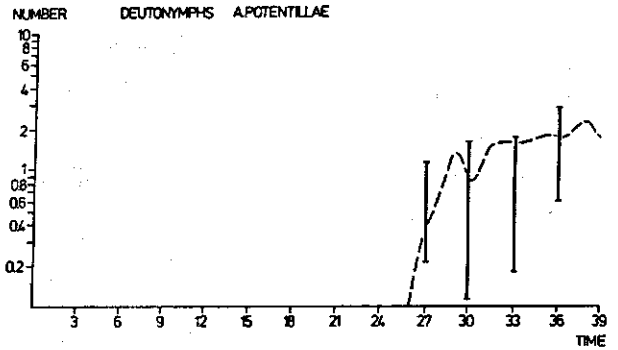


Fig. 76 | Simulated and experimental numbers of *Amblyseius potentillae* in a population experiment in a greenhouse of *Panonychus ulmi*; and simulated colour values of the predatory stages. The confidence intervals for egg, protonymph, deutonymph, adult male and adult female of *Amblyseius potentillae* are given. The broken line represents the simulated numbers.






NUMBER
DEUTONYMPHS A.POTENTILLAE
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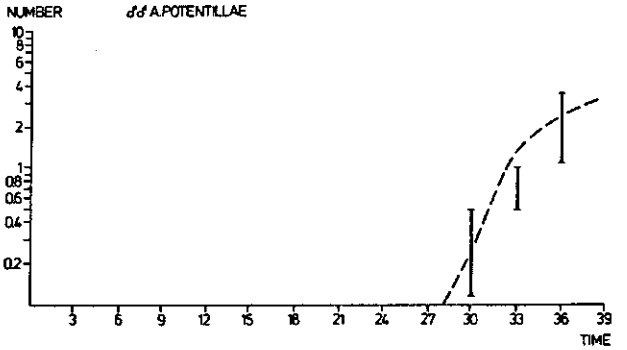
6
4
2
1
0.8
0.6
0.4
0.2
3 6 9 12 15 18 21 24 27 30 33 36 39
TIME


NUMBER
♂♂ A.POTENTILLAE
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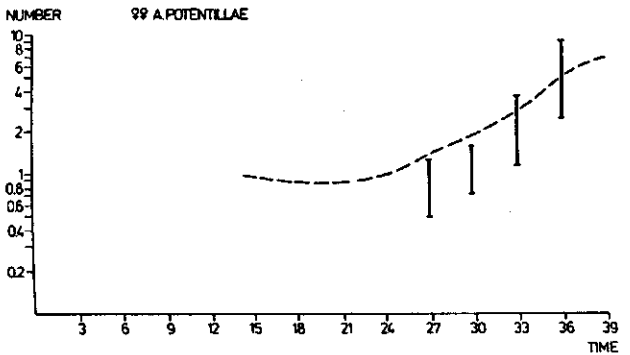
6
4
2
1
0.8
0.6
0.4
0.2
3 6 9 12 15 18 21 24 27 30 33 36 39
TIME


NUMBER
♀♀ A.POTENTILLAE
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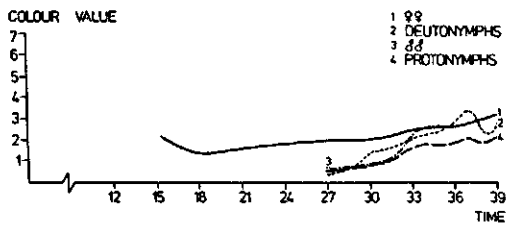
6
4
2
1
0.8
0.6
0.4
0.2
3 6 9 12 15 18 21 24 27 30 33 36 39
TIME


COLOUR VALUE
1 ♀♀
2 DEUTONYMPHS
3 ♂♂
4 PROTONYMPHS
7
6
5
4
3
2
1
12 15 18 21 24 27 30 33 36 39
TIME

9.4. Field

9.4.1 Population fluctuations during the season

Population fluctuations of fruit-tree red spider mite and predatory mites were determined in 8 orchards smaller than 1 ha during 1974. Cultivation measures were according to the system of integrated pest control. The orchards were infested with predatory mites, some of these one or two years earlier, by the introduction of twigs from cherry orchards or neglected apple orchards with abundant numbers of predatory mites. Most predators were introduced in late summer or in autumn. Other methods of infestation with laboratory-reared predatory mites were less successful, (van de Vrie et al., in prep).
The densities of all stages of prey and predator were determined by counting the numbers in 100 randomly chosen leaves, sample size and technique being discussed in detail by van de Vrie et al., (in prep). The leaf surface of each sample was determined planimetrically; the results are given in Table 36 in terms of mean, standard deviation and standard error throughout the season. The meso-weather is the same for all orchards and leaf area index is about the same because of the system of pruning.
Only samples taken from Golden Delicious trees are accounted for so that the observations may be considered as replicate except for the initial numbers of prey and predator. The number of adult females and

Table 36 Leaf surface in cm^2 of 100 leaves of Golden Delicious trees, throughout the season.

	$\bar{x}$	$s(\bar{x})$
21 May	1786.5	43.9
06 June	1912.9	24.6
20 June	1952.1	19.8
01 July	1954.6	21.0
15 July	1977.9	12.2
30 July	20.35.7	26.3
12 August	2000.1	7.9
20 August	2064.9	25.6
28 August	2034.7	22.8
05 September	2091.1	11.1
01 October	2073.6	25.7

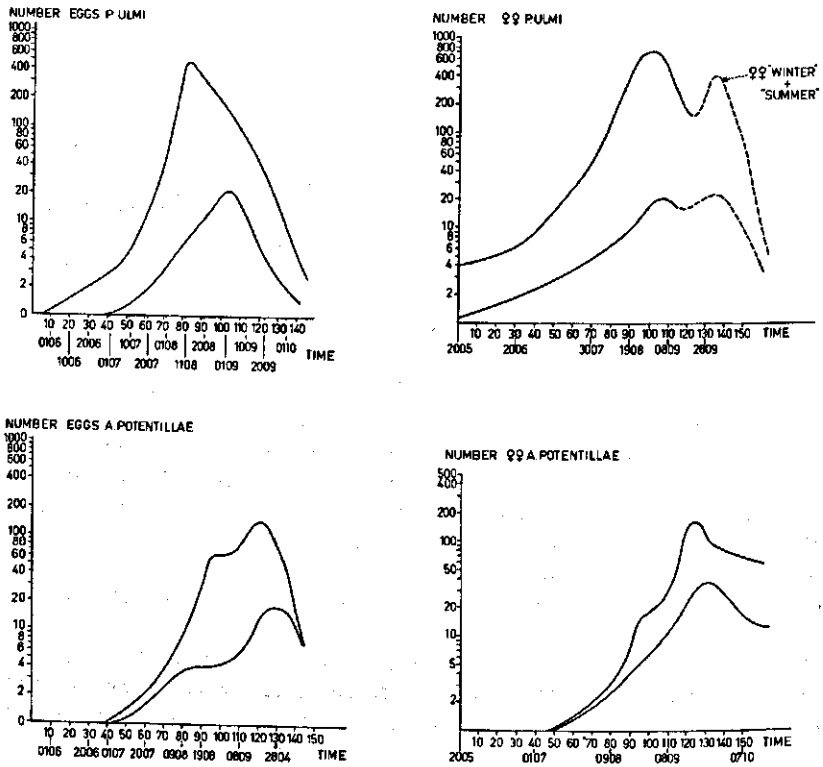


Fig. 77 | Population densities of *Amblyseius potentillae* and *Panonychus ulmi* observed in different orchards. Only the extremes are given for eggs and adult females of prey and predator, at the end of the season both 'summer' and 'winter' females are present.

eggs of the prey and predator in all orchards are presented in Figure 77. The observations for the orchards with the highest and lowest density are joined by lines. Population densities of prey and predator are less than 10 per 100 leaves in spring (mid May – mid June) and the ratio of prey-predator females may vary from 8 to 0.05.

Prey and predator densities increase from then on until mid August when both species reach their maximum. In none of the orchards involved did prey densities surpass the damage level, 300 adult mites per 100 leaves. The large density differences are attributed to differences in the initial density. The average initial densities in the orchards

are represented by squares, together with 90% confidence intervals. These confidence intervals appear so large that it is practically impossible to determine the initial number of prey in each of the orchards at an accuracy which justifies the simulation of the densities observed later. To circumvent this problem the results for the 8 orchards are averaged, it being realized that predators of orchard A do not eat preys of orchard B. Initial values for the simulated 'average' results are found here by an iterative process. In addition the effect of initial numbers of prey and predator are studied in a sensitivity analyses, Section 10.2. It is realized that, the data obtained by this procedure of averaging and initialization may be only used for verification of the pattern of growth and development, but not for the absolute numbers nor for the details of interference between prey and predator. However these verifications were already done in Section 9.3. In the beginning of the season considerable numbers of very small mites, *Aculus spp.*, which serve as alternative prey were found in all orchards. Counting was impossible so that estimates according to density classes were made. 0, 1 – 10. 11 – 50, 51 – 100 and >100 mites per leaf correspond to density classes 0, 1, 2, 3 and 4, respectively.

Fig. 78 presents the estimates throughout the season. The population density of the gall mites reaches its maximum in July, so that there are large quantities of these alternative prey when the density of the fruit-tree red spider mite is often very low. Thus the predator can survive lean periods (Mc Murtry & van de Vrie, 1973); (Chant, 1966).

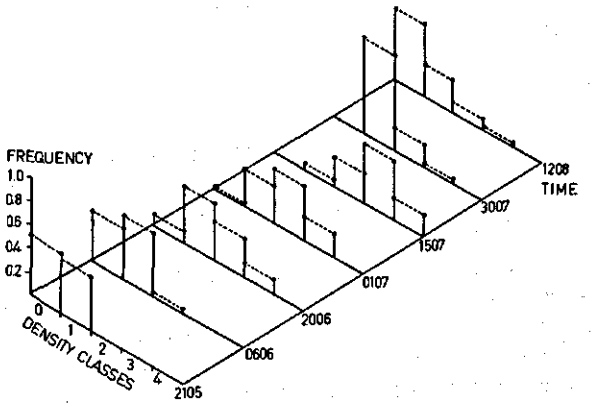


Fig. 78 | Density levels of *Aculus spp.* at the experimental fruit orchard at Wilhelminadorp during the season 1975, frequency distribution of density classes, the averages of 16 plots are given.

To account for these alternative prey a lower limit of 0.5 for the colour value of the predator is introduced in the models Section 8.2.
Fig. 79 gives the observed average densities and the simulated densities for adult females and eggs of the prey and predator, and also the observed and simulated colour values of the adult female predator. The simulated functions are based on an initial number of 4 prey females that have just matured, 1 predator female per 100 leaves on 1st June, the observed surface of the leaves and the weather data of 1974 in the orchards. There appears to be a good overall agreement between the simulated and measured results, especially for the position of the maximum numbers of prey and predator, the time lag between these maxima and the density level of prey and predator with respect to each other.
Also the observed and simulated colour values of the adult predator are in good agreement. The details of the growth and development are now much better visualized than by the experimental results only. At first it is possible to recognize successive generations in the adult prey, a phenomenon which disappears in later stages. No generations are recognized for the predators, because of their long adult life and short juvenile period (Collyer, 1964).
The number of generations can easily be deduced from the simulation. It is practically impossible to count the juvenile stages of the animals accurately but the simulation visualizes the course of their densities very clearly (Fig. 80). The disappearance of the prey and predator population in autumn is due to the induction of the diapause. The moment of diapause induction and the period of diapause induction were verified separately.

9.4.2 The diapause induction

The moment of diapause induction was determined in 1974 in various orchards in the south western part of the Netherlands. Orchards with different prey densities were chosen, an orchard with an adult female density of more than 20 per leaf, one with a density between 10 and 20 and five orchards with densities below 10 per leaf. The moment of diapause induction was determined by inspecting first year shoots for winter eggs. Second or older year shoots are not suitable for this purpose because the dead winter eggs from earlier years cannot be distinguished from fresh winter eggs. The moment of diapause induction ranged from 10–25 August and the fifty percent level of winter eggs was reached from 1 September to 1 October. The details in Table 37 show that this difference in the moment of diapause induction

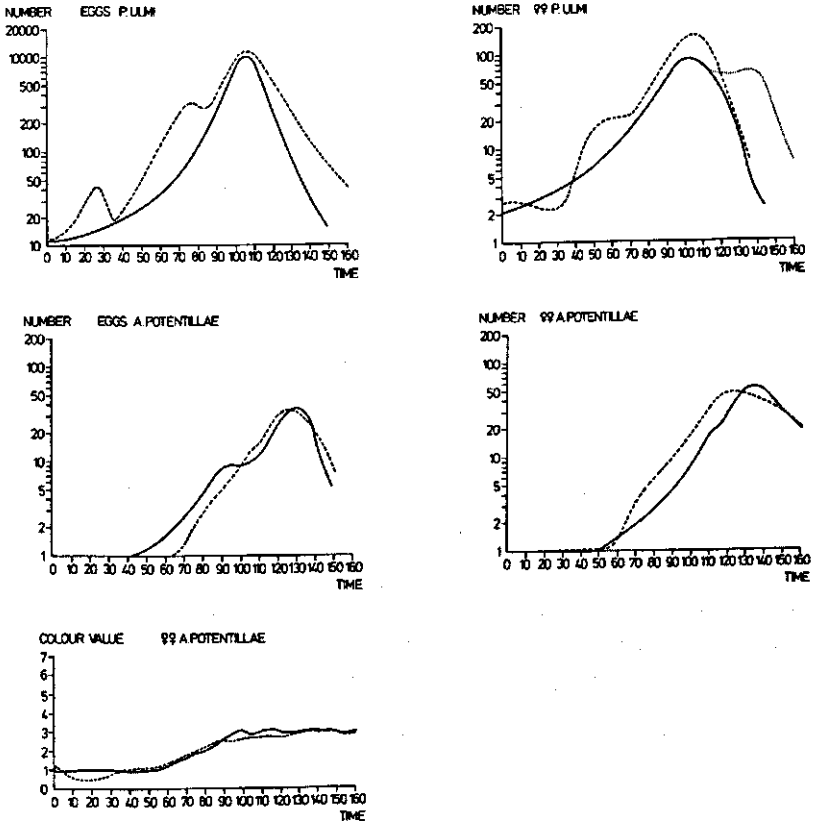
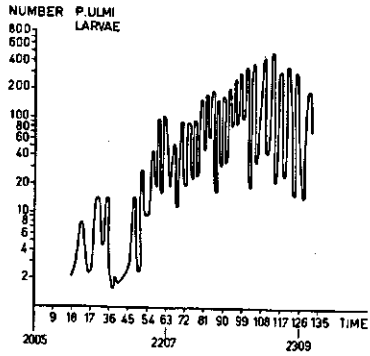
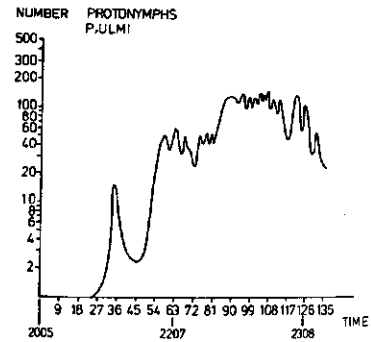
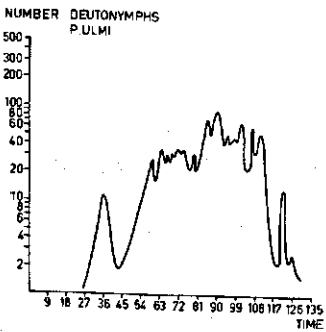
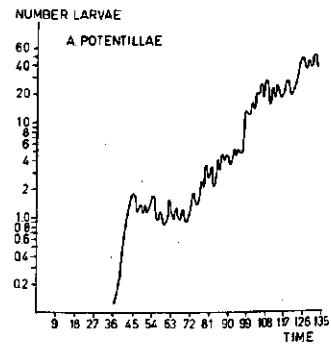


Fig. 79 | Simulated and average experimental density curve during the season 1974 for adult females and eggs of *Panonychus ulmi* and *Amblyseius potentillae*; simulated and average experimental colour value for adult female predators. The broken line represents the simulated numbers, only 'summer' females are given.









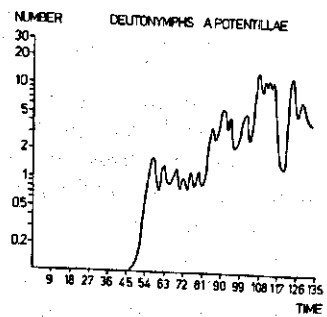


Fig. 80 | Simulated density curves of some juvenile stages of *Panonychus ulmi* and *Amblyseius potentillae* during the season.

Table 37 Field observations of diapause induction in *P. ulmi* in 1974. Dates of first winter eggs and 50% of total winter eggs, determined by expressing the data on logarithmic paper (van de Vrie et al. in prep.)

Number of adult female mites per 100 leaves on 10 August	First winter eggs	50% of total winter eggs
> 250	before 10 August	before 10 September
150 – 250	between 10 August and 20 August	between 10 September and 20 September
< 150	after 20 August	after 20 September

is related to density and probably caused by food supply. The moment of diapause induction in orchards where population densities of the adult female range from 1 – 10 per leaf is the same. Densities of 10 per leaf are seldom reached in practice, therefore these results are compared in Table 38 with those of the model in Section 8.2.3, in which food effects are neglected. There is good correspondence between experiment and simulated data. Calculations with the model further showed that the reversibility of the diapausing process has no quantitative effect (less than 10% difference between models in which reversibility is accounted for and models that do not include reversibility) and can be neglected in the population model.

Table 38 Simulated and measured moments of diapause induction in 1974.

	Date of diapause induction			
	simulated with duration of twilight			measured
	1h	0h	0.5h	
First winter eggs	24 August	5 August	15 August	after 20 August
50% of total winter eggs	1 October	1October	1 October	after 20 September

10 Sensitivity analysis

Sensitivity analysis is done to evaluate the effect of structural changes in a model and to determine the relative importance of the rates and parameters, to improve insight in the system and to guide management and further experiments. Sensitivity analysis on structural changes consists of eliminating parts of the program by multiplying the rates in these parts by zero. This type of sensitivity analysis is done to determine the effect of strong interference on the system as for example selective spraying. Sensitivity analysis of rates, parameters and initial values consists of varying inputs and parameters over a certain range and comparing the effect on the end result. All rates, initial values and parameters acting at more than one place in the INITIAL or DYNAMIC part of the model are considered. If the effect of the factor considered is relatively small, further experimentation in this direction is not urgent but when a large effect is found further study and analyses should be concentrated on that section of the model.
Sensitivity analysis is only done with the verified population model for the field situation (reference model) and with the micro-weather simulator that is connected to a population model for the prey.
After the sensitivity analysis an error in the definition of RTTAFF (residence time in age classes of adult female predators) was found. A run with a corrected version proved that deviations from the results on the reference model are of minor importance, Fig 81.

10.1 Population model

10.1.1 Predation

To determine the effect of predation on the density curves three runs were made. In the first run no predators were introduced in the model, STA = 132, and thus the population density of prey was simulated without the effect of biotic mortality. Fig. 82 presents the results of these simulations for the adult female and the eggs of the prey: these graphs are typical for the other stages. In the same figure the results of the simulations together with the reference model are represented by broken lines.

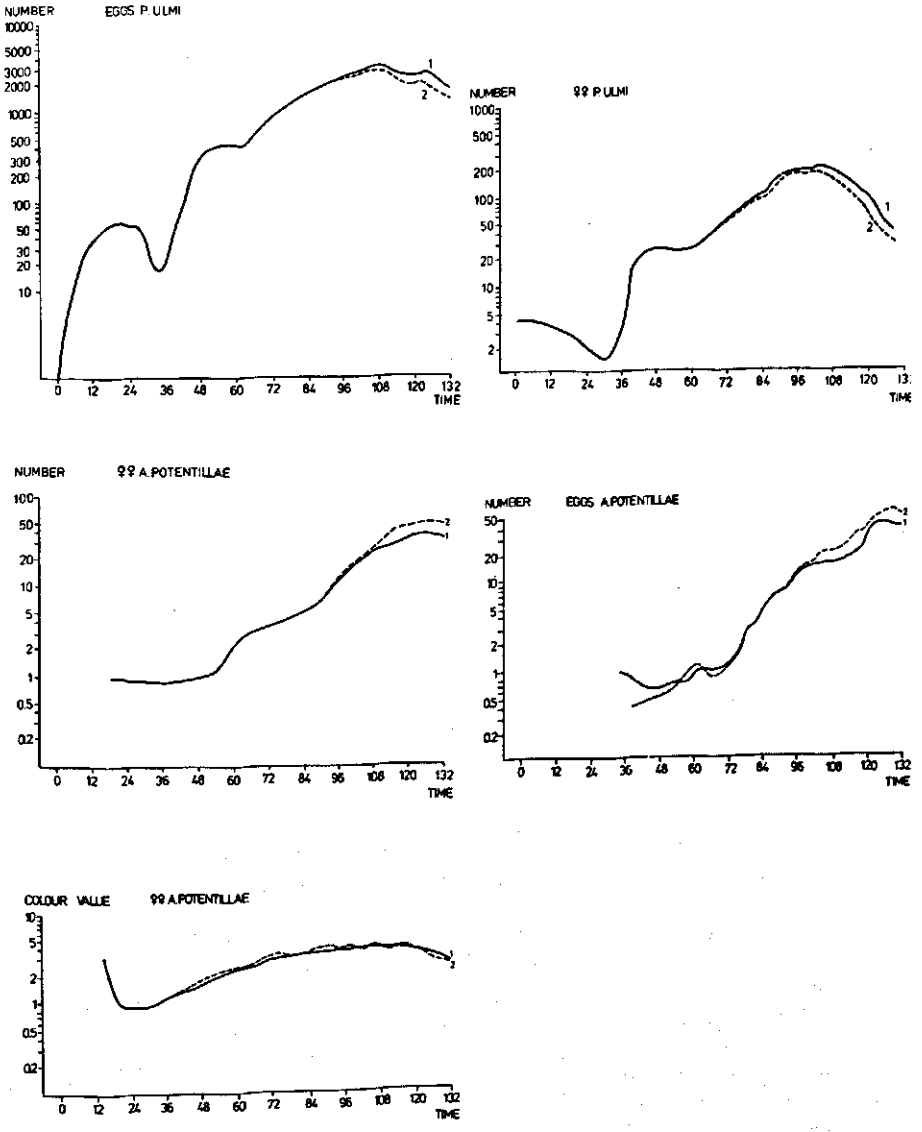


Fig. 81 | Simulation results for the numbers of adult females and eggs of *Panonychus ulmi* and *Amblyseius potentillae* and colour value of the adult female predator with the corrected simulation model and the reference model.

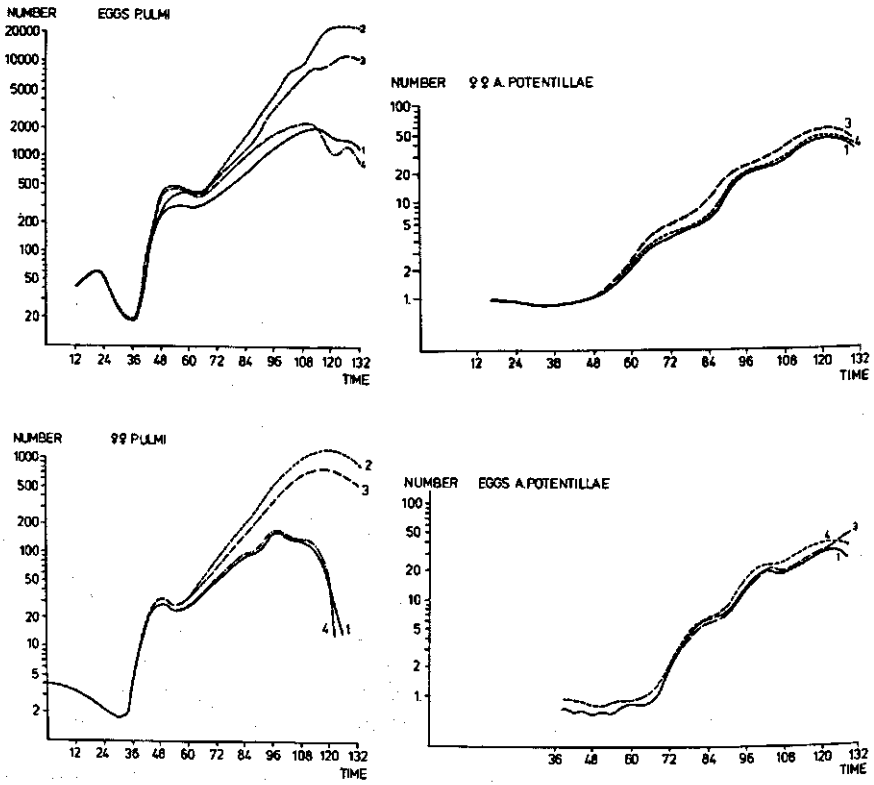


Fig. 82 | Simulation results for the numbers of adult females and eggs of *Panonychus ulmi* and *Amblyseius potentillae*.
1. reference model; 2. without any predation; 3. without predation by adult female predators; 4. without predation by juvenile and adult male predators.

In both situations increase in the number of the eggs is about the same until the beginning of July. Then when predators are absent, the number of prey eggs rapidly increases and reaches a maximum at the end of August about ten times that of the reference curve. The course of the adult female population density curve shows the same pattern, the maximum again being about ten times the reference curve maximum, far above the damage level.
There are no differences in the very beginning because the very low densities of both prey and predators result in negligible predation. A very small number of fruit-tree red spider mites without predators at the start of the season will certainly cause damage unless measures are

taken such as the introduction of a very low number of predatory mites at the start of the season to prevent the prey population from exploding. Thus it is concluded that the presence of predatory mites explains the low densities of the fruit-tree red spider mite in many orchards in practice, although their numbers are rather small. The second and third runs were to investigate the relative contribution of the different predatory stages: in the second run the predation by the adult female predator is neglected (SENP 1, SENP 5, SENP 8, SENP 10 and SENP 12 equal zero) and in the third run the predation by the juvenile stages and the adult males is set to zero (SENP 2 = SENP 3 = SENP 4 = SENP 6 = SENP 7 = SENP 9 = SENP 11 = 0). The colour of the different predatory stages deprived of predation are adjusted to the average colour value of the same stage in the reference model.
This adjustment is made to prevent the introduction of numerical response effects in this analysis for predation rates of the different stages and is applied in both runs. Fig. 82 shows the results for the adult females, the eggs of prey and predator, the results of the reference model again being given by broken lines. If the predation activity of juveniles and adult males is neglected, the population growth of the prey reaches a level just below the damage level, the general pattern of the curve being the same as for the reference curve, Fig. 82. The colour value of the predator not deprived of predation remains for the whole season between 2–4 as in the reference model.
When the predatory activity of the adult female predator is neglected, the effect is much larger as is shown in Fig. 82 where the adult female prey is presented. The course of the population is again the same but the maximum that is reached is more than 5 times that of the reference curve. The relatively low contribution of the juvenile stages and of the adult males to the total predation activity may be explained by the short juvenile period and the low predation rate of these stages because the absolute gut content and velocity are smaller. It is mainly the adult female predator that keeps the prey population below the damage level because of its high predation rate (24 larvae per day at 25°C, Section 6.2), its long life-span and the increase of oviposition rate up to the end of the colour scale. These characteristics enable the adult female predator to suppress high prey densities by an increased predation rate as well as an increased oviposition rate, as is shown in the next sections. Moreover because the predator can survive lean periods by switching to alternative prey and can do without food for long periods, it is a powerful regulator.
These results permit simplification of the population model. Juvenile and adult male predation may be neglected provided that their gut

content is set equal to that of the adult female predator.
The latter assumption is reasonable as the presence of prey is demonstrated by the adult female predator's colour and thus preys are also available for the other predatory stages whose contribution to the predation is relatively low.

10.1.2 Initialization

One of the main problems in pest management is the development of criteria for taking measures to prevent damage, i.e. what ratio between prey and predator is acceptable at what time of the year and what are the consequences if no spraying or other control measures are applied. To determine such criteria for the spider mite system, several runs were made with the model in which various combinations of initial prey and predator numbers and different moments of introduction of prey or predators were tried out. These changes in the model are realized by varying the value of the parameters, IPAFS, initial number of prey females, ITAFS, initial number of predator females, STA, time of introduction of the female predator and STPU, time of introduction of the female prey. The results of these runs are presented in Fig. 83–85; only the numbers of the adult females of prey and predator, the numbers of prey eggs and larvae and the colour value of the adult female predator are given that deviate most from the reference curve. Fig. 83 shows that with an initial density of 4 adult females of the prey per 100 leaves, introduction of one adult female predator per 100 leaves before 15 June suffices to keep the prey density below the damage level (3 adult females per leaf). The colour value of the predator is about 0.5, its lower limit, until 10–20 July and then slowly increases until values of 3–4 are reached at the end of August.
There is some phase difference between the different treatments but the density of female prey is about the same so that the predation activity evidently reaches the same level, as can be seen from the colour value at the end. In Fig. 84, the effect of different initial numbers of prey is shown. Up to an initial prey-predator ratio of 10:1, the damage level is not reached and the colour value of the predator still does not exceed 4. An initial prey density of 100 adult females (prey-predator ratio 100) causes prey densities far above the damage level but also induces a rapid increase of the predator population so that maximum densities of the adult female predator population are more than 4 per leaf. The prey population is then within the same season suppressed to very low levels and the predator-prey ratio at the end of the season, on 10 September, is about 10. Then the predator, is also very pale in colour so that the

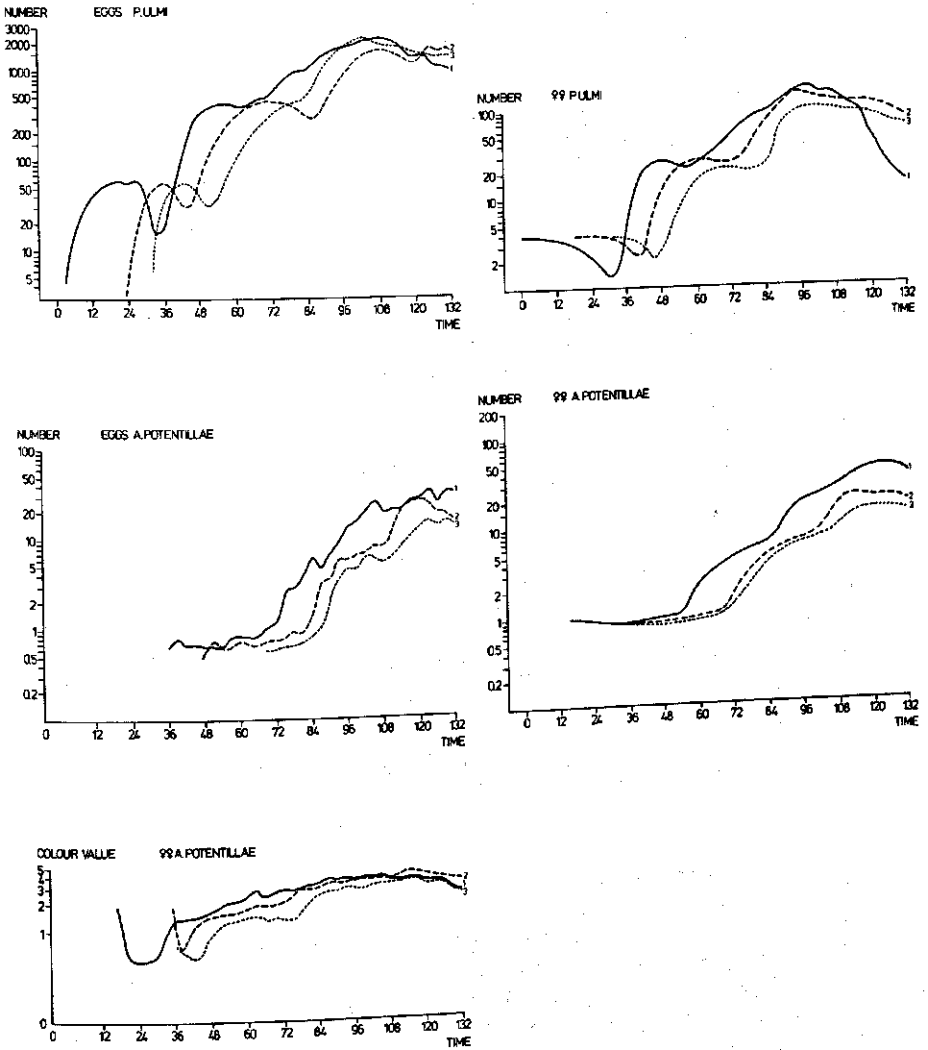


Fig. 83 | Simulation results for the numbers of adult females and eggs of *Panonychus ulmi* and *Amblyseius potentillae* and the colour value of the adult female predator.
1. reference model; 2. predator and prey are introduced on 20 May; 3. predator is introduced on 15 June, prey on 20 May.

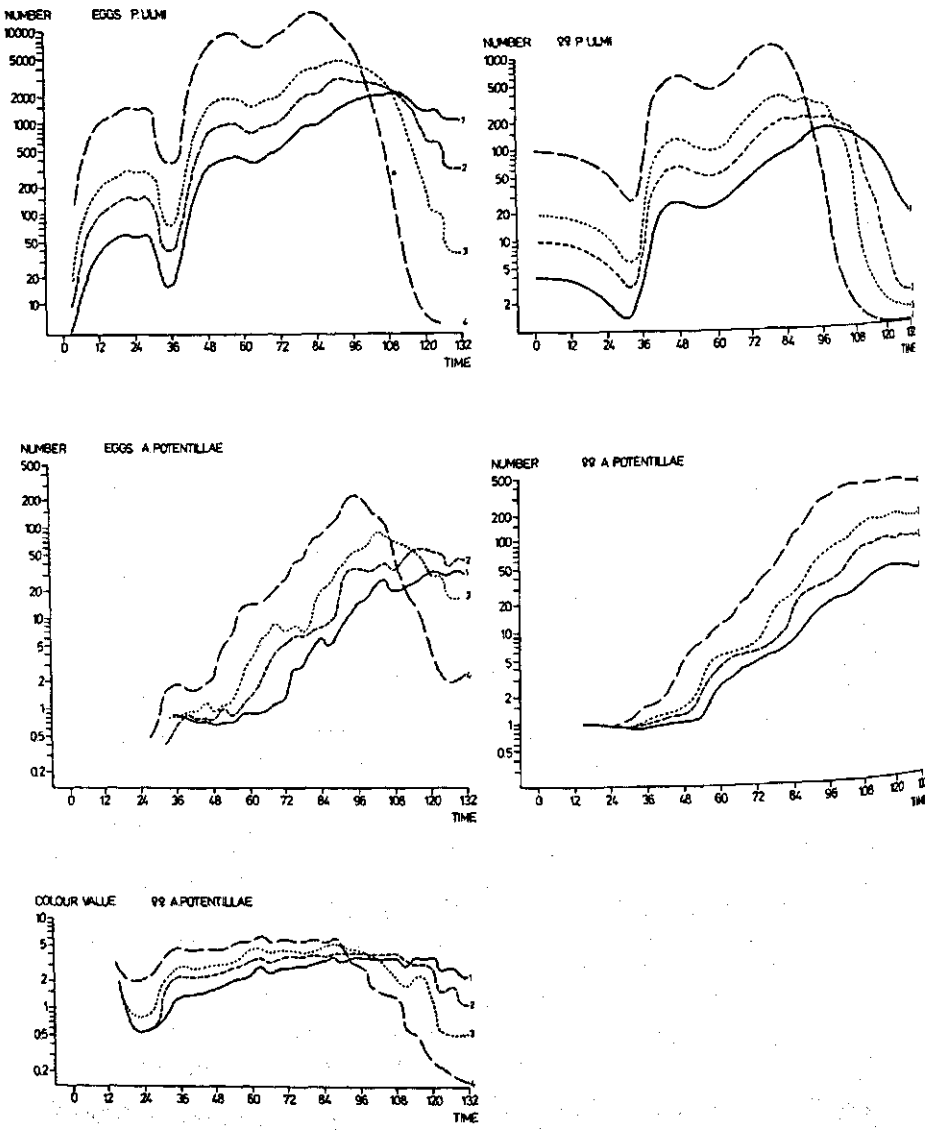


Fig. 84 | Simulation results for the numbers of adult females and eggs of *Panonychus ulmi* and *Amblyseius potentillae* and the colour value of the adult female predator when the initial prey population on 20 May is; 1. reference model; 2. 10 adult females; 3. 20 adult females; 4. 100 adult females.

rates of development and oviposition of the predator are considerably reduced. With insufficient alternative prey there is little chance for the predator to survive the lean autumn period. However at that time many diapausing animals are already present, so that the initial predator density in the next season will still be considerable.
The results of the runs with different initial predator densities are given in Fig. 85. It is shown that an initial predator density of 20 females per 100 hundred leaves versus 4 adult females of the prey keeps the prey population far below the damage level: maximally 6 adult females of the prey per 100 leaves are found. The predators are then very hungry and colour value never exceed 1.5. The maximum predator population density is about twice as small as that of the reference model but these numbers are high enough to prevent prey numbers from exploding. All these results confirm the field experience that a high initial predator-prey ratio prevents the prey population from increasing and results in a relatively low final level of the predator density. Further it is concluded that the predator prey ratio at the start of the summer may range from 0.1 to 20.
It is therefore acceptable to introduce predatory mites at the end of June or the start of July. Then only minor amounts of predators are required. If introductions are done later, relatively large numbers of predators have to be used (roughly $>$ 50 per tree, so $>$ 100 000 per ha i.e. 90 000 cherry leaves or 1000 twigs with a predator density of 0.5 females per leaf). The rather wide range in initial densities and moments of initialization without reaching damage levels confirms experience with release programs, in the field.

10.1.3 Driving variables

During the stage of model development and experimentation, some runs with the preliminary model were made to evaluate the effect of small changes in the driving variables and to determine the required accuracy of these variables. It was shown in Section 7.2.1 that systematic errors in temperature of more than 0.5°C already caused considerable changes in the end result. With a systematic increase in temperature the prey population develops faster, and then the predator population rapidly increases and suppresses the prey population in an earlier stage of development. Thus the maximum of the prey population is reached at the beginning of August instead of mid or end August. Two runs with the final program with changed values of SEN showed the effects of systematic increases or decreases in temperature, Fig. 86. A very warm summer, a systematic increase of 2°C, produces

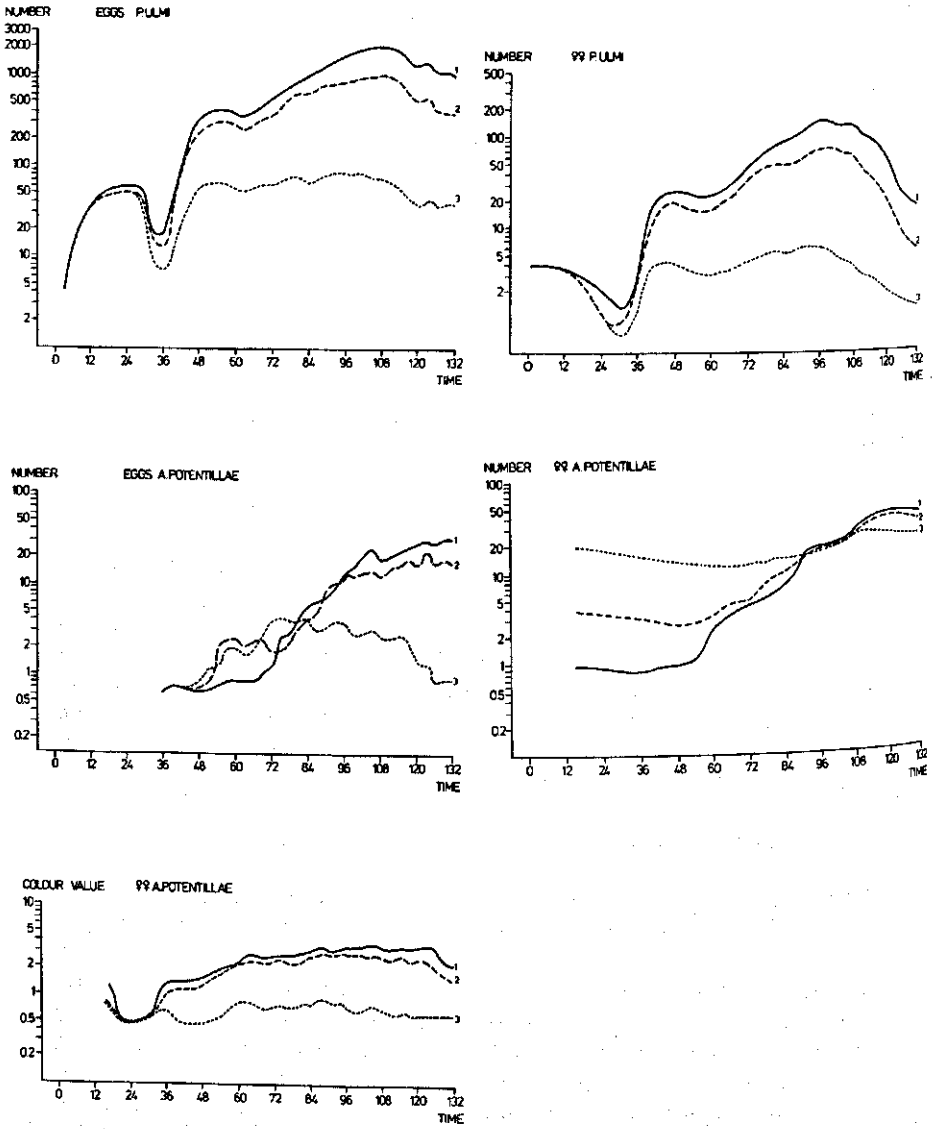


Fig. 85 | Simulation results for the numbers of adult females and eggs of *Panonychus ulmi* and *Amblyseius potentillae* and the colour value of the adult female predator when the initial predator population on 1 June is; 1. 1 adult female (reference model); 2. 4 adult females; 3. 20 adult females.

the described deviations; a very cold summer, a systematic decrease of 2°C, retards population growth of the prey, which finally reaches its maximum at the end of August, at a value far below the reference curve. Hence a cold summer may cause prey population densities below the reference curve and a warm summer gives maxima of the same size as the reference curve but at an earlier stage of the season.

The other important abiotic parameter that requires sensitivity analysis is the surface of the leaves. All simulations were done for the well determined surface of 100 July leaves of the cultivar Golden Delicious, by multiplying all relative predation rates by a standard factor that expresses the quotient of the standard surface of the process experiments of Section 6.2 to the surface of the 100 leaves samples. In this way it was implicitly assumed that the upper surface of the leaves and the surface of the twigs and branches could be neglected because of the relatively short time the animals spend there. The calculations were done for Golden Delicious and should be easily transferable to other apple cultivars.

The sampling unit is 100 leaves for all cultivars, but the surface of these units may differ, for example for Golden Delicious 2000 cm^2 and for Schone v. Boskoop > 4000 cm^2, (van de Vrie et al., in prep.). These differences in surface mean differences in density of prey and predator so that predation rate may be smaller and the colour value of the predators lower which may effect again numerical and functional responses. All these difficulties would have been prevented if sample units of 1000 cm^2 had been used instead of 100 leaves. To evaluate the effect of difference in surface per sample unit, several runs were made with various multiplication factors.

Fig. 87 presents the results of some runs with rather large changes in multiplication factor, it being shown that smaller deviations from the standard factor only caused minor deviations in the end result. Only deviations that are more than 1.5 or less than 0.75 times the standard factor considerably influence the course and maximum of the density curve for adult females and eggs of the predator. The 100 leaf surface of different cultivars does not show a wide range (2000–4500 cm^2).

The many combinations of the prey and predator population densities found in the field are therefore not induced by characteristics of the tree but are mainly attributable to the initial prey-predator ratios that may vary in a wide range due to the stochastical character of the winter mortality of both prey and predator. Some additional runs with very small systems, comparable with the systems used by McMurtry & van de Vrie (1973) and with different temperature combinations showed

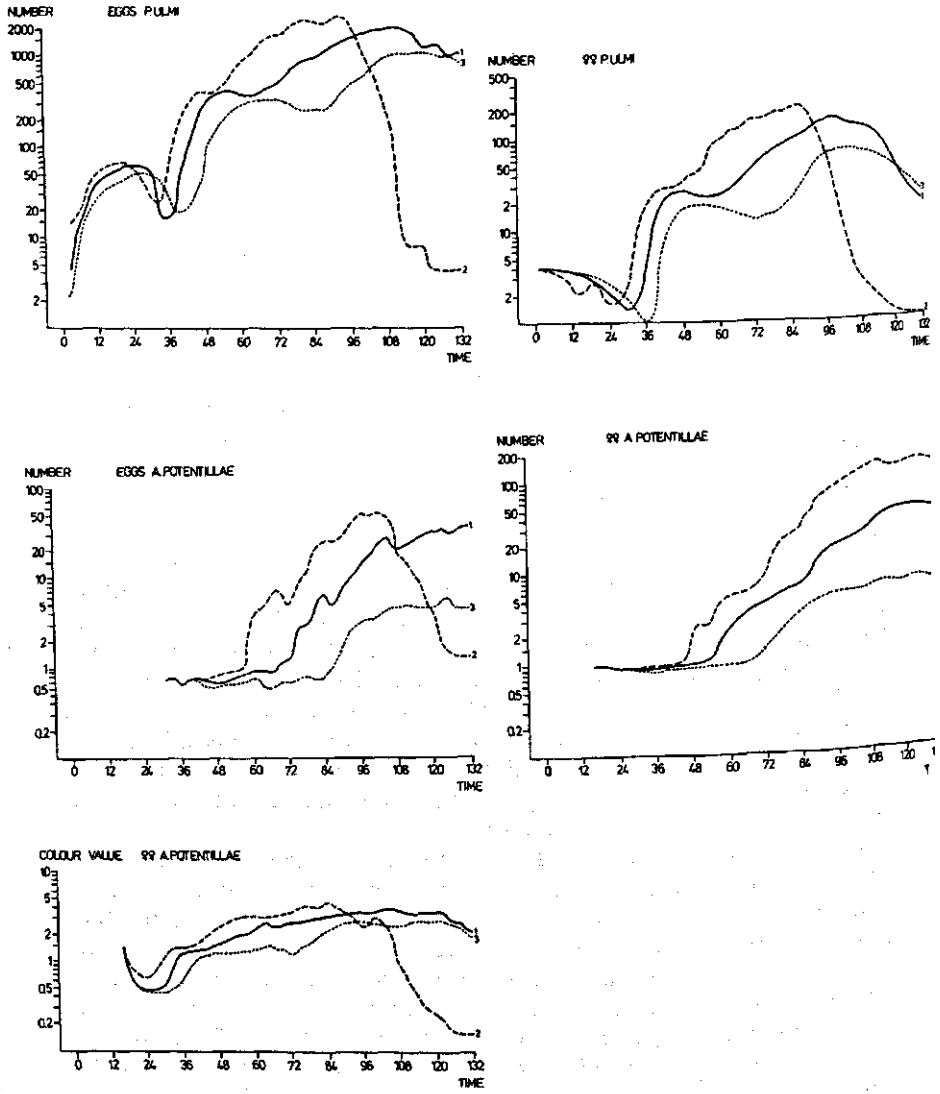


Fig. 86 | Simulation results for the numbers of adult females and eggs of *Panonychus ulmi* and *Amblyseius potentillae* and the colour value of the adult female predator.
1. reference model; 2. temperature is systematically 2°C higher; 3. temperature is systematically 2°C lower.

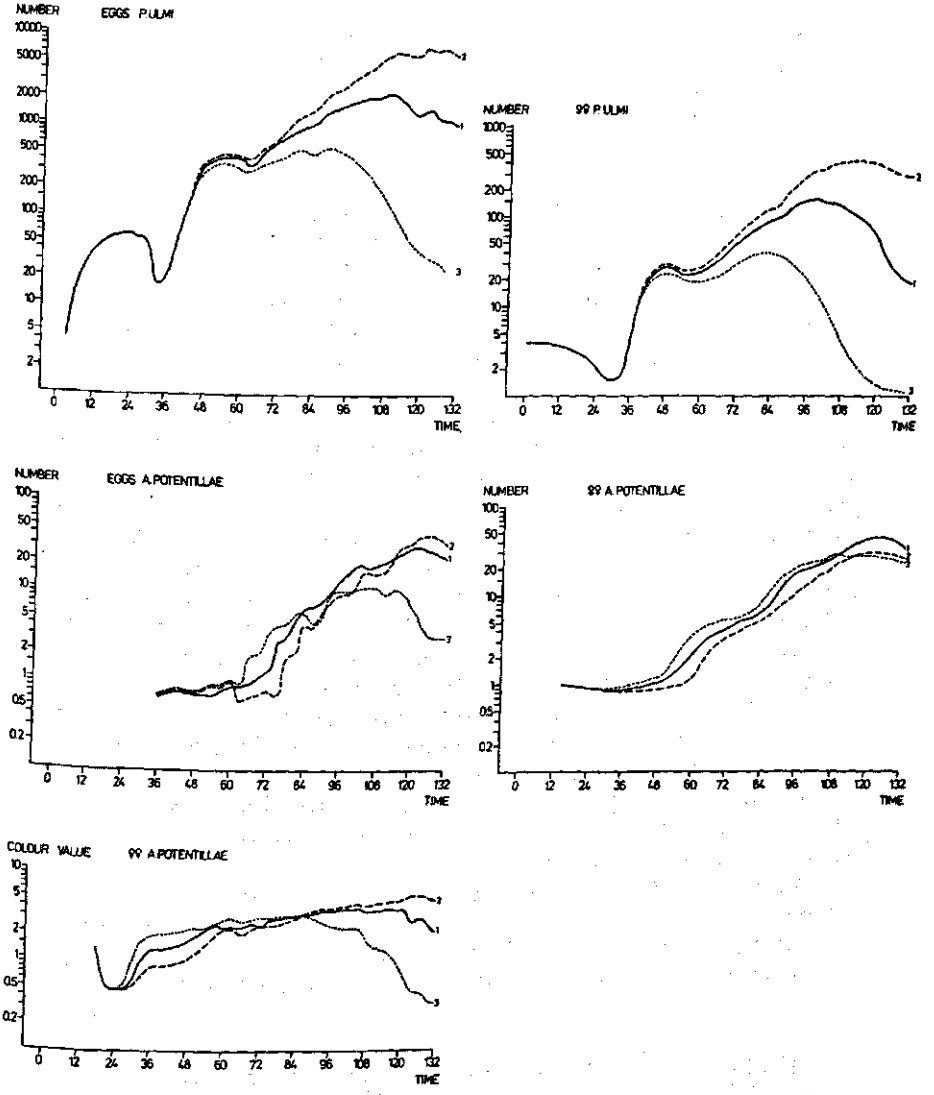


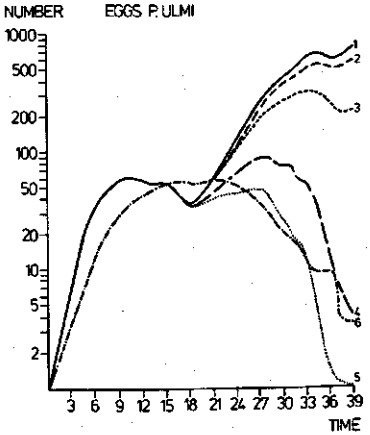
Fig. 87 | Simulation results for the numbers of adult females and eggs of *Panonychus ulmi* and *Amblyseius potentillae* and the colour value of the adult female predator when the multiplication factor for surface transformation (CFS) is 1. 1.92 E — 3 = 0.00192 (reference model); 2. 0.96 E — 3 = 0.00096; 3. 3.84 E — 3 = 0.00384.

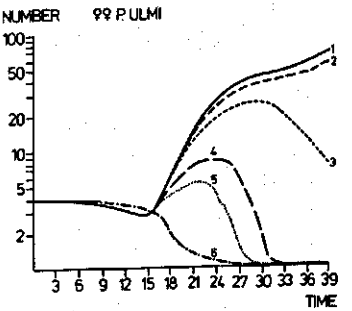
that the prey population is controlled within 30 days, Fig. 88. These results presented for adult females and eggs of prey and predator confirm the experimental results of McMurtry & van de Vrie.

10.1.4 Rates of mortality, development and oviposition

To determine priorities for future research, to improve and simplify the models, the effect of the different factors is evaluated. So all rates are multiplied by sensitivity factors, SEN 1–33 for the rates of development and abiotic mortality; SENA 1–10, for the rates of oviposition of the prey; SENB 1–10, for the rates of oviposition of the predator; SENC 1–8, for the rates of increase and decrease in colour value of the predator; SENP 1–12 for the relative rates of predation; SEN 16, SEN 21, SEN 25 and SEN 28 are multiplication factors affecting the numerical responses for development and oviposition. When all factors have the value 1, the density curves originally simulated for the prey and predator result. For each single factor to be analysed two runs were made, one with SEN...= 1.2 and one with SEN...= 0.8. For most relations these values cause deviations just outside their 90% confidence interval. All other sensitivity factors were kept at the value 1, so combinations of sensitivity factors and changes within the 90% confidence interval were omitted for time reasons. Changes to both sides were applied to detect asymmetry in response.
Figs 89–92 present the results of some runs for the adult females and eggs of prey and predator and the colour values of the adult female predators, only the most extreme results being given.
Because of the many sensitivity factors and the differences in their effect on the population curve it is necessary for further discussion to subdivide them in two groups.
1. Factors that have no effect on the pattern of the population curves of both prey and predator and affect the maxima of prey densities within the 10 percent range. Most factors belong to this group.
2. Factors causing changes in the pattern of the population curves or

Fig. 88 | Simulation results for the numbers of adult females and eggs of *Panonychus ulmi* and *Amblyseius potentillae* and colour value of the adult female predator: 1. without predator; max. temp. = 22°C, min. temp. = 19°C; 2. with one initial predator and the multiplicationfactor for surface transformation, CFS = 1.92 E — 3; 3. CFS = 1. E — 2; 4. CFS = 5. E — 2; 5. CFS = 1. E — 1; 6. CFS = 1. E — 1, max. temp. = 20°C; min. temp. = 10°C.


NUMBER
EGGS P. ULMI
1000
500
200
100
50
20
10
5
2
3 6 9 12 15 18 21 24 27 30 33 36 39
TIME


NUMBER
♀♀ P. ULMI
100
50
20
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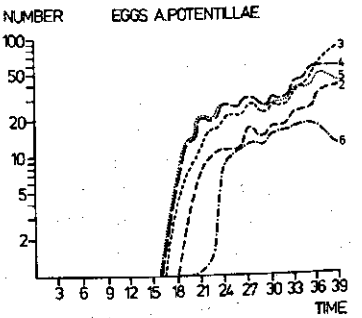
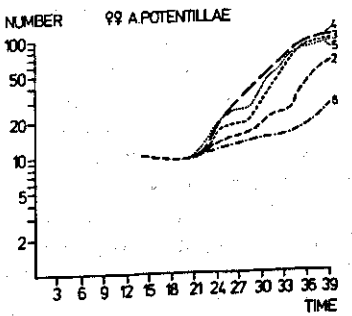
5
2
3 6 9 12 15 18 21 24 27 30 33 36 39
TIME


NUMBER
EGGS A. POTENTILLAE
100
50
20
10
5
2
3 6 9 12 15 18 21 24 27 30 33 36 39
TIME


NUMBER
♀♀ A. POTENTILLAE
100
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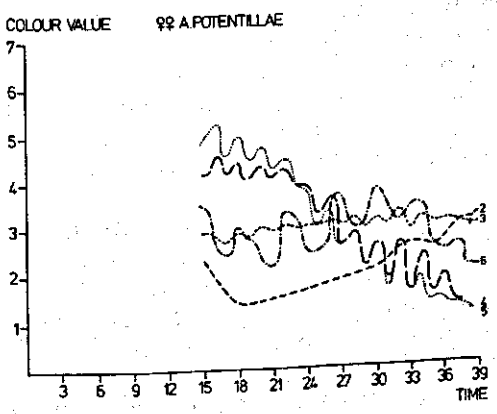
TIME


COLOUR VALUE
♀♀ A. POTENTILLAE
7
6
5
4
3
2
1
3 6 9 12 15 18 21 24 27 30 33 36 39
TIME

deviations in the maxima of the prey densities outside the 10 percent range.
Minor changes are caused by the factors affecting the abiotic mortality rates of eggs of *P. ulmi*, SEN3'1,4'; of juveniles of *P. ulmi*, SEN 6'1,6'; of diapausing juveniles of *P. ulmi* SEN 9'1,4'; of pre-oviposition females of *P. ulmi*, SEN 11; of eggs of *A. potentillae*, SEN 13; of juveniles of *A. potentillae*, SEN 15; of diapausing juveniles of *A. potentillae*, SEN 20 and of preoviposition females of *A. potentillae*, SEN 24. The small effect of these factors is due to the already very low abiotic mortality as is shown in Fig. 25 and Table 17. The first group also includes the sensitivity factors for developmental periods of diapausing juveniles and eggs of *P. ulmi*, SEN 7 and SEN 1; of eggs, juveniles and diapausing juveniles of *A. potentillae*, SEN 18, SEN 22 and SEN 26. The small effect of the developmental periods of these stages is explained by their low contribution to predation. Eggs of the prey are not eaten, deutonymphs of the prey are relative unattractively, eggs and larvae of the predator do not predate and protonymphal and deutonymphal predation activity is low.
Changes in the lower limit of the colour value of the predator from 0.5 to 1.0 cause relatively important changes in the population curve, Fig. 89. The prey population reaches higher densities than the reference model and these may be caused by the high predation rate in the early summer that is apparently more important than the numerical response due to the higher lower limit of colour value. The absolute effect of these changes is nevertheless small. The effect on the increase or decrease in colour value, SENC 1–8, is also small and scarcely affects the course of colour in time. This once more confirms the assumption of negligible temperature effects on prey utilization, so that improving measurements on prey utilization does not seem very useful.
Multiplication of the oviposition rate of the prey (0.8 and 1.2) also has little effect on the population numbers, an increase of prey numbers being easily buffered by the functional and numerical response of the predator. The colour value only shows a minor change. The multiplication factors were chosen such that the relations deviated just outside their confidence intervals.
However this is not so for all numerical response factors. Multiplication of these relations by the multiplication factors that are used for all other relations (1.2 and 0.8) results in small deviations in the end result. But the limited confidence interval obtained for the relations colour value against development rate and maturation rate, (Section 7.3) necessitates a wider range of multiplication factors (0.5–2.0). When these are applied, strong deviations from the reference curve result

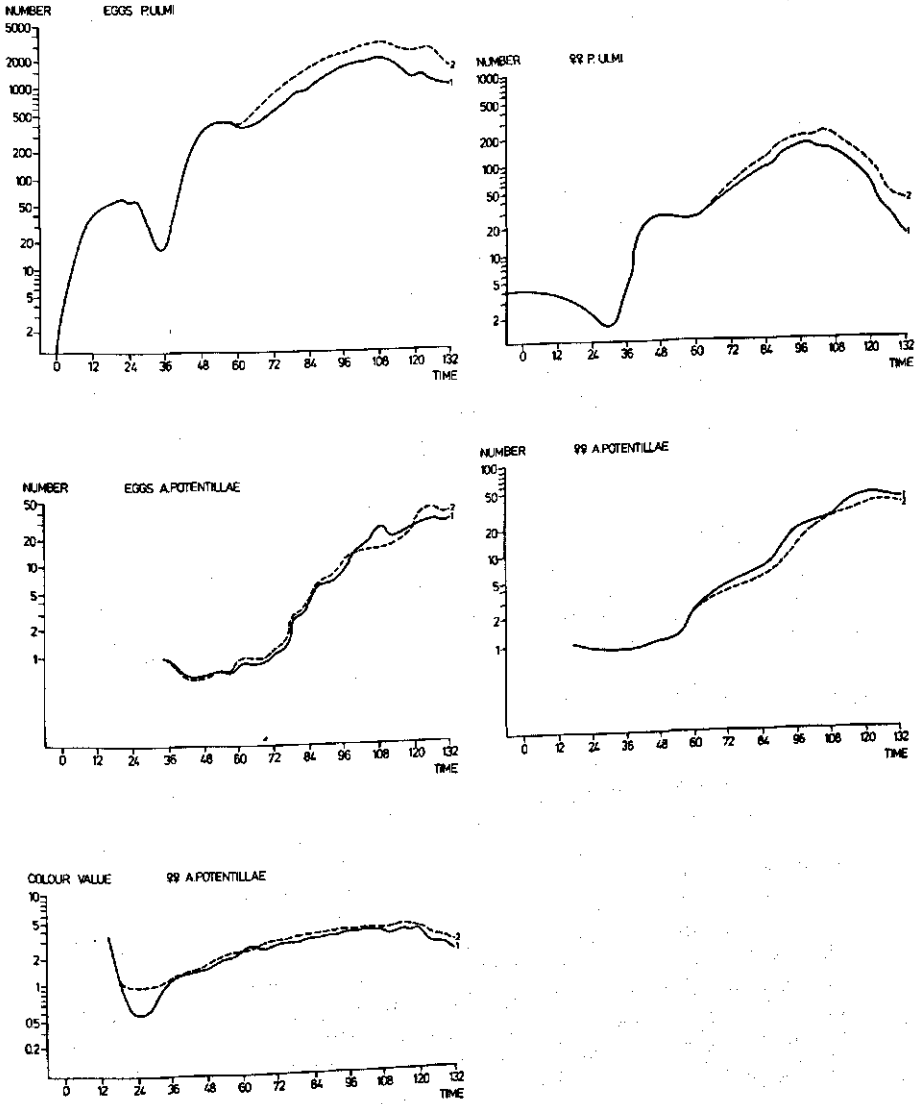


Fig. 89 | Simulated population fluctuations for adult females and eggs of *Amblyseius Panonychus ulmi* and *Amblyseius potentillae* and colour value of *Amblyseius potentillae* throughout the season when the lower limit of the colour value is 1. 0.5 (reference model); 2. 1.0.

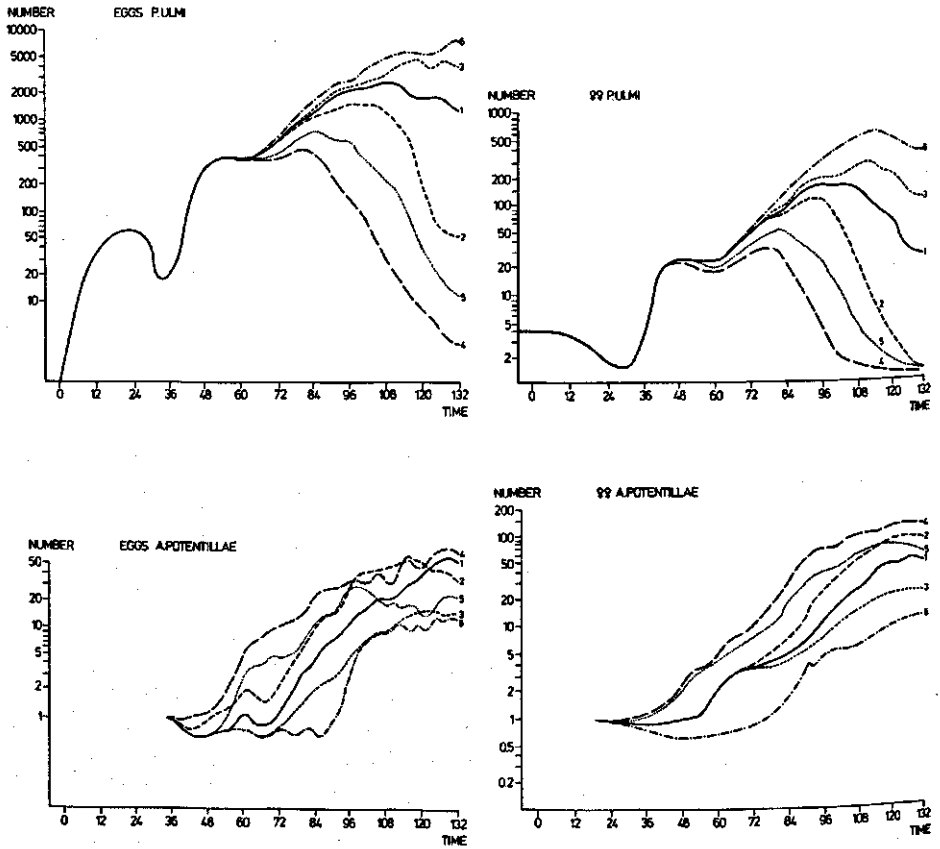


Fig. 90 | Simulation results for the numbers of adult females and eggs of *Panonychus ulmi* and *Amblyseius potentillae* when 1. reference model; 2. colour value against oviposition rate of adult female predator is multiplied by 2.; 3. colour value against oviposition rate adult female predator is multiplied by 0.5; 4. colour value against delay in development of juvenule stages is multiplied by 0.5 and colour value against oviposition rate of adult female predator is multiplied by 2.0; 5. colour value against delay in development is multiplied by 2.

(Fig. 90). An increased effect of delaying development due to low colour values gives prey densities above the damage level at the end of the season and a decreased effect results in a regulation of the prey population far below the damage level. In the same figure the results of simulations with multiplication factors 2.0 and 0.5, for the relation colour value against oviposition rate are given. It is concluded that changes in numerical response have important effects and should be determined more accurately, than was possible in this study.
The second group of factors causing relatively considerable deviations in pattern or maxima of the curves in comparison with the reference curve when multiplication factors range from 0.8 to 1.2, includes the length of the juvenile period of the prey, SEN 4, the oviposition rate of the predator SENB'1,10' and the relative predation rates SENP' 1,12'. However with the multiplication factors considered no changes in the general pattern of the population curves occur, only the size and the position of the maximum of the population density of both prey and predator is affected, as is shown in Figs 91 to 92.

All density curves are compared with the reference curve. The relatively strong effect of lengthening or shortening the juvenile period of the prey is explained by the relatively large contribution of its larvae and protonymphs to the predation process. Lengthening the juvenile period causes a much lower maximum of the prey density and shortening the juvenile period, Fig. 91, causes much higher maxima. Although prey density is considerably affected, the changes in colour of the predator are only very small. The changes in the population density curve due to the sensitivity factor for rate of oviposition of the predators are principally found in mid and late August Fig. 92, an increased oviposition rate causing a much smaller final prey population and a decreased oviposition rate causing a much higher final prey population. This is due to the more rapid decrease of the prey population when SENB = 1.2 and a slow decrease when SENB = 0.8, induced by the relatively high or low predator density. Thus the overwintering prey population is affected in an important way by the oviposition rate of the predator, the course of the population in time being scarcely influenced. The changes in relative predation rate result in prey density curves that have the same pattern as the reference curve as is shown in Fig. 91. The changes in predation rates have less influence than a change in the juvenile period of the preys. Multiplication of the relative predation rates of the adult female predator only results in population density curves that scarcely deviate from the curves found when all predation rates were multiplied. Multiplication

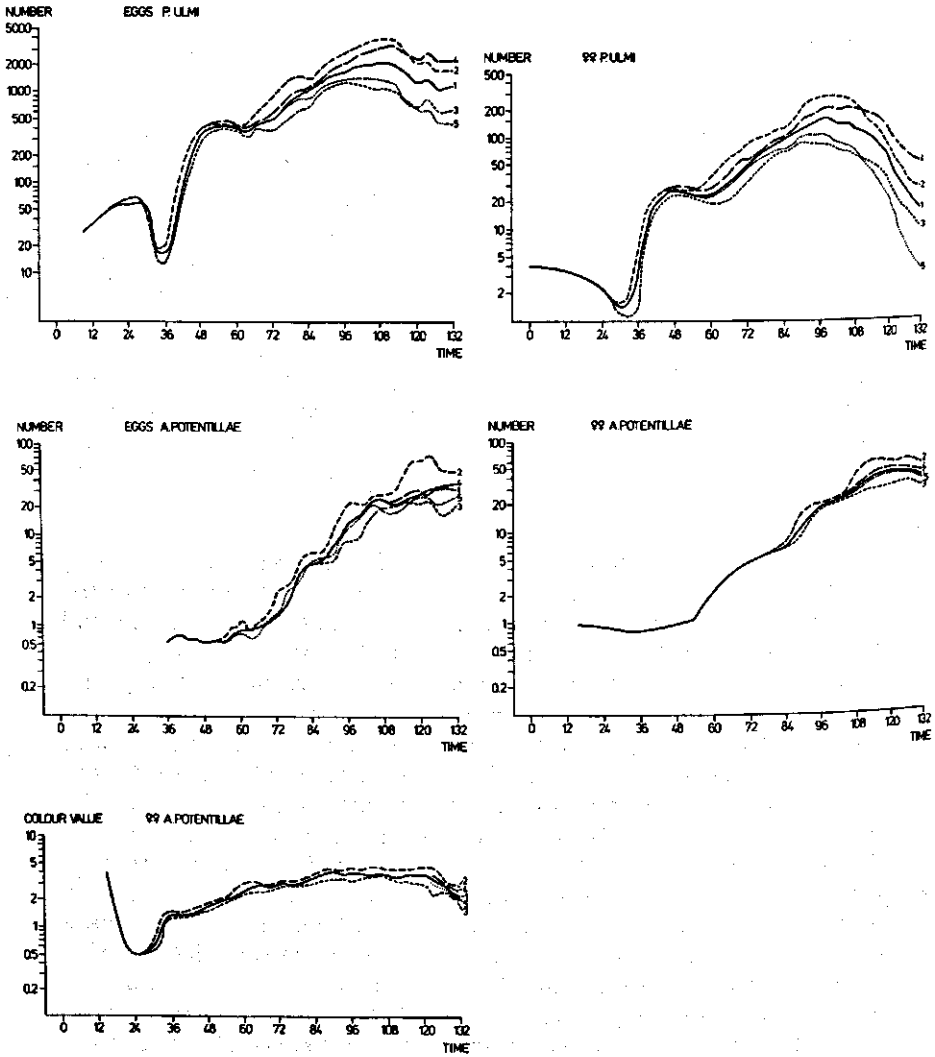


Fig. 91 | Simulation results for the numbers of adult females and eggs of *Panonychus ulmi* and *Amblyseius potentillae* and colour value of the adult female predator for 1. reference model; 2. length of juvenile period prey is multiplied by 0.8; 3. length of juvenile period prey is multiplied by 1.2; 4. relative predation rate of adult female predator is multiplied by 0.8; 5. relative predation rate of adult female predator is multiplied by 1.2.

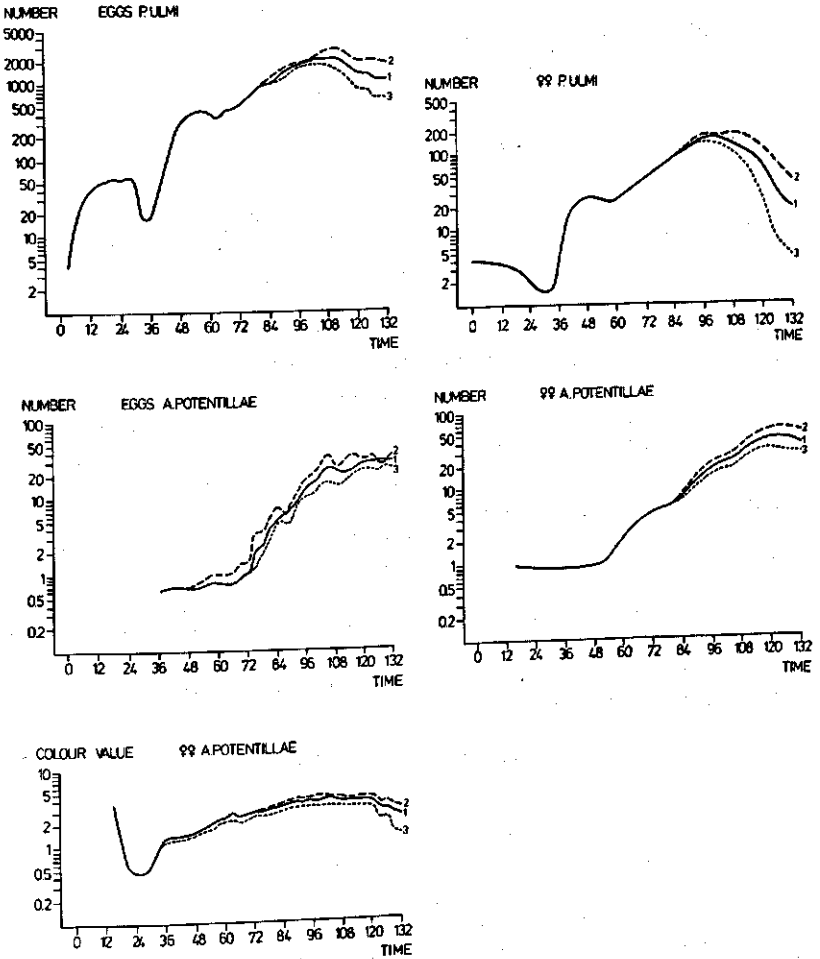


Fig. 92 | Simulation results for the numbers of adult females and eggs of *Panonychus ulmi* and *Amblyseius potentillae* and colour value of the adult female predator for 1. reference model; 2. oviposition rate of adult female predator is multiplied by 1.2; 3. oviposition rate of adult female predator is multiplied by 0.8.

of the predation rates of the juvenile predator stages and the adult male predator gives curves for prey and predator that do not deviate at all from the reference curve confirming again the result of Section 10.1.1.

The colour value is always hardly affected so that numerical effects on the predator population are not likely.
Apparently the combined effect on prey utilization and relative predation rate buffers the effect on the colour value.

10.2 Micro-weather model

Like the population model, the micro-weather simulator was submitted to a sensitivity analysis to determine the relative importance of the parameters and rates involved. This sensitivity analysis was done in the same way with multiplication factors of the rates and parameters. The following factors were involved; width of the row, leaf area index, scattering coefficient, height of the row, direction of the rows, stomatal resistance, laminar resistance, and leaf distribution function. In Table 39 a scheme for the sensitivity analysis is presented, each factor being varied sometimes relative to the absolute value of the parameters and sometimes relative to the range of possible values, examples of the latter being temperature and width of the row.
The criterion for this sensitivity analysis is the difference between air temperature and weighted mean of the leaf temperatures. This differ-

Table 39 Scheme for sensitivity analysis for the micro-weather simulator coupled to the population model. Each factor is varied separately, factors 1–3 affecting the leaf temperatures, factors 4–7 affecting the fraction of leaves that belong to each of the classes.

Factor	Reference model	Variations	
1. Scattering coefficient	0.4	0.3	0.5
2. Laminar resistance multiplied by	1.0	0.9	1.1
3. Stomatal resistance multiplied by	1.0	0.9	1.1
4. Leaf area index	4	3	5
5. Leaf distribution function	0.222,0.193,0.165	0.0,0.0,0.0	1.0,0.0,0.0
	0.125,0.097,0.085	0.0,0.0,0.0	0.0,0.0,0.0
	0.057,0.034,0.023	0.0,0.0,1.0	0.0,0.0,0.0
6. Direction of row to the azimuth	45°	0°	90°
7. Width of the path	2	1	0
Width of the row	2	1	2

Table 40 Final numbers of eggs and mites (all stages) of *Panonychus ulmi*, expressing the cumulated weighted mean of air and leaf temperatures, for various combinations of parameters of the microclimate simulator.

	Numbers of	
	eggs	mites
Air temperature		
Oviposition rate x 0.9	59249	24607
Oviposition rate x 1.0	90367	36861
Leaf temperature		
Reference model	76466	28167
Laminar resistance x 1.1	75346	27868
Laminar resistance x 0.9	77646	29045
Stomatal resistance x 1.1	78869	29532
Stomatal resistance x 0.9	73649	27212
Scattering coefficient = 0.5	63180	34102
Scattering coefficient = 0.3	88308	22989
Direction of row = 0°	76206	28353
Direction of row = 90°	74502	27539
Leaf area index = 5	70204	25804
Leaf area index = 3	85848	32854
Leaf position		
erectophile	71471	28611
planophile	76681	26512
Width of row = 1	78829	29493
Width of path = 1		
Closed crop	80848	30382

ence is cumulatively expressed in the growth of the egg fraction of the prey population model connected to the micro-weather simulator and therefore the final egg number is used as a measure of the effect of the different parameters and rates.

In table 40 the results are given for the different modifications. It appears that only SCAT and LAI have an important effect on the difference and that all the other factors such as leaf distribution and width of the row are of minor importance for these temperature effects. This relative importance of the scattering coefficient makes accurate determination of this variable necessary in situations where the micro-weather simulator is used.

11 Final discussion

11.1 Aspects of the present work

To evaluate the present work and to give some suggestions for further research the following concluding remarks are made. Initial prey-predator ratios may vary over a wide range without the danger of reaching prey densities above the damage level later in the seasons, so that a management system can be based on a survey of predators and prey, sometime in spring. The model of the hatching process, Section 8.2.1 is easily incorporated in the population model and then initialization of the population model may be based on a survey of winter eggs and overwintering female predators at their overwintering sites. Since it is impossible to distinguish visually between living and dead winter eggs, it is necessary to know enough about the overwintering process to compute the fraction of viable eggs in spring.
The most important factors in the system are rate of oviposition, predation rate of the adult female predator and the length of the juvenile period of the prey. Of minor importance are relative changes in abiotic mortality of prey and predator, predation rate of adult males and juveniles, and length of the pre-oviposition period of prey and predator. It seems acceptable to simplify the model by neglecting abiotic mortality of prey and predator and predation rate of juveniles and adult males, and by reducing the number of age classes. The effect of relative changes in numerical response for the values of 0.8 and 1.2 is not large. But at present there is so little information on delay in development of the predator due to insufficient food, that uncertainty of multiplication factors within the range 0.5–2.0 cannot be excluded especially at low colour values. The deviations between the population density curves are then considerable, although less important than those due to structural changes. The lack of quantitative knowledge on numerical response requires further experimentation to improve the model. This experimentation may be done iteratively in combination with simulation until the same accuracy of model output is obtained as was realized for the numerical response of adult females.
The experimental results of the present work may be applied in other fields of research. For example, the linear relation between colour value of the predator and oviposition rate of adult female predators,

(Section 6.3.2) may be used in testing secondary effects of pesticides. At present new pesticides are carefully screened, the harm they do to useful fauna elements being taken into account. However, satisfactory criteria and simple testing techniques are often not available. For predatory mites the predation rate could be an acceptable criterion. The direct measurement of this predation rate is a time-consuming and cumbersome procedure. It can be replaced by measuring oviposition rate of standardized females, for example young females that have just been mated, because there is a linear relation between colour value and rate of oviposition up to the end of the colour scale.
The colour scale as a measure of satiation is applicable in other predatory mite species, since it is shown (van de Vrie, pers. commun.) that colour changes are in several species direct related to changes in behaviour.
The population models may also be used to evaluate the prospects for regulating prey with other predatory mites imported from abroad that possess resistance to organophosphorus pesticides, because the quantitative data or reliable estimates required are well defined and limited in number. The experimenting techniques to obtain these data are well developed.
The models may also be an aid in explaining the phenomena observed in the field that some predatory mite species may replace other species. For this purpose two different predators are easily introduced into the models and their mutual interference through predation on the same food source is thereby simulated.
To apply the models to other predator-prey systems the relations between predation rate and prey density must be determined at various temperatures. These tedious and time-consuming determinations should be limited by using models in which only the maxima of the functional response curves are introduced. The other points of the relations can then be found iteratively by comparing simulated results with the results of independent small-scale population experiments as described in Section 9.3. In this way the most time-consuming experiments in the low prey densities can be omitted and only process experiments at high prey densities are required.

In the present work simulations were done for 100 leaves, the sample size normally used for density determinations of prey and predator. An evaluation of sample size and sample technique has been given by van de Vrie et al., (in prep.).
For the present studies these 100 leaf samples represent the whole orchard and the results of simulations are therefore applicable to the

entire field. For this study the distribution of the mites in the orchard, whether normal or negative binomial, is of no importance as the calculations concern the mean of the whole orchard. Further detail in the models is only required when the differences within the orchard are so large that consideration of averages for the whole orchard is an unrealistic simplification.

Often large differences in density of prey and predator are found between equally treated orchards. These may be caused by the variation in initial numbers of prey and predator in spring, (Section 10.1.2), due to the stochastical character of winter mortality. Another cause for these differences between orchards may be pesticide application. The models may be used to evaluate the effect of an occasional spraying that kills a certain proportion of prey and predator population.

11.2 Future prospects

The present study shows all steps of model building and evaluation. The first step concerns the description of the system, its limits and its structure; the second step comprises quantification and mathematical description of the different relations. The third step, often closely connected and here clearly interwoven with the second step, concerns the interconnection of the different relations; it is, in fact, the construction of the computer models according to well-defined techniques. The final step is the evaluation and the sensitivity analysis of the model. This systematic way of model building has many advantages and although these have already been mentioned implicitly, they are once more considered.

Organization of information
All available data are collected and as far as possible used. If there are not sufficient data or reliable estimates available, it is clear which additional experiments should be done. The required accuracy of these experiments is determined by the possible accuracy of the independent higher order experiments that are needed for verification of the models. In Chapter 5, this iterative way of modelling and experimenting is shown for the determination of the bionomical characteristics of prey and predator. This method of working saves considerable experimenting time that would have been spent if all experiments were done with the same level of accuracy (standard error/mean). Moreover relatively unimportant relations, i.e. those contributing little to the end result, can be omitted.

Future research
Simulation can be applied to determine directions of future research and to weigh research priorities. Even when final aims of research have been formulated, there are many ways to achieve the results. Often much attention is paid initially to aspects that contribute little to the end result whereas aspects of major importance are studied in much less detail. The chances of such errors of judgement are less, if the experimental research is from the onset complemented by model building and simulation, not so much because preliminary models reflect the real systems, but because they honestly reflect one's opinion about the system in semi-quantitative terms. The approach is well illustrated by the use that is made of micro-meteorological modelling in this study.

Rigidity in the technique of modelling.
In the present study the state variable approach is used throughout. This approach, given form with the simulation language CSMP, enables the biologist or agronomist to handle all aspects of modelling while keeping fully in touch with the experimental situation. It prevents communication errors between modeller and experimenter and makes the models readible and usable for outsiders. For instance the technique applied for simulating development and ageing that takes into account the measured dispersion is generally applicable. It is used for simulating flow of water, transport of solutes and heat in soils, germination and development of plants, and biochemical processes.

Scope of this approach
Because of the present status of crop growth models, they can be combined with the population models on phytophagous and predacious arthropods of this study. Upon quantification of the relation between host plant and phytophagous animal, these combined models may be used for calculating the reduction in yield due to various numbers of phytophagous animals at different times. In the present models the host plant is assumed to be an infinite food source, this being justified by the prey densities considered. In other situations the models may help in formulating well-defined threshold levels for the phytophagous animal. These threshold values are determined by economic factors in addition to plant physiological factors. Changing prices may be taken into account so that the combined models could become a useful tool in pest management.

Application of the present models.
The models may be used for calculating ratios of prey and predator females sometime in spring, which can be accepted without the danger of exceeding the 'damage level' (defined according to the OILB), later in the season for a given climate situation.
Year to year weather differences in the Netherlands are large enough to influence population growth of prey and predator, so that it may be useful to monitor this development with models based on actual weather, measured at a local station. Weather differences within orchards at different places are, however, so small that it would not be worthwhile to monitor the development based on weather observations in situ.

Summary

During the last decade, integrated pest control systems have been developed for several crops. One of the main fields of research in integrated control has been the control of orchard pests. Experience with modified spraying programmes in apple orchards, the increasing resistance of spider mites to acaricides, and knowledge on the bionomics of many pest species have been major factors in promoting the development of integrated pest control systems. Attempts were made to introduce predatory mites or to improve their effectiveness in the control of the fruit-tree red spider mite, one of the major pests in commercial fruit orchards. These experiments clearly showed how these natural enemies can reduce and maintain spider mite populations below the economic threshold level. At present predacious mites are widely applied in the control of spider mites in apple orchards. However, the resulting changes in the system have still not been quantitatively assessed, and it is only speculation to explain the mode of operation of the system if there is no information about the underlying ecological processes. For a stable pest control system one must know how spider mite and predacious mite populations interact with each other and with the host plant, and how the system is influenced by abiotic factors (temperature, relative air humidity, wind and rain) and by cultivation methods (including the use of fertilizers as well as insecticides and fungicides). In several countries with a developed agriculture, research has therefore been started to monitor the effect of predators on pest populations.

This study presents basic models for the fruit-tree red spider mite (*Panonychus ulmi*) and the native predacious mite, *Amblyseius potentillae*. The models are constructed according to the state variable approach, as is described in Chapter 3. The models developed with this technique bridge the gap between biological control with predacious mites in the field and the analytical methods of natural sciences, thus assisting in the introduction and management of biological control agents of the fruit-tree red spider mite.
The simulation models are based on extensive knowledge of the effect of temperature, humidity, food and daylength on the prey as well as the predator. The relations between rates of development, mortality,

oviposition and diapause with temperature and other physical factors were determined from literature studies, estimation and many laboratory experiments, Chapter 5. Many of the temperature responses of rates proved to be linear and reacted momentaneously to temperature fluctuations.

The predator-prey interaction (between predacious mite and fruit-tree red spider mite) in these models, which closely approximates the field situation, is based on a detailed analysis of the predation process. This predator-prey interaction is very complex. Five developmental stages of the prey (larva, protonymph, deutonymph, adult male and female), and four developmental stages of the predator (protonymph, deutonymph, adult male and female) are involved. The attractiveness of the different stages of the prey varies and depends partly on the satiation level of the predator. For example, the adult female predator (the most voracious stage) shows a strong preference for the younger stages of the prey, but 'hungry' predators are much less selective. The rate of ingestion and the utilization of a killed prey also depends on the satiation level of the predator. Fransz's detailed analysis of the predation process in the system two-spotted spider mite and predacious mite and the explanatory models he developed for this process showed that a simple system (one standardized predator and a constant number of preys) reaches an equilibrium within a few hours. Hence the degree of filling of the gut of the predator oscillates with a small amplitude, at a level depending on predator and prey density and on the temperature of the system. This enables the complex predation process to be incorporated in a model for a population of higher order by simply expressing relative predation rate and prey utilization as functions of temperature and state of the predator. The satiation level of the predator can be quantified visually, because well-fed predators are dark, while hungry predators are whitish and transparent. A colour scale has been developed which relates the behaviour of the predator expressed in success ratio (number of successful encounters to the total number of encounters) to the quantity of leaf and animal pigments in the predator, which together constitutes its colour.

Experiments were carried out to determine the rate of decrease in colour value, which is supposed to equal the digestion rate, the relation between predation rate and prey density, and the relation between predation rate and colour value at various temperatures. The required relations for relative predation rate and prey utilization are easily derived from these functions. Oviposition rate and the development rate from egg to adult of the predator (numerical response) also depend

on its satiation level and on temperature. These relations are also experimentally quantified, Section 6.3.
The details of information required on the driving variables, temperature and food condition were determined by experiment and simulation. The effect of nutritive condition of the tree on the prey was determined in water culture experiments and related to the nitrogen content of the leaves in commercial apple orchards. It is shown, Section 7.2, that the nutritive condition of the trees in practice do not affect the rates of development and oviposition of the fruit-tree red spider mite. To determine the required details about micro-weather an adapted and verified micro-weather simulator was coupled to the population model. The small differences between simulation results when leaf temperatures are the driving variables and simulations in which air temperature is the driving variable justified further calculations in the field with air temperature, Section 7.3.
The assumptions in the model underlying the treatment of the predation process were verified by comparing results of an independent experiment on predation in replacement series of 'prey stages', with simulation results. It is also shown that the procedure, for determining yields of a plant species growing in competition, from sowing density experiments in monoculture, may be applied for calculating predation rates of a species in 'mixed cultures' from its functional response curve in monoculture (see Section 9.2).

The models for hatching winter eggs, for population growth throughout the season and for diapause are verified at different levels of integration by independent population experiments. The most simple verification is the measurement of population growth in small ecosystems under controlled conditions in situations with and without predators and then to compare results with those of simulation.

Verification in the field is done by comparing simulation results with population measurements in several orchards. The correspondence in general pattern of population fluctuations of prey and predator and the good correspondence between simulated and measured colour values of the predators enables the model to be used for sensitivity analysis and management.
Sensitivity analysis showed that particular key factors are absent and that a wide range of initial prey-predator ratio's may be tolerated. It is further shown that the predation activity of the younger stages and the adult males is relatively unimportant and that the female predator is the important regulator due to its high predation capacity, its long life-

span and an increase in rate of oviposition until the predator is well fed. The system is rather sensitive to length of prey's juvenile period, predation rate, and oviposition rate of the adult female predator and the delay in development of the predator due to insufficient food.

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References

Andersen, V.S., 1947. Untersuchungen über die Biologie und Bekämpfung der Obstbaumspinnmilbe Paratetranychus pilosus Can. et Fanz. Diss. Univ. Bonn, 118 p.

Anderson, N.H., & C.V.G. Morgan, 1956. The role of Typhlodromus spp. in British Columbia Apple Orchards. Proc. 10th int. Congr. Ent. Montreal 1956; 4: 659–665

Avery, D.J., 1964. Carbon dioxide exchange by plum and apple leaves damaged by fruit tree red spider mite, Rep. E. MallingRes. stn, 1961: 77–80.

Baeumer, K., & C.T. De Wit, 1968. Competitive interference of plant species in monocultures and mixed stands. Neth. J. agric. Sci. 16: 103–122.

Balevsky, A., 1967. Tetranychid mites occurring on fruit crops. (In Bulgarian with German and Russian summaries.) Sofia, Izdat. Bulgar. Akad. Nauk. Inst. Zasht. Rast. Gara Kostinbrod, 157 pp.

Beament, J.W.L., 1951. The structure and formation of the egg of the fruit tree red spider mite, Metatetranychus ulmi Koch. Ann. Appl. Biol. 38: 1–24.

Becker, H., 1952. Ueber den Einfluss konstanter Temperaturen, relativer Luftfeuchtigkeit und Licht auf die Frühjahrsentwicklung der Wintereier der Obstbaumspinnmilbe, Paratetranychus pilosus Can. et Fanz. Anz. Schädlingsk. 25: 116–18.

Bengston, M., 1965. European red mite (Panonychus ulmi) and its adaptation to the Stanthorpe district, Queensland. Qd J. agric. Sci. 22: 177–185.

Berker, J., 1955. Die natürlichen Feinde der Tetranychiden. Z. Ang. Ent. 43: 115–172.

Blair, C.A., 1951. Damage to apple leaves by the fruit tree red spider mite, Metatetranychus ulmi Koch. Rep. E. Malling Res. Stn., 1950: 152–54.

Blair, C.A. & J.R. Groves, 1952. Biology of the fruit tree red spider mite, Metatetranychus ulmi Koch in South East England. J. hort. Sci. 27: 14–43.

Bokhorst, D., 1970. Chemical light measurements in glasshouses, Proc. conf. C.I.G.R. Wageningen, p. 225–239.

Bondarenko, N.V., 1964. Mites on fruit trees. In Russian. Zasht. Rast. Vredit. Bolez. 6: 41–42.

Boulanger, L.W., 1958. The effect of European red mite feeding injury on certain metabolic activities on Red Delicious apple leaves. Maine Agric. Exp. Stn Bull. 570, 34 pp.

Burnett, T., 1970. Effects of temperature on a greenhouse acarine predator-prey population. Can. J. Zool. 48: 555–562.

Bursell, E. 1970. An Introduction to Insect Physiology, Academic Press, London, New York.

Bursell, E., 1974. Environmental aspects — Humidity. In: Rockstein (Ed.) Physiology of Insects. Vol. 2, chapter 2.

Cagle, L.R., 1946. Life history of the European red mite. Tech. Bull. Virginia agric. Exp. Stn 113: 1-31.

Chant, D.A. 1959. Phytoseid mites (Acarina: Phytoseiidae) Part I. Bionomics of seven species in South Eastern England. Part II. A taxonomic review of the family Phytoseiidae with the description of thirty eight new species. Can. Ent. 91 (Suppl. 12), 166 pp.

Chant, D.A., 1961. The effect of prey density on prey consumption and oviposition in adults of Typhlodromus occidentalis Nesbitt (Acarina: Phytoseiidae) in the laboratory. Can. J. Zool. 39: 311-315.

Chant, D.A., 1966. Integrated control systems. In: Scientific aspects of pest control. Nat. Acad. Sci. Publ. 1402. Washington D.C.

Chant, D.A. & C.A. Fleschner, 1960. Some observations on the ecology of phytoseid mites (Acarina: Phytoseiidae) in California. Entomophaga, 5: 131-139.

Chapman, P.J., S.E. Lienk & O.F. Curtis, 1952. Responses of apple trees to mite infestations. J. Econ. Ent. 45: 815-21.

Collyer, E., 1958. Some insectary experiments with predacious mites to determine their effects on the development of Metatetranychus ulmi (Koch) populations. Ent. Exp. Appl. 1: 138-146.

Collyer, E., 1964. A summary of experiments to demonstrate the role of Typhlodromus pyri Scheut. in the control of Panonychus ulmi (Koch) in England. C.r. Ier Congrès int. d'Acarologie, Fort Collins, Colo, USA (1963): 363-71.

Collyer, E., 1964. Phytophagous mites and their predators in New Zealand orchards. N.Z. J. Agri. Res. 7: 551-568.

Collyer, E., 1964. The effect of an alternative food supply on the relationship between two Typhlodromus species and Panonychus ulmi (Koch) Acarina. Ent. Exp. & Appl. 7: 120-124.

Collyer, E., 1974. European Red mite, Panonychus ulmi, life cycle. Information series, Dep. Sci. Invert. Res. 1974 105/5.

Cowan, I.R., 1968. The interception and absorption of radiation in plant stands. J. appl. Ecol. 5: 367-379.

Cranham, J.E., 1972. Influence of temperature on hatching of wintereggs of fruit tree red spider mite, Panonychus ulmi (Koch). Ann. appl. Biol. 70: 119-37.

Cutright, C.R., 1963. The European red mite in Ohio. Ohio agric. Exp. stn Res. Bull. 953, 32 pp.

Dosse, G. 1956, Ueber die Entwicklung einiger Raubmilben bei verschiedene Nahrungstieren (Acarina — Phytoseiidae) Pflanzenschutz-berichte 16: 122-136.
Ehara, S., 1964. The tetranychid mites of Japan. Cr. 1er Congrès int. d'Acarologie, Fort Collins, Colo (1963): 409-14.
Evenhuis, H.H., 1958. Een oecologisch onderzoek over de appelbloedluis Eriosoma lanigerum (Hausm.) en haar parasiet Aphelinus mali (Hald.) in Nederland. Tijdschr. PlZiekt. 64: 1-103.
FAO., 1973. Panel of Experts. Proc. FAO Conf. Ecology. Rel. Plant Pest Contr. Rome.
Fjelddalen, J., 1952. Red spider mites of top and small fruit. Biology and Control. Frukt baer 2: 56-72.
Fluiter, H.J. de, 1957. De bestrijding van ziekten en plagen in twee belangrijke fruitteeltgebieden in Canada. Meded. Dir. Tuinb. 20: 167-175.
Fransz, H.G., 1974. The functional response to prey density in an acarine system. Simulation Monograph. Pudoc, Wageningen. 149 pp.
Gates, D.M., 1962, Energy exchange in the Biosphere, Harper & Row, London/New York.
Geijskes, D.C., 1938. Waarnemingen over het fruitspint in verband met zijn bestrijding. Tijdschr. PlZiekt. 44: 49-80.
Gilliatt, F.C., 1935. The European red mite, Paratetranychus pilosus Can. et Fanz. in Nova Scotia. Can. J. Res. D. Zool. 13: 1-17.
Goudriaan, J., 1973. Dispersion in simulation models of population growth and salt movement in the soil. Neth. J. agric. Sci. 21: 269-281.
Goudriaan, J., (in prep.). 1977. (Department of Theoretical Production Ecology, De Dreijen 4, Wageningen) Simulation Monograph. Pudoc, Wageningen.
Goudriaan, J. & P. Waggoner, 1972. Simulating both aerial microclimate and soil temperature from observations above the canopy. Neth. J. agric. Sci. 20: 104-124.
Groves, J.R., 1951. A synopsis of the world literature on the fruit tree red spider mite, Metatetranychus ulmi Koch and its predators. Commonw. Inst. Ent., London 180 pp.
Günthart, E., 1945. Ueber Spinnmilben und deren natürliche Feinde. Mitt. schweiz. ent. Ges. 19: 279-308.
Hamstead, E.O., & E. Gould, 1957. Relation of mite populations and seasonal leaf nitrogen levels in apple orchards. J. econ. Ent. 50: 109-10.
Helle, W. & M. van de Vrie, 1974. Problems with spider mites. Outlook Agric. 8: 119-125.
Herbert, H.J. 1959. Note on the feeding ranges of six species of predacious mites (Acarina: Phytoseiidae) in the laboratory. Can. Ent. 91: 812.

Herbert, H.J., 1961. Influence of various numbers of prey on rate of development, oviposition and longevity of Typhlodromus pyri Scheuten (Acarina : Phytoseiidae) in the laboratory. Can. Ent. 93: 381–384.
Herbert, H.J., 1970. Limits of each stage in populations of the European Red mite, Panonychus ulmi. Can. Ent. 102: 64–68.
Herbert, H.J. & K.P. Butler, 1975. Sex ratio of the European red mite, Panonychus ulmi (Acarina: Tetranychidae), in apple orchards in Nova Scotia. Can. Ent. 107: 825–828.
Holling, C.S., 1966. The functional response of invertebrate predators to prey density. Mem. Ent. Soc. Can. 48, 86 pp.
Hopmans, P.A.M., (in prep.). (Department of Horticulture, Haagsteeg, Wageningen).
Hueck, H.J., 1951. Influence of light upon the hatching of wintereggs of the fruit tree red spider. Nature, London 167: 993–994.
Hueck, H.J., 1953. The population dynamics of the fruit tree red spider. (Metatetranychus ulmi Koch 1836 Acari, Tetranychidae) with special reference to the influence of DDT. Diss. Univ. Leiden, 148 pp.
Huffaker, C.B., M. van de Vrie, & J.A. McMurtry, 1969. The ecology of tetranychid mites and their natural control. Ann. Rev. Ent. 14: 125–74.
Huffaker, C.B., J.A. McMurtry, & M. van de Vrie, 1970. Ecology of Tetranychid Mites and Their Natural Enemies: A Review II Hilgardia 39 (1).
Jackson, J.E., & J.W. Palmer, 1972. Interception of light by model hedgerow orchards in relation to latitude, time of the year and hedgerow configuration and orientation. J. appl. Ecol. 9: 341–357.
Janssen, J.M.G., 1974. Simulation of germination of winter annuals in relation to microclimate and microdistribution. Oecologia (Berlin) 14: 197–228.
Jary, S.G., & M.D. Austin, 1937. Dep. Ent., Jl. S.-east. agric. Coll. Wye 39: 9–15.
Keulen, H. van, 1975. Simulation of water use and herbage growth in arid regions. Simulation Monographs. Pudoc, Wageningen, 18488.
Kropczynska, D., 1970. Biology and ecology of the predatory mite Typhlodromus finlandicus (Oud) (Acarina: Phytoseiidae) (In Polish with English summary) Zesz. probl. Postep. Naulk roln. 109: 11–42.
Kropczynska, D. & M. van de Vrie, 1967. The distribution of phytophagous and predacious mites on apple leaves. Boll. Zool. Agr. Bachic. II(7): 107–112.
Kuenen, D.J., 1943. Spint op vruchtbomen, Tijdschr. PlZiekten. 49: 130–31.
Kuenen, D.J., 1946. Het fruitspint en zijn bestrijding. Meded. Tuinb Voorl Dienst 44, 68 pp.
Kuenen, D.J. 1949. The fruit tree red spider mite (Metatetranychus ulmi Koch, Tetranychidae, Acari) and its relation to its host plant. Tijdschr. Ent. 91: 83–102.

Kuenen, D.J. & A. Post, 1958. Influence of treatment on predators and other limiting factors of Metatetranychus ulmi (Koch). Proc. 10th Int. Congr. Ent., Montreal (1956) 4: 611-15.

Lablans, W.N., et al. (In prep.). (K.N.M.I., Utrechtseweg 297, Den Bilt).

Landsberg, J.J., D.B.B. Powell, & D.R. Butler, 1973. Microclimate in an apple orchard. J. appl. Ecol. 10. 881-896.

Lees, A.D., 1953a. Environmental factors controlling the evocation and termination of diapause in the fruit tree red spider mite, Metatetranychus ulmi Koch (Acarina, Tetranychidae). Ann. Appl. Biol. 40: 449-86.

Lees, A.D., 1953b. The significance of light and dark phases in the photoperiodic control of diapause in Metatetranychus ulmi. Ann. appl. Biol. 40: 487-97.

Leski, R. & S. Predki, 1964. Investigations on the biology of the European red mite Panonychus ulmi (Koch) (Acarina : Tetranychidae). In Polish with English summary. Polskie Pismo ent., B. 20: 157-188.

Lienk, S.E. & P.J. Chapman, 1958. Effect of wintertemperature of 1956-1957 on the survival rate of European red mite eggs. J. Econ. Ent. 44: 623.

Lienk, S.E., P.J. Chapman & O.F. Curtis, 1956. Responses of apple trees to mite infestations II. J. Econ. Ent. 49: 350-353.

Listo, J., E.M. Listo & V. Kanervo, 1939. A study on the fruit tree red spider mite (Paratetranychus pilosus Can. et Fanz). In Finnish with English summary. Valt. Maatalouskoet. Julk. 99, 143 pp.

Livisic, I.Z., 1964. Synopsis of the fauna of Tetranychus mites in fruit orchards. In Russian with English summary. Sb. nauch. Trud. gos. Nikitsk. botan. sad. 37: 135-148.

Lord, F.T., 1949. The influence of spray programs on the fauna of apple orchards in Nova Scotia III. Mites and their predators. Can. Ent. 81: 202-230.

Louwerse, W. & J.L.P. van Oorschot, 1969. An assembly for routine measurements of photosynthesis, respiration and transpiration of intact plants under controlled conditions. Photosynthetica 3: 305-315.

McMurtry, J.A. & G.T. Scriven, 1966. Effects of artificial foods on reproduction and development of four species of Phytoseid mites. An. Ent. Soc. Am. 59 (2): 267-269.

McMurtry, J.A., C.B. Huffaker & M. van de Vrie, 1970. Ecology of Tetranychid mites and their natural enemies, a review. I. Tetranychid enemies: Their biological characters and the impact of spray practices. Hilgardia 40: 331-390.

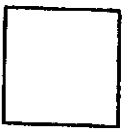
McMurtry, J.A. & M. van de Vrie, 1973. Predation by Amblyseius potentillae (Garman) on Panonychus ulmi (Koch) in simple ecosystems (Acarina: Phytoseiidae, Tetranychidae). Hilgardia 42: 17-34.

Martin, H. & Worthing (Eds), 1970. Pesticide manual (4th edition). British Crop Protection Council, Boreley, Ombersley, Droitwich, Worcs.
Massee, A.M. & W. Steer, 1929. Tar-distillate washes and red spider. J. Min. Agric. (London) 36: 253–257.
Mathys, G., M. Baggiolini & J. Stahl, 1968. Influence of pesticides and fertilizers on the behaviour of phytophagous mites in orchards and under laboratory conditions. Entomophaga 13: 357–372.
Mori, H., 1957. The influence of temperature and relative humidity upon the development of the eggs of fruit tree red spider mite Metatetranychus ulmi (Koch) (Acarina : Tetranychidae) — Jour. Fac. Agric. Hokkaido (imp.) Univ. 50: 363–70.
Mori, H., 1961. Comparative studies of thermal reaction in four species of spider mites. (Acarina: Tetranychidae). J. Fac. Agric. Hokkaido (imp) Univ. 51: 574–91.
Mori, H., 1967. A review of biology on spider mites and their predators in Japan. Mushi 40: 47–65.
Musa, S., & G. Dosse, 1966. Preliminary studies on Panonychus ulmi Koch in Lebanon Magon, Inst. Rech. Agr. Liban. 8 (Ser.Sci.): 1–14.
Newcomer, E.J. & M.A. Yothers, 1929. Biology of the European red mite in the Pacific Northwest, U.S. Dept. Agric. Tech. Bull. 89, 70 pp.
Parent, B., & A.A. Beaulieu, 1957. Life history of the European red mite. Can. Ent. 89: 328–33.
Parlange, J.Y., P.E. Waggoner, & G.H. Heichel, 1971. Boundary layer resistance and temperature distribution on still and flapping leaves. I. Theory and laboratory experiments. Pl. Physiol. 48: 439–442.
Penman, H.L., 1948. Natural evaporation from open water, bare soil and grass. Proc. Roy. Soc. A. 193: 120–146.
Picket, A.D., 1949. A critique on insect chemical control methods. Can. Ent. 81: 67–76.
Post, 1962. Effect of cultural measures on the population density of the fruit tree spider mite, Metatetranychus ulmi Koch (Acari: Tetranychidae). Diss. Univ. Leiden, 110 pp.
Putman, W.L. 1965. Paper chromatography to detect predation on mites Can. Ent. 97: 435–441.
Putman, W.L., 1970a. Threshold temperatures for the European red mite, Panonychus ulmi (Koch) (Acarina: Tetranychidae) Can. Ent. 102: 421–425.
Putman, W.L., 1970b. Some effects of wind on the European red mite, Panonychus ulmi (Koch) (Acarina: Tetranycidae) Can. Ent. 102:659–667.
Putman, W.L., 1970c. Some aspects of sex in the European red mite, Panonychus ulmi. Can. Ent. 102:612–617.

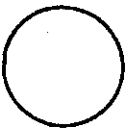
Putman, W.L., 1970d. Effects of water and high humidity on the European red mite. Panonychus ulmi (Acarina: Tetranychidae) Can. Ent. 102:955–961.
Rabbinge, R., P.J.M. Mols & M. van de Vrie, 1976, (In prep.). (Department of Theoretical Production Ecology, De Dreyen 4 and Department of Entomology, Binnenhaven 7, Wageningen).
Rabbinge, R. & M. van de Vrie, (In prep.). (Department of Theoretical Production Ecology, De Dreyen 4, and Department of Entomology, Binnenhaven 7, Wageningen).
Rodriguez, J.G., 1958. The comparative NPK nutrition of Panonychus ulmi (Koch) and Tetranychus telarius (L) on apple trees. J. Econ. Ent. 51: 369–373.
Ross, W.A. & W. Robinson, 1922. Notes on the plum spider mite or European red mite. Rep. Ent. Soc. Ontario 52: 33–42.
Rota, P., 1961–1962. Osservazioni sugli Acari Tetranychidi dannosi alle piante coltivate ed ornamentali in Italia. Boll. Zool. agric. Bachic. 2: 31–136.
Saba, F., 1964. Mitteilung über Schadmilben im Vorderen Orient. Anz. Schädlingsk. 37: 17–19.
Shul'gin, I.A., A.F. Kleshnin, M.I. Verbolova & Y.Z. Posol'nyi, 1960. An investigation of the optical properties of leaves of woody plants using the SF-4 spectrophotometer. Soviet Pl. Physiol 7: 247–52.
Sømme, L., 1966. Mortality of wintereggs of Metatetranychus ulmi (Koch) during the winter of 1965–66. Norsk. ent. Tidskr. 13: 420–23.
Steiner, A.A., 1961. A universal method for preparing nutrient solutions of a certain desired composition. Pl. Soil 15; 134–154.
Stigter, C.J. & B. Lammers, 1974. Leaf diffusion resistance to water vapour and its direct measurement. III Results regarding the improved diffusion porometer in growth rooms and fields of indian corn (Zea mays) Meded. Landb Hogesch. Wageningen 74–21.
Stigter, C.J., J. Goudriaan, & F. Bottemanne, 1976 (In prep.). (Agric. Univ., Dep. of Physics and Meteorology, Duivendaal, Wageningen.)
Storms, J.J.H., 1969. Observation on the relationship between mineral nutrition of apple rootstocks in gravel culture and the reproduction of Tetranychus urticae (Acarina: Tetranychidae). Ent. Exp. Appl. 12: 297–311.
Thompson, W.R., 1930. The biological control of insect and plant pests. E.M.B. 29.
Trägard, I., 1915. Contribution towards the knowledge of spinning mites Tetranychus. (In Swedish with English summary) Meddn Cent Anst. Forörs Väs. Jordbr Omrad. Stockh. 109, 60 pp.
Uvarov, B.P., 1931. Insects and climate. Trans. entomol. Soc. Lond 79: 1–247.
Veerman, A., 1970. The pigments of Tetranychus cinnabarinus Boisd. (Acarina: Tetranychidae). Comp. Biochem. Physiol. 1970. 36: 749–763.

Vrie, M. van de, 1956. Over de invloed van spintaantasting op de opbrengst en groei van vruchtbomen. Tijdschr. Pl Ziekt. 62: 243–57.
Vrie, M. van de, 1964. Invloed van carbaryl op de vermeerdering van de fruitspintmijt. Jaarversl. Proefstn Fruitteelt Volle Grond: 112–13.
Vrie, M. van de, 1966. Population sampling for integrated control. Proc. FAO-Symp. Integr. Pest Contr. Rome (1965):2: 57–75.
Vrie, M. van de, 1973. Studies on prey-predator interactions between Panonychus ulmi and Typhlod omus potentillae. (Acarina: Tetranychidae, Phytoseïidae) on apple in the Netherlands. Proc. FAO Conf. Ecology. Rel. Plant Pest Contr. Rome, 1973:145–160.
Vrie, M. van de, & A. Boersma, 1970. The influence of the predaceous mite Typhlodromus (A) potentillae (Garman) on the development of Panonychus ulmi (Koch) on apple grown under various nitrogen conditions Entomophaga 15: 291–304.
Vrie, M. van de, J.A. McMurtry, & C.B. Huffaker, 1972. Ecology of Tetranychid Mites and their Natural Enemies: A Review III Biology, Ecology and Pest Status and Host-Plant Relations of Tetranychids. Hilgardia 41: 343–432.
Vrie, M. van de, R. Rabbinge & M.W. Sabelis. (In prep.). (Agric. Univ., Department of Theoretical Production Ecology, De Dreyen 4, and Department of Entomology, Binnenhaven 7, Wageningen).
Wertheim, S.J., 1973. De belichting als produktiefaktor. Fruitteelt 63: 250–251.
Wit, C.T. de, 1960. On competition. Versl Landbouwk. Onderz. 66. 8. Pudoc, Wageningen, 82 pp.
Wit, C.T. de, 1965. Photosynthesis of leaf canopies. Agric. Res. Rep. 663 Pudoc, Wageningen, 57 pp.
Wit, C.T. de & J. Goudriaan, 1974. Simulation of ecological processes. Simulation Monographs. Pudoc, Wageningen, 159 pp.
Wybou, A., 1949. Notice sur l'araignée rouge des arbres fruitiers (Paratetranychus pilosus, Bryobia praetiosa). Fruit belge 17: 110.
Wybou, A., 1951. De Acari der vruchtbomen. Versl. Nav. Inst. Aanm. Wetensch. Onderz. Nijverh. Landb. (IWONL), 126 pp.

Appendix I. List of the symbols used in the relational diagrams



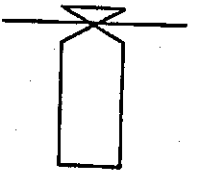
STATE VARIABLE OR VALUE OF AN INTEGRAL



AUXILIARY VARIABLE

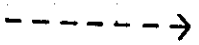
(ABCD)

DRIVING OR FORCING VARIABLE



RATE OF FLOW OF MATERIAL INTO OR FROM AN INTEGRAL

FLOW OF MATERIAL, INTO OR FROM AN INTEGRAL



FLOW OF INFORMATION

ABCD

PARAMETER

MORTALITY

Appendix II. List of abbreviations

NAME	DESCRIPTION	UNIT
AFPN'1,2'	RELATIVE RATE OF MORTALITY OF PREOVIPOSITION FEMALES OF PANONYCHUS ULMI	DAY-1
AFS '1-10'	ADULT FEMALES 'SUMMER' OF P.ULMI,AGE CLASS 1-10	NUMBER
AMS '0-3'	ADULT MALE 'SUMMER' OF P.ULMI, AGE CLASS 0-4	NUMBER
AMSKD	SQUARE OF THE RELATIVE DISPERSION OF LIFE SPAN OF ADULT MALE 'SUMMER' OF P.ULMI	
AMSMR	RELATIVE RATE OF MORTALITY OF ADULT MALE 'SUMMER' OF P.ULMI	DAY-1
CAF	COLOUR VALUE PER ADULT FEMALE A.POTENTILLAE	COLOUR FEMALE-1
CAM	COLOUR VALUE PER ADULT MALE A.POTENTILLAE	COLOUR MALE-1
CDN	COLOUR VALUE PER DEUTONYMPH OF A.POTENTILLAE	COLOUR DEUT.-1
CFS	MULTIPLICATION FACTOR OF RELATIVE PREDATION RATES ACCOUNTING FOR THE SURFACE OF THE SYSTEM	
COSDEC	COSINE DECLINATION	
CPN	COLOUR VALUE PER PROTONYMPH OF A.POTENTILLAE	COLOUR PROTON.-1
CSLT	COSINE LATITUDE	
CTAF	INVERSE COLOUR VALUE PER ADULT FEMALE OF A.POT.	COLOUR-1 FEMALE
CTAM	INVERSE COLOUR VALUE PER ADULT MALE OF A.POT.	COLOUR-1 MALE
CTDN	INVERSE COLOUR VALUE PER DEUTONYMPH OF A.POT.	COLOUR-1 DEUTONYMPH
CTPN	INVERSE COLOUR VALUE PER PROTONYMPH OF A.POT.	COLOUR-1 PROTONYMPH
DAY	NUMBER OF THE DAY	
DAYL	LENGTH OF THE DAY	HOURS
DEADP	DEVELOPMENT TO PREOVIPOSITION FEMALES P.ULMI	NUMBER DAY-1
DEAFS	DEVELOPMENT TO ADULT FEMALES P.ULMI 'SUMMER FORMS'	NUMBER DAY-1
DEAMS	DEVELOPMENT TO ADULT MALES P.ULMI'SUMMER FORMS'	NUMBER DAY-1
DEATSF	DEVELOPMENT TO ADULT FEMALES A.POTENTILLAE	NUMBER DAY-1
DEC	DECLINATION OF THE SUN	
DECAF	DECREASE OF COLOUR VALUE OF ADULT FEMALES	COLOUR TIME-1
DECAM	DECREASE OF COLOUR VALUE OF ADULT MALES	COLOUR TIME-1
DECDN	DECREASE OF COLOUR VALUE OF DEUTONYMPHS	COLOUR TIME-1
DECPN	DECREASE OF COLOUR VALUE OF PROTONYMPHS	COLOUR TIME-1
DEJU	DEVELOPMENT TO JUVENILES (P.ULMI)	NUMBER DAY-1
DEJUS	DEVELOPMENT TO JUVENILES SENSITIVE TO DIAPAUSE INDUCING CONDITIONS (P.ULMI)	NUMBER DAY-1
DETE	DEVELOPMENT OF EGGS OF A.POTENTILLAE	NUMBER DAY-1
DETJ	DEVELOPMENT OF JUVENILES OF A.POTENTILLAE	NUMBER DAY-1
DETJS	DEVELOPMENT OF JUVENILES SENSITIVE TO DIAPAUSE INDUCING CONDITIONS (A.POTENTILLAE)	NUMBER DAY-1
DLONG	DIFFERENCE IN HOURS WITH STANDARD SOLAR TIME	HOURS
DTEMD	FIRST ORDER AVERAGE OF TEMPERATURE	DEGREE CELSIUS
DTEMI	INITIAL AVERAGE OF TEMPERATURE	DEGREE CELSIUS
EKO	SQUARE OF THE RELATIVE DISPERSION OF DEVELOPMENT PERIOD OF EGGS OF P.ULMI	
EMOR'1,4'	RELATIVE RATE OF MORTALITY OF EGGS OF P.ULMI IN AGE CLASS 1-4	DAY-1
EQT1	COLOUR VALUE OF ADULT FEMALES OF A.POTENTILLAE	COLOUR CH-2
EQT2	COLOUR VALUE OF DEUTONYMPHS OF A.POTENTILLAE	COLOUR CH-2
EQT3	COLOUR VALUE OF PROTONYMPHS OF A.POTENTILLAE	COLOUR CH-2
EQT4	COLOUR VALUE OF ADULT MALES OF A.POTENTILLAE	COLOUR CH-2
F1	OVIPOSITION RATE OF FEMALES P.ULMI	EGGS DAY-1
FP'1,10'	OVIPOSITION RATE OF FEMALES P.ULMI IN AGE CLASS 1-10	EGGS DAY-1 FEMALE-1
FT	OVIPOSITION RATE OF FEMALES A.POTENTILLAE	EGGS DAY-1
FT'1,10'	OVIPOSITION RATE OF FEMALES A.POTENTILLAE IN AGE CLASS 1-10	EGGS DAY-1 FEMALE-1
GSAFS	STAGE OF SENESCENCE OF ADULT FEMALES P.ULMI 'SUMMER FORMS'	DEVELOPMENT UNITS
GSAMS	STAGE OF SENESCENCE OF ADULT MALES P.ULMI 'SUMMER FORMS'	DEVELOPMENT UNITS
GSE	STAGE OF DEVELOPMENT OF EGGS P.ULMI	DEVELOPMENT UNITS
GSJ	STAGE OF DEVELOPMENT OF JUVENILES P.ULMI	DEVELOPMENT UNITS
GSJS	STAGE OF DEVELOPMENT OF JUVENILES P.ULMI SENSITIVE TO DIAPAUSE INDUCING CONDITIONS	DEVELOPMENT UNITS
GTE	STAGE OF DEVELOPMENT OF EGGS A.POTENTILLAE	DEVELOPMENT UNITS
GTJ	STAGE OF DEVELOPMENT OF JUVENILES A.POTENTILLAE	DEVELOPMENT UNITS
GTJS	STAGE OF DEVELOPMENT OF JUVENILES A.POTENTILLAE SENSITIVE TO DIAPAUSE INDUCING CONDITIONS	DEVELOPMENT UNITS

GTSF	STAGE OF SENESCENCE OF ADULT FEMALES OF A.POTENTILLAE 'SUMMER FORMS'	DEVELOPMENT UNITS
GTSFF	STAGE OF SENESCENCE OF ADULT FEMALES A.POTENTILLAE 'SUMMER FORMS'	DEVELOPMENT UNITS
GTSM	STAGE OF SENESCENCE OF ADULT MALES A.POTENTILLAE 'SUMMER FORMS'	DEVELOPMENT UNITS
HA	HOUR ANGLE	RADIALS
HOUR	HOUR OF THE DAY	HOUR
INCAF	RATE OF INCREASE OF COLOUR VALUE ADULT FEMALES A.POTENTILLAE	COLOUR UNITS DAY-1
INCAM	RATE OF INCREASE OF COLOUR VALUE ADULT MALES A.POTENTILLAE	COLOUR UNITS DAY-1
INCDN	RATE OF INCREASE OF COLOUR VALUE DEUTONYMPHS A.POTENTILLAE	COLOUR UNITS DAY-1
INCPN	RATE OF INCREASE OF COLOUR VALUE PROTONYMPHS A.POTENTILLAE	COLOUR UNITS DAY-1
J'0-6'	NUMBER OF JUVENILES OF P.ULMI IN AGE CLASS 0-6	NUMBER
JKO	SQUARE OF THE RELATIVE DISPERSION OF DURATION OF JUVENILE PERIOD OF P.ULMI	
JMOR'1,6'	RELATIVE MORTALITY RATE OF JUVENILES OF P.ULMI IN AGE CLASS 1-6	DAY-1
JS'0-4'	NUMBER OF JUVENILES OF P.ULMI SENSITIVE TO DIAPAUSE INDUCTION IN AGE CLASS 0-4 'SUMMER'	NUMBER
JSKO	SQUARE OF THE RELATIVE DISPERSION OF THE DURATION OF JUVENILES SENSITIVE TO DIAPAUSE INDUCING CONDITIONS OF P.ULMI	
JSMR	RELATIVE MORTALITY RATE OF JUVENILES OF P.ULMI SENSITIVE TO DIAPAUSE INDUCING CONDITIONS 'SUMMER FORMS'	
LAT	LATITUDE LOCATION	DAY-1 DEGREES
LF1	LOGARITHM OF TOTAL REPRODUCTION RATE OF P.ULMI	NUMBER
LFT	LOGARITHM OF TOTAL REPRODUCTION RATE OF A.POT.	NUMBER
LGAFS	LONGEVITY ADULT FEMALES P.ULMI 'SUMMER FORMS'	DAYS
LGAMS	LONGEVITY ADULT MALES P.ULMI 'SUMMER FORMS'	DAYS
LGLE	DURATION EGG PERIOD P.ULMI	DAYS
LGLJ	DURATION JUVENILE PERIOD P.ULMI	DAYS
LGLJS	DURATION DEVELOPMENT PERIOD JUVENILES SENSITIVE TO DIAPAUSE INDUCING CONDITIONS P.ULMI	DAYS
LGPAFS	DURATION PRE-OVIPOSITION PERIOD FEMALES P.ULMI	DAYS
LGPAFW	LONGEVITY 'WINTER'FEMALES P.ULMI	DAYS
LGTJ	DURATION JUVENILE PERIOD A.POTENTILLAE	DAYS
LGTJS	DURATION DEVELOPMENT PERIOD JUVENILES SENSITIVE TO DIAPAUSE INDUCING CONDITIONS A.POTENTILLAE	DAYS
LGTSF	DURATION PRE-OVIPOSITION PERIOD FEMALES A.POT.	DAYS
LGTSFF	LONGEVITY ADULT FEMALES A.POT. 'SUMMER FORMS'	DAYS
LGTSM	LONGEVITY ADULT MALES A.POT. 'SUMMER FORMS'	DAYS
LGTTE	DURATION EGG PERIOD A.POTENTILLAE	DAYS
LPAFS	LOGARITHM NUMBER ADULT FEMALES P.ULMI	NUMBER
LPAMS	LOGARITHM NUMBER ADULT MALES P.ULMI	NUMBER
LPDN	LOGARITHM NUMBER DEUTONYMPHS P.ULMI	NUMBER
LPE	LOGARITHM NUMBER EGGS P.ULMI	NUMBER
LPL	LOGARITHM NUMBER LARVAE P.ULMI	NUMBER
LPPN	LOGARITHM NUMBER PROTONYMPHS P.ULMI	NUMBER
LSNHS	SINE OF SUN ELEVATION TODAY AT LAST TIME STEP	
LTAFS	LOGARITHM NUMBER ADULT FEMALES A.POTENTILLAE 'SUMMER FORMS'	NUMBER
LTAMS	LOGARITHM NUMBER ADULT MALES A.POTENTILLAE 'SUMMER FORMS'	NUMBER
LTE	LOGARITHM NUMBER EGGS A.POTENTILLAE	NUMBER
LTDN	LOGARITHM NUMBER DEUTONYMPHS A.POTENTILLAE	NUMBER
LTL	LOGARITHM NUMBER LARVAE A.POTENTILLAE	NUMBER
LTPN	LOGARITHM NUMBER PROTONYMPHS A.POTENTILLAE	NUMBER
MASF'1,10'	RATE OF MORTALITY ADULT FEMALES A.POTENTILLAE IN AGE CLASS 1-10	NUMBER DAY-1
MAXT	DAILY MAXIMUM TEMPERATURE	DEGREE CELSIUS
MINT	DAILY MINIMUM TEMPERATURE	DEGREE CELSIUS
MRJS'1,2'	RELATIVE MORTALITY RATE OF A.POTENTILLAE JUVENILES SENSITIVE TO DIAPAUSE INDUCING CONDITIONS	
MRTE'1,3'	RELATIVE MORTALITY RATE OF EGGS OF A.POTENTILLAE IN AGE CLASSES 1-3	DAY-1
MRTJ'1,4'	RELATIVE MORTALITY RATE JUVENILES A.POTENTILLAE IN AGE CLASSES 1-4	DAY-1

MTPSF'1,2'	RELATIVE MORTALITY RATE PRE-OVIPOSITION FEMALES A.POTENTILLAE IN AGE CLASSES 1-2	DAY-1
NUMR1	NUMERICAL RESPONSE FACTOR 1, COLOUR LEVEL DEPENDENCY OF OVIPOSITION RATE A.POTENTILLAE	
NUMR2	NUMERICAL RESPONSE FACTOR 2 , COLOUR LEVEL DEPENDENCY DEVELOPMENT PERIOD JUVENILES A.POT.	
NUMR3	NUMERICAL RESPONSE FACTOR 3 , COLOUR LEVEL DEPENDENCY DEVELOPMENT PERIOD JUVENILES SENSITIVE TO DIAPAUSE INDUCING CONDITIONS OF A.POTENTILLAE	
NUMR4	NUMERICAL RESPONSE FACTOR 4 , COLOUR LEVEL DEPENDENCY MATURATION PERIOD OF ADULT FEMALES OF A.POTENTILLAE	
PAFST	TOTAL NUMBER PRE-OVIPOSITION FEMALES P.ULMI	NUMBER
PAFST'1=2'	NUMBER PRE-OVIPOSITION FEMALES IN AGE CLASS 1=2	NUMBER
PAFW	NUMBER 'WINTER'FEMALES P.ULMI	NUMBER
PRED1	RELATIVE PREDATION RATE LARVAE P.ULMI BY ADULT FEMALES OF A.POTENTILLAE	DAY-1
PRED2	RELATIVE PREDATION RATE LARVAE P.ULMI BY DEUTONYMPHS OF A.POTENTILLAE	DAY-1
PRED3	RELATIVE PREDATION RATE LARVAE P.ULMI BY PROTONYMPHS OF A.POTENTILLAE	DAY-1
PRED4	RELATIVE PREDATION RATE LARVAE P.ULMI BY ADULT MALES OF A.POTENTILLAE	DAY-1
PRED5	RELATIVE PREDATION RATE PROTONYMPHS P.ULMI BY ADULT FEMALES OF A.POTENTILLAE	DAY-1
PRED6	RELATIVE PREDATION RATE PROTONYMPHS P.ULMI BY DEUTONYMPHS OF A.POTENTILLAE	DAY-1
PRED7	RELATIVE PREDATION RATE PROTONYMPHS P.ULMI BY ADULT MALES OF A.POTENTILLAE	DAY-1
PRED8	RELATIVE PREDATION RATE DEUTONYMPHS P.ULMI BY ADULT FEMALES OF A.POTENTILLAE	DAY-1
PRED9	RELATIVE PREDATION RATE DEUTONYMPHS P.ULMI BY ADULT MALES OF A.POTENTILLAE	DAY-1
PRED10	RELATIVE PREDATION RATE ADULT MALES P.ULMI BY ADULT FEMALES OF A.POTENTILLAE	DAY-1
PRED11	RELATIVE PREDATION RATE ADULT MALES P.ULMI BY ADULT MALES OF A.POTENTILLAE	DAY-1
PRED12	RELATIVE PREDATION RATE ADULT FEMALES P.ULMI BY ADULT FEMALES OF A.POTENTILLAE	DAY-1
PRMO'1-22'	RELATIVE MORTALITY RATE BY PREDATION IN DIFFERENT CLASSES AND STAGES	DAY-1
PV1	UTILIZATION OF KILLED LARVAE P.ULMI BY ADULT FEMALES A.POTENTILLAE	COLOUR PREY-1
PV2	UTILIZATION OF KILLED PROTONYMPHS P.ULMI BY ADULT FEMALES A.POTENTILLAE	COLOUR PREY-1
PV3	UTILIZATION OF KILLED DEUTONYMPHS P.ULMI BY ADULT FEMALES A.POTENTILLAE	COLOUR PREY-1
PV4	UTILIZATION OF KILLED ADULT FEMALES P.ULMI BY ADULT FEMALES A.POTENTILLAE	COLOUR PREY-1
PV5	UTILIZATION OF KILLED LARVAE P.ULMI BY DEUTONYMPHS A.POTENTILLAE	COLOUR PREY-1
PV6	UTILIZATION OF KILLED PROTONYMPHS P.ULMI BY DEUTONYMPHS A.POTENTILLAE	COLOUR PREY-1
PV7	UTILIZATION OF KILLED LARVAE P.ULMI BY PROTONYMPHS A.POTENTILLAE	COLOUR PREY-1
PV8	UTILIZATION OF KILLED LARVAE P.ULMI BY ADULT MALES A.POTENTILLAE	COLOUR PREY-1
PV9	UTILIZATION OF KILLED PROTONYMPHS P.ULMI BY ADULT MALES A.POTENTILLAE	COLOUR PREY-1
PV10	UTILIZATION OF KILLED DEUTONYMPHS P.ULMI BY ADULT MALES A.POTENTILLAE	COLOUR PREY-1
PV11	UTILIZATION OF KILLED ADULT MALES P.ULMI BY ADULT MALES A.POTENTILLAE	COLOUR PREY-1
RDCV1	RELATIVE RATE OF DECREASE IN COLOUR VALUE OF ADULT FEMALES A.POTENTILLAE	DAY-1
RDCV2	RELATIVE RATE OF DECREASE IN COLOUR VALUE OF DEUTONYMPHS A.POTENTILLAE	DAY-1
RDCV3	RELATIVE RATE OF DECREASE IN COLOUR VALUE OF PROTONYMPHS A.POTENTILLAE	DAY-1
RF'1,8'	MULTIPLICATION FACTORS OF THE RELATIVE PRELATION RATES TO USE THE EXPERIMENTALLY DETERMINED RELATION FOR OTHER PREY-PREDATOR COMBINATIONS	
RISE	TIME OF SUNRISE	HOUR
RTAFS	RESIDENCE TIME PER AGE CLASS ADULT FEMALES P.ULMI	DAYS

RTAMS	RESIDENCE TIME PER AGE CLASS ADULT MALES P.ULMI	DAYS
RTE	RESIDENCE TIME PER AGE CLASS EGGS P.ULMI	
RTJ	RESIDENCE TIME PER AGE CLASS JUVENILES P.ULMI	DAYS
RTJS	RESIDENCE TIME PER AGE CLASS JUVENILES SENSITIVE TO DIAPAUSE INDUCING CONDITIONS OF P.ULMI	DAYS
RTPAFS	RESIDENCE TIME PER AGE CLASS PRE-OVIPOSITION FEMALES P.ULMI	DAYS
RTTE	RESIDENCE TIME PER AGE CLASS EGGS A.POTENTILLAE	DAYS
RTTJ	RESIDENCE TIME PER AGE CLASS JUVENILES A.POT .	DAYS
RTTJS	RESIDENCE TIME PER AGE CLASS JUVENILES SENSITIVE TO DIAPAUSE INDUCING CONDITIONS OF A.POTENTILLAE	DAYS
RTTSF	RESIDENCE TIME PER AGE CLASS PRE-OVIPOSITION FEMALES OF A.POTENTILLAE	DAYS
RTTSFF	RESIDENCE TIME PER AGE CLASS ADULT FEMALES OF A.POTENTILLAE	DAYS
RTTSM	RESIDENCE TIME PER AGE CLASS ADULT MALES A.POT.	DAYS
SEN	PARAMETER THAT INCREASES OR DECREASES THE ACTUAL TEMPERATURE SYSTEMATICALLY	
SEN*1-33*	MULTIPLICATION FACTORS FOR THE RELATIONS FOR AGEING RATES,DEVELOPMENT RATES AND MORTALITY RATES,TO TEST THEIR RELATIVE IMPORTANCE	
SENA*1-10*	MULTIPLICATION FACTORS FOR THE OVIPOSITION RATES OF P.ULMI	
SENB*1-10*	MULTIPLICATION FACTORS FOR THE OVIPOSITION RATES OF A.POTENTILLAE	
SENC*1-8*	MULTIPLICATION FACTORS FOR THE RATES OF INCREASE AND DECREASE IN COLOUR OF THE DIFFERENT PREDATORY STAGES	
SENP*1-12*	MULTIPLICATION FACTORS FOR THE RELATIVE PREDATION RATES	
SINDEC	SINE DECLINATION	
SL*1-10*	SLOPES OF THE LINEAR RELATION BETWEEN OVIPOSITION RATE AND TEMPERATURE IN AGE CLASSES 1-10 OF P.ULMI	NUMBER EGGS DAY-1 C-1
SNHS	SINE ELEVATION OF THE SUN	
SNLT	SINE LATITUDE	
SPU	START TIME OF P.ULMI IN THE MODEL	DAYS
SRP	SEX RATIO OF P.ULMI	
SRT	SEX RATIO OF A.POTENTILLAE	
STA	START TIME A.POTENTILLAE IN THE MODEL	DAYS
STAR	START TIME OF THE MODEL	DAYS
TASF	NUMBER ADULT FEMALES A.POTENTILLAE*SUMMER FORMS*	NUMBER
TASF*1-10*	NUMBER ADULT FEMALES A.POTENTILLAE IN AGE CLASS 1-10	NUMBER
TASM	NUMBER ADULT MALES A.POTENTILLAE	NUMBER
TASH*0-3*	NUMBER ADULT MALES A.POTENTILLAE IN AGE CLASS 0-3	NUMBER
TAWF	NUMBER OVERWINTERING FEMALES A.POTENTILLAE	NUMBER
TE*0-3*	NUMBER EGGS A.POT. IN AGE CLASS 0-3	NUMBER
TEKO	SQUARE OF THE RELATIVE DISPERSION OF DEVELOPMENT PERIOD OF EGGS A.POTENTILLAE	NUMBER
TEMP	ACTUAL TEMPERATURE	DEGREE CELSIUS
TEMS	TEMPERATURE SUM	DEGREE CELSIUS
TJ*0-4*	NUMBER JUVENILES A.POT. IN AGE CLASS 0-4	NUMBER
TJKO	SQUARE OF THE RELATIVE DISPERSION OF DEVELOPMENT PERIOD JUVENILES OF A.POTENTILLAE	
TJS*0-2*	NUMBER JUVENILES SENSITIVE TO DIAPAUSE INDUCING CONDITIONS IN AGE CLASS 0-2	NUMBER
TJSKO	SQUARE OF THE RELATIVE DISPERSION OF DEVELOPMENT PERIOD OF JUVENILES SENSITIVE TO DIAPAUSE INDUCING CONDITIONS OF A.POTENTILLAE	
TOMOF	SUMMARIZED MORTALITY RATE ADULT FEMALES A.POT.	NUMBER DAY-1
TOMOR	SUMMARIZED MORTALITY RATE ADULT FEMALES P.ULMI	NUMBER DAY-1
TOMORF	ACCUMULATED DEAD ADULT FEMALES A.POTENTILLAE	NUMBER
TOMORT	ACCUMULATED DEAD ADULT FEMALES P.ULMI	NUMBER
TPAFS	NUMBER FEMALES P.ULMI	NUMBER
TPAFSO	NUMBER PRE-OVIPOSITION FEMALES P.ULMI	NUMBER
TPAMS	NUMBER MALES P.ULMI	NUMBER
TPE	NUMBER EGGS P.ULMI	NUMBER
TPDC	NUMBER DEUTOCHRYSALIS P.ULMI	NUMBER
TPDN	NUMBER DEUTONYMPHS P.ULMI	NUMBER
TPL	NUMBER LARVAE P.ULMI	NUMBER
TPPC	NUMBER PROTOCHRYSALIS P.ULMI	NUMBER
TPPN	NUMBER PROTONYMPHS P.ULMI	NUMBER
TPSF*0-2*	NUMBER PRE-OVIPOSITION FEMALES A.POTENTILLAE	

	IN AGE CLASS 0-2	NUMBER
TPTC	NUMBER TELEIOCHRYSALIS P.ULMI	NUMBER
TSFKO	SQUARE OF THE RELATIVE DISPERSION OF MATURATION PERIOD FEMALES OF A.POTENTILLAE	
TSMKO	SQUARE OF THE RELATIVE DISPERSION OF SPAN OF MALES A.POTENTILLAE	
TTAFS	NUMBER ADULT FEMALES A.POTENTILLAE	NUMBER
TTAMS	NUMBER ADULT MALES A.POTENTILLAE	NUMBER
TTE	NUMBER EGGS A.POTENTILLAE	NUMBER
TTDN	NUMBER DEUTONYMPHS A.POTENTILLAE	NUMBER
TTL	NUMBER LARVAE A.POTENTILLAE	NUMBER
TTPN	NUMBER PROTONYMPHS A.POTENTILLAE	NUMBER
UL'1.4'	LOWER LIMIT FOR THE COLOUR VALUE OF ADULT FEMALES,DEUTONYMPHS,PROTONYMPHS AND ADULT MALES OF A.POTENTILLAE,RESPECTIVELY, DUE TO THE PRESENCE OF ALTERNATE PREYS	COLOUR UNITS
VALAMP	DAILY AMPLITUDE OF THE TEMPERATURE	DEGREE CELSIUS
VALAV	DAILY AVERAGE OF TEMPERATURE	DEGREE CELSIUS
VALSR	TEMPERATURE AT SUNRISE	DEGREE CELSIUS
VALSS	TEMPERATURE AT SUNSET	DEGREE CELSIUS
WEP	ACCUMULATED NUMBER WINTER EGGS P.ULMI	NUMBER

ADDITIONAL LIST OF ABBREVIATIONS FOR THE MODEL ON DIAPAUSING OF P.ULMI

WE	NUMBER WINTER EGGS P.ULMI	NUMBER
SE	NUMBER SUMMER EGGS P.ULMI	NUMBER
AFW	NUMBER 'WINTER'FEMALES P.ULMI	NUMBER
AFW'0-5'	NUMBER 'WINTER'FEMALES IN AGE CLASS 0-5	NUMBER
AFWKO	RELATIVE DISPERSION OF LIFE SPAN ADULT FEMALES	
LOAFW	LONGIVITY ADULT FEMALES P.ULMI	DAYS
RTAFW	RESIDENCE TIME ADULT FEMALES P.ULMI PER AGE CLASS	DAYS
GSAFW	SENESCENCE STAGE ADULT FEMALES P.ULMI	DEVELOPMENT UNITS
JW'0-4'	NUMBER JUVENILES SENSITIVE TO DIAPAUSE INDUCING CONDITIONS P.ULMI 'WINTER FORMS'	DAYS
JWKO	RELATIVE DISPERSION DEVELOPMENT PERIOD JUVENILES SENSITIVE TO DIAPAUSE INDUCING CONDITIONS	DAYS

ADDITIONAL LIST OF ABBREVIATIONS FOR THE MODEL ON HATCHING OF WINTER EGGS OF P.ULMI

EI	INITIAL NUMBER WINTER EGGS	NUMBER
COLDP	LENGTH OF THE COLD PERIOD	DAYS
ININ	INITIAL STAGE OF DEVELOPMENT OF THE WINTER EGGS	DEVELOPMENT UNITS
TEMI	FIRST ORDER AVERAGE OF TEMPERATURE WITH A TIME CONSTANT OF TWO DAYS	DEGREE CELSIUS
DEWE	DEVELOPMENT RATE WINTER EGGS	DEVELOPM.UNITS DAY-1
GSH	DEVELOPMENT STAGE WINTER EGGS	DEVELOPMENT UNITS
LOLEW	AVERAGE LENGTH OF HATCHING PERIOD OF WINTER EGGS	DAYS
RTEW	RESIDENCE TIME OF EGGS PER AGE CLASS	DAYS
EW'1-2'	NUMBER OF EGGS PER AGE CLASS 1-2	NUMBER
TPEW	TOTAL NUMBER OF WINTER EGGS	NUMBER
PL	ACCUMULATED NUMBER OF LARVAE	NUMBER

ADDITIONAL LIST OF ABBREVIATIONS FOR THE MODEL ON PREDATION IN A REPLACEMENTSERIES

TPL	NUMBER OF PREDATED LARVAE P.ULMI	NUMBER
TPPN	NUMBER OF PREDATED PROTONYMPHS P.ULMI	NUMBER
TPDN	NUMBER OF PREDATED DEUTONYMPHS P.ULMI	NUMBER
TPAFS	NUMBER OF PREDATED ADULT FEMALES P.ULMI	NUMBER
TPAMS	NUMBER OF PREDATED ADULT MALES P.ULMI	NUMBER
PPLI	DENSITY OF LARVAE P.ULMI	NUMBER CM-2
PPNI	DENSITY OF PROTONYMPHS P.ULMI	NUMBER CM-2
PDNI	DENSITY OF DEUTONYMPHS P.ULMI	NUMBER CM-2
PAFI	DENSITY OF ADULT FEMALES P.ULMI	NUMBER CM-2
PAMSI	DENSITY OF ADULT MALES P.ULMI	NUMBER CM-2
MUF1	MULTIPLICATION FACTOR FOR TEMPERATURE DEPENDENCY OF PREY UTILIZATION OF LARVAE P.ULMI	
MUF2	MULTIPLICATION FACTOR FOR TEMPERATURE DEPENDENCY OF PREY UTILIZATION OF PROTONYMPHS P.ULMI	
MUF3	MULTIPLICATION FACTOR FOR TEMPERATURE DEPENDENCY OF PREY UTILIZATION OF DEUTONYMPHS P.ULMI	
MUF4	MULTIPLICATION FACTOR FOR TEMPERATURE DEPENDENCY OF PREY UTILIZATION OF ADULT FEMALES P.ULMI	

ADDITIONAL LIST OF ABBREVIATIONS FOR THE MICRO-WEATHER SIMULATOR

RA	RESISTANCE LAMINAR LAYER	SEC M-1
WIDTH	WIDTH OF THE LEAVES PROJECTED IN A DIRECTION PERPENDICULAR TO THE WIND	M
CFSR1	FRACTION OF LEAVES RECEIVING DIFFUSE LIGHT ONLY	
CFSR2-11	FRACTION OF LEAVES RECEIVING BOTH DIFFUSE AND DIRECT LIGHT WITH DIFFERENT DIRECTIONS WITH RESPECT TO THE SUN	
CFSR12	FRACTION OF LEAVES COMPLETELY IN THE SHADE	

THE DETAILED COMMENTS IN THE LISTING OF THE PROGRAM MAKE FURTHER EXPLANATION OF ABBREVIATIONS SUPERFLUOUS.