INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps. Each original is also photographed in one exposure and is included in reduced form at the back of the book.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.
Modeling and optimality of spider mite management systems in greenhouses

Cheng, Zhibin, Ph.D.

The Ohio State University, 1993
MODELING AND OPTIMALITY OF SPIDER MITE
MANAGEMENT SYSTEMS IN GREENHOUSES

DISSERTATION

Presented in Partial Fulfillment of the Requirements for
the Degree Doctor of Philosophy in the Graduate
School of the Ohio State University

By

Zhibin Cheng, B.S.

* * * * *

The Ohio State University

1992

Dissertation Committee:
D.J. Horn
D.K. Pearl
R.K. Lindquist
B.R. Stinner

Approved by

Adviser
Department of Entomology
To my parents
ACKNOWLEDGEMENTS

I am most grateful to my adviser Dr. David J. Horn for his continuous encouragement, guidance and friendship during my graduate study. I also express sincere appreciation to the other members of my advisory committee, Drs. Dennis K. Pearl, Richard K. Lindquist and Benjamin R. Stinner, for their suggestions and comments. The technical assistance of Mr. Foster F. Purrington is gratefully acknowledged.

The study was made possible with the support of the Ohio State University, especially the USDA research funds through Professors Horn, Pearl and Bartoszynski. To my wife, Qun, I offer sincere thanks for her unshakable faith in me and her willingness to endure with me the vicissitudes of my endeavors. To my daughter, SaSa, I thank her for understanding my frequent absences.
VITA

Feburary 20, 1951 ............. Born - Wuhan, China
1982 .......................... B.S., The East China
Institute of Technology, Nanjing, China
1982-1987 ..................... Faculty member,
Huazhong University of
Science and technology,
Wuhan, China
1987-1988 ..................... Visiting Scientist, The
Ohio State University,
Wooster, Ohio
1988-present ................. Graduate Research
Associate, The Ohio State
University, Columbus, Ohio

PUBLICATIONS

Cheng, Z., 1984. The successive residual identification
model for prediction. J. of Huazhong U. of Sci. and
Tech. 4: 29-35.

Cheng, Z., Li, B., Zou, C. and Que, T., 1986. Parameter
estimation in a nonlinear population model with two
parameters: A yeast population growth as an example.

Modelling, 43: 275-281.

FIELD OF STUDY

Major Field: Entomology
TABLE OF CONTENTS

DEDICATION .............................................. ii
ACKNOWLEDGEMENTS ....................................... iii
VITA .................................................... iv
LIST OF TABLES ........................................ xi
LIST OF FIGURES ....................................... xiv
CHAPTER PAGE

I. INTRODUCTION ........................................ 1
1.2. Outbreaks of the two-spotted spider mite, *Tetranychus urticae*, in modern agroecosystems .......................... 2
1.3. Changes in strategy for control of the two-spotted spider mite, *Tetranychus urticae* ........................................ 4
1.4. Experiment-based approaches to control of the two-spotted spider mite, *Tetranychus urticae*, in greenhouses ............... 6
1.5. Systems approaches to control of the two-spotted spider mite, *Tetranychus urticae* ................................ 9

1.5.1. Analytic approach and system identification .................... 9

1.5.2. Simulation models and control models ............................ 15

1.6. Developing optimality of spider management system in modern agricultural practices ............................. 17

1.6.1. Mathematical model ........................................ 17

1.6.2. Method for optimization .......................... 19

1.7. Scope of study ........................................ 20

II. EXPERIMENTAL VALIDATION OF A PREDATOR-PREY STOCHASTIC MODEL ON LIMA BEANS .............. 22

2.1. Introduction ............................................... 22

2.2. Validation of the model on a single plant .......................... 26

2.2.1. Introduction ............................................... 26

2.2.2. Materials and methods .......................... 27

2.2.3. Results and discussion .......................... 28

2.3. Validation of the model on a four-plant system .......................... 37

2.3.1. Introduction ............................................... 37
2.3.2. Materials and methods ............. 37
2.3.3. Results and discussion ............. 40

III. DEATH, SURVIVAL AND REPRODUCTION OF MITE POPULATIONS UNDER STARVATION ............... 46
3.1. Introduction .......................... 46
3.2. Stochastic models of death processes
during starvation ........................ 50
   3.2.1. Introduction ....................... 50
   3.2.2. Data collection ................... 51
   3.2.3. Estimation of mean death rate of a
           population ........................ 56
   3.2.4. Poisson death process .......... 59
   3.2.5. Results ............................ 68
   3.2.6. Discussion ......................... 68
3.3. Gut content of Phytoseiulus
     persimilis ............................ 69
   3.3.1. Introduction ...................... 69
   3.3.2. Materials and methods .......... 71
   3.3.3. Results and discussion ........... 75
3.4. Reproduction of Phytoseiulus
     persimilis and Tetranychus urticae
during starvation ........................ 76
   3.4.1. Introduction ...................... 76
   3.4.2. Materials and methods .......... 77

vii
3.4.3. Results and discussion .......... 77

IV. PRELIMINARY STUDY FOR EXTENSION OF A
STOCHASTIC MODEL FROM LABORATORY LIMA BEANS
TO COMMERCIAL GREENHOUSE CUCUMBERS .......... 80
4.1. Introduction .......................... 80
4.2. Maturation and repreduction parameters
of the prey, Tetranychus urticae, feeding
on lima beans and cucumbers ............. 81
4.2.1. Introduction ....................... 81
4.2.2. Materials and methods .............. 82
4.2.3. Results and discussion ............. 83
4.3. Predation, reproduction and maturation
parameters of the predator, Phytoseiulus
persimilis on lima beans and
 cucumbers ............................. 88
4.3.1. Introduction ........................ 88
4.3.2. Materials and methods .............. 89
4.3.3. Results and discussion ............. 90

V. AN ALTERNATIVE APPROACH TO MODELING AND
OPTIMALITY OF A SPIDER MITE MANAGEMENT
SYSTEM ....................................... 96
5.1. Introduction .......................... 96
5.2. A fuzzy biological control model of

Tetranvchus urticae ................... 99

5.2.1. Introduction ....................... 99

5.2.2. Materials and methods ............. 100

5.2.3. State and control variables of

mite/cucumber system .................. 102

5.2.4. Fuzzy biological control model .... 109

5.2.5. Results ............................ 110

5.2.6. Sensitivity analysis ............... 118

5.2.7. Discussion ......................... 121

5.3 Optimal use of Phytoseiulus persimilis

for biological control of Tetranvchus

urticae on greenhouse cucumbers based

on a hypothetical economic

criterion ............................... 122

5.3.1. Introduction ....................... 122

5.3.2. State transition of the fuzzy

biological control model ............. 122

5.3.3. Optimal problem of mite/cucumber

biological control system .......... 126

5.3.4. Dynamic programming: Bellman's

principle of optimality .............. 130

5.3.5. Results and discussion .......... 131

GENERAL DISCUSSION AND CONCLUSIONS ......... 135
LIST OF TABLES

<table>
<thead>
<tr>
<th>TABLE</th>
<th>Parameters for initial simulations based on Pearl's stochastic model. (All values are rates per mite per day, at 25°C, in various systems.)</th>
<th>PAGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>Parameters for initial simulations based on Pearl's stochastic model. (All values are rates per mite per day, at 25°C, in various systems.)</td>
<td>25</td>
</tr>
<tr>
<td>2.</td>
<td>Results of the single plant experiments: some important parameter estimates in Pearl's model by a simulation-based estimation based on the data from single plant systems</td>
<td>30</td>
</tr>
<tr>
<td>3.</td>
<td>Results of the four-plant experiment: migration related parameter estimates in Pearl's model by a simulation-based estimation based on the data from four-plant systems</td>
<td>39</td>
</tr>
<tr>
<td>4.</td>
<td>Survivors of PPE and 2SSM adult females during starvation at T=25°C, RH=75±15% and L:D=12:12</td>
<td>54</td>
</tr>
<tr>
<td>5.</td>
<td>Survivors of PPE and 2SSM adult males during starvation at T=25°C, RH=75±15% and L:D=12:12</td>
<td>55</td>
</tr>
<tr>
<td>6.</td>
<td>Estimations of gut content coefficient (b_0), food digestion rate (b_1) and mean death rate (D'(t)) of both sexes of PPE and 2SSM by regressions based on data in Tables 4 and 5</td>
<td>58</td>
</tr>
<tr>
<td>7.</td>
<td>Mean eggs laid by single PPE and 2SSM females after differing starvation periods. T=25°C, RH=75±15% and photophase D:L=12:12</td>
<td>78</td>
</tr>
</tbody>
</table>
8. Oviposition rates of 2SSM feeding on Lima bean (P. limensis L.) and cucumber (C. sativus L.) leaf discs at 2 different temperatures, L:D = 12:12 and RH = 80±15% .................. 84

9. Maturation time of 2SSM feeding on 2 different leaf discs at temperature T = 25°C, L:D = 12:12 and RH = 80±15% ............ 86

10. Maturation time of 2SSM feeding on 2 different leaf discs at temperature T = 25°C, L:D = 12:12 and RH = 80±15% ............ 87

11. Predation and oviposition rates of PPE adult females feeding on 2SSM eggs at T = 25°C, L:D = 12:12 and RH = 80±15% ............... 92

12. Maturation time of PPE feeding on 2SSM at T = 25°C, L:D = 12:12 and RH = 80±15% ........ 93

13. Census of mean population densities of 2SSM and PPE adults with mean control of predator on a single cucumber plant .................. 101

14. Conceptual data of adult population densities and control for the mite/cucumber system. The data were obtained by fuzzy 0-1 mapping ...... 106

15. The possibility matrices of the mite/cucumber control system with respect to the transition between current state and predicted 2SSM state driven by different controls ............... 113

16. The possibility matrices of the mite/cucumber control system with respect to the transition between current state and predicted PPE state driven by different controls ............... 115

17. Comparison of a verbal mite/cucumber control system and a simulation of its fuzzy control model ............................. 117

18. Effects of increasing 10% of membership functions on changes of the elements in R₁ and R₂ ........................................... 120

19. A hypothetic cost of control and loss of cucumber damage caused by the 2SSM for 80 cucumber plant .................................. 129
Minimized goal function $g_0[e(1)]$ of control cost and cucumber loss caused by the 2SSM in the mite/cucumber control system during 45 days
### LIST OF FIGURES

<table>
<thead>
<tr>
<th>FIGURES</th>
<th>PAGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. The major procedures of system identification</td>
<td>13</td>
</tr>
<tr>
<td>2. Simulation-based fit to the single plant experiments: populations of 2SSM on each plant at 25°C. Sample output from 16 simulations with comparison of the experimental data</td>
<td>31</td>
</tr>
<tr>
<td>3. Simulation-based fit to the single plant experiments: populations of PPE on each plant at 25°C. Sample output from 8 simulations with comparison of the experimental data</td>
<td>33</td>
</tr>
<tr>
<td>4. Simulation-based fit to the single plant experiments: population of 2SSM females on each plant at different temperatures. Sample output from 16 simulations with comparison of the experimental data</td>
<td>35</td>
</tr>
<tr>
<td>5. Simulation-based fit to the 4-plant experiment: spatial and temporal distribution of 2SSM egg population following initial release of 2 females at day 0 on plant 3. Sample output from 16 simulations</td>
<td>41</td>
</tr>
<tr>
<td>6. Simulation-based fit to the 4-plant experiment: spatial and temporal distribution of 2SSM female population following initial release of 2 females at day 0 on plant 3. Sample output from 16 simulations</td>
<td>43</td>
</tr>
</tbody>
</table>
7. Logistic and linear regressions for the survivorships of PPE during a period of starvation. Simulation: solid circles with dotted lines for females and a solid line for males; experimental data: open circles with solid lines for females and open circles for males ................. 60

8. Logistic regressions for the survivorships of 2SSM during a period of starvation. Simulation: solid circles with dotted lines; experimental data: open circles with solid lines ............................. 62

9. Sample output from 10 simulations with comparison of the experimental data (from experiments 1 and 3). Data are mean survivors of each PPE population during starvation; bars are ± SD. Simulation: solid circles; experimental data: open circles ........................................ 64

10. Sample output from 10 simulations with comparison of the experimental data (from experiments 2 and 4). Data are mean survivors of each 2SSM population during starvation; bars are ± SD. Simulation: solid circles; experimental data: open circles ........................................ 66

11. Weight increase (before and after three-hour feeding) of a PPE adult and number of 2SSM eggs eaten (during three-hour feeding) by a PPE adult after differing starvation periods; bars are ± SD. Weight increase: solid circles with solid lines; eggs eaten: open circles with dashed lines ......................... 73

12. Fuzzy 0-1 mappings .............................. 104

13. Conceptual paired state variables of PPE and 2SSM in the mite/cucumber system after taking fuzzy mappings on the experimental data .................................................. 107

14. The performance functions Q_1 (for X variable) and Q_2 (for Y variable) against the number of iterations for the "max-prod" structure of the mite/cucumber control system ................. 111

15. Control rules of mite/cucumber system ...... 124
16. A N-stage decision process of the mite/cucumber control system (N=15) ......... 127
CHAPTER I

INTRODUCTION

In this dissertation, two species of mites, *Tetranychus urticae* Koch (Acarina: Tetranychidae) and its predator, *Phytoseiulus persimilis* Athias-Henriot (Acarina: Phytoseiidae) are intensively investigated as models of predator-prey interactions and for developing pest management systems in greenhouses.


The two-spotted spider mite (hereinafter 2SSM), *T. urticae*, develops from egg through larva, protonymph, deutonymph, to adult stages. The three active, feeding immature stages are each followed by intervening stages of quiescence called the protochrysalis, deutochrysalis and teleiochrysalis, respectively (Crooker, 1985). Development of the 2SSM is closely related to temperature, host plant, humidity, light and other factors; extreme environmental
conditions can cause the mites to enter diapause. This species is arrhenotokous; unmated females produce only haploid eggs which develop into males, whereas mated females produce both haploid and diploid eggs, which develop into males and females, respectively. Under normal conditions, the sex ratio within a stable population varies around 1:2 (male:female). *P. persimilis* (hereinafter PPE) is a specialized predator of a number of *Tetranychus* species (Huffaker et al., 1970) and successfully controls the 2SSM in many crops. The success of this predatory mite in controlling the 2SSM is due to its voracity, high rate of oviposition (Sabelis, 1985), rapid developmental rate (Chant, 1961a), resistance to some acaricides or pesticides (Zebitz et al., 1981) and effective searching ability (Sabelis and Dicke, 1985). There are four developmental stages of this species: egg, larva, nymph and adult. Only mated adult females produce eggs which develop into both males and females. The sex ratio within a stable population is usually 1:3 (male:female).

1.2 OUTBREAKS OF THE TWO-SPOTTED SPIDER MITE, *Tetranychus urticae*, IN AGROECOSYSTEMS

Spider mites are potentially major pests of important food, fiber and ornamental crops (Pritchard and Baker, 1955). The 2SSM is the most polyphagous species of
Tetranychidae and a large variety of host plants is known. It is a major pest of vegetables (Hussey et al., 1965; French et al., 1976; Dixon, 1973; Gould, 1971), fruits (McMurtry, 1969; Sances et al., 1982a, b; Hoy, 1985) and ornamentals in greenhouses (Jeppson et al., 1975; Van de Vrie, 1985). The potential of the 2SSM injury to host plants has become increasingly evident during the last few decades. The 2SSM feeds on the parenchyma cells of leaves; their stylets are inserted through the leaf epidermis and cell contents are removed by sucking. In the past, the 2SSM caused severe damage which resulted in heavy losses in such crops as citrus, avocado, beans, tomatoes, cucumbers, cotton, apples, pears, plums, strawberries and many other horticultural and ornamental crops. The damage caused by the 2SSM is obvious; when outbreaks occur, the infested leaves are either completely yellowed or abscise, resulting in loss of yield. Outbreaks of the 2SSM do not occur in natural ecosystems where low productivity of mites is a character. Natural factors such as diseases and predators regulate the spider mite population around an equilibrium. However, in modern agroecosystems where production levels are high, broad-spectrum pesticides are frequently used to protect yields. Pesticides often have a more adverse effect on the natural enemies of the mites than on the mites themselves, who have developed resistance to many pesticides; therefore a stable population equilibrium does
not exist and mite outbreaks can occur. In modern agroecosystems, especially in modern greenhouses, plant culture is mainly practised in protected climatic conditions. Temperature, relative humidity, soil conditions or artificial growing media, fertilizing, watering, daylength and atmospheric conditions are controlled within narrow ranges, and are often automated with sophisticated computerized equipment (Van de Vrie, 1985). Where crops are grown under nearly optimal conditions, i.e. growth is not limited by water or nutrients, and forms a sufficient food source for the 2SSM, the development is enhanced and outbreaks can result (Van de Vrie et al., 1972). Outbreaks of the 2SSM are therefore typical in high-energy-input agroecosystems.

1.3 CHANGES IN STRATEGY FOR CONTROL OF THE TWO-SPOTTED SPIDER MITE, Tetranychus urticae

Frequent use of broad-spectrum pesticides in modern agriculture so affects the natural enemies of spider mites as to release them from natural control, and spider mites have developed resistance to most acaricides (Horn, 1988). Outbreaks can develop even shortly after the pesticide application, because the 2SSM has developed resistance to pesticides that previously gave effective control (Helle, 1965; Helle and Van de Vrie, 1974; Dittrich, 1975; Jeppson
et al., 1975). The 2SSM has developed resistance rapidly to organophosphates (OPs), including parathion and many other acaricides (Hoy, 1985). Resistant 2SSM is common in greenhouses worldwide. The development of resistance in greenhouses is favored by the relative isolation of the 2SSM populations, the extended season for development, the absence of diapause and repeated pesticide applications (Cranham and Helle, 1985). The problem of heavy acaricide use and sole reliance on chemical controls during the past several decades had become obvious. Researchers began to realize that the main strategy for controlling spider mites should be changed from reliance on heavy and repeated use of pesticides to alternatives such as biological control (Huffaker et al., 1970; James, 1990; Jaroski and Pliva, 1990), genetic control (Feldmann, 1977, 1979, 1985; Feldmann et al., 1981; Hoy and Cave, 1988; Nelson and Stafford, 1972), control by breeding resistant plants (Brody and Karban, 1990; De Ponti, 1977a, b, 1978, 1985; Gould, 1978a, b; Gould et al., 1982; Karban, 1990; Stoner and Stringfellow, 1967; Tulisalo, 1969, 1972) and control by fungal epidemics (Carner, 1976; Dresner, 1949; Robertson and Carroll, 1988; Smitley et al., 1986). Effectiveness of a specific method or a combination of methods depends on specific agricultural practices and requirements of grower and consumer. Since my study investigated optimal use of PPE for controlling the 2SSM, I limit discussion to
biological control in its traditional sense of using a natural enemy to control a pest population.

1.4 EXPERIMENT-BASED APPROACHES TO CONTROL OF THE TWO-SPOTTED SPIDER MITE, *Tetranychus urticae*, IN GREENHOUSES

Since the first report of laboratory investigation into the effectiveness of the phytoseiid mite, *Phytoseiulus persimilis* (= *Phytoseiulus riegeli* Dosse) in the control of *T. urticae* (= *Tetranychus telarius* (L.)) (Dosse, 1958), this predator has been studied as a control agent of the 2SSM and related species infesting greenhouse crops especially cucumbers and tomatoes (Amano and Chant, 1977, 1978; Bravenboer, 1963, 1975; Bravenboer and Dosse, 1962; Bravenboer and Theune, 1960; Burges, 1974; Chant, 1961a; Dixon, 1973; Gould, 1976; Hussey, 1964, 1965; Hussey et al., 1965; Liang and Huffaker, 1960; Legowski, 1966; McMurtry and Scriven, 1975; Mori and Chant, 1966a, b; Parr, 1972; Parr and Hussey, 1967; Pruszynski, 1976; Simmonds, 1972; Takafuji and Chant, 1976). All these investigations were experiment-based and characterized by "trial and error". Systems approaches were not attempted although the importance of maintaining the appropriate balance between predator and prey with regard to timing of introduction and number of predators released was nevertheless considered
essential to successful control. Chant (1961b) demonstrated the predatory efficiency of PPE on potted Lima bean plants infested with *T. telarius* (L.). At a predator:prey ratio of 1:50, almost complete control was obtained within 21 days. Hussey et al. (1965) developed an experiment-based theoretical pattern of spider mite control on cucumbers through observation of leaf damage based on greenhouse experiments. They suggested that for cucumber plants maintained for 30 weeks, only two introductions of the predator and an acaricide application are necessary, and they must be timed to prevent the leaf-injury sustained during management from exceeding the maximum leaf damage tolerated by cucumber plants without yield loss (Hussey and Parr, 1963). In the study of Hussey et al. (1963, 1965), the consistent presence of predators in the system and an economical criterion (a leaf damage index) were major aspects of successful control. Parr and Hussey (1967) also carried out a production scale experiment with greenhouse cucumbers (200 plants) to ascertain the minimum level of predator introduction likely to achieve efficient and economical control of the 2SSM in commercial greenhouses. In their design, the "pest in first" technique was employed; spider mite populations were initiated by infesting each plant with 20 females when the plants had five leaves, and then they released PPE in four different ways. Through this experiment they found that release of several predators on
every fifth plant was the most economical and efficient way of introduction. Hussey (1967) further concluded that when attempting to use biological control in greenhouses it is essential to realize that commercially acceptable results will be achieved only if sufficient numbers of predators are systematically introduced. Markkula and Tiittanen (1976) investigated the effectiveness and expense of "pest in first" and "natural infestation" (release no additional 2SSM, and control acts only after plants show damage) methods in commercial cucumbers. They found that both methods were equally suitable for controlling the 2SSM but the "pest in first" method proved more expensive.

There is no doubt that experiment-based biological control or its integration with chemical control of the 2SSM on greenhouse cucumbers is a first step in developing optimal biological and chemical control of this species. Such studies have been conducted in commercial greenhouses and both ecological and economical factors were considered as criteria to evaluate the effectiveness of a control strategy. However, in experiment-based studies, development of an effective control strategy depended mainly on investigators' intuition and experiences. Comparative studies performed to seek a better control strategy were selected from a narrow range of potential control policies. Apparently, it is too expensive and time consuming to find an optimal control strategy by doing production scale
experiments with every different potential control policy. Therefore, experiment-based research is unable to solve optimality problems. However, experiment-based research for successful control of the 2SSM has provided considerable insights toward development of optimal control on this pest in modern agricultural practices.

1.5 SYSTEMS APPROACHES TO CONTROL OF THE TWO-SPOTTED SPIDER MITE, *Tetranychus urticae*

As discussed in section 1.3, the experiment-based approach is a valid tool for seeking better controls for the 2SSM. An additional challenge for 2SSM management is to develop an optimal management system which is economically and ecologically efficient. Systems approaches including modeling and optimization should be introduced into current research of spider mite management for a thorough understanding of the dynamics of predator-prey-plant interactions and pest management. Hassell (1978) predicted systems approach would soon be an effective adjunct to integrating biological control with other methods to pest management.

1.5.1 Analytic approach and system identification

Because of the importance of systems approaches to 2SSM
management, there has been an increasing number of mathematical models developed for spider mite predator-prey-plant systems since the 1970's (Rabbinge and Hoy, 1980; Shaw, 1984, 1985; Sabelis et al., 1988; Nachman, 1987a, 1988; Pearl et al., 1989). In modeling research, an analytic approach is a commonly used method for studying system dynamics in the natural sciences. With an analytic approach, the interactions of system components can be described as mathematical equations if the mechanisms of these interactions are known. Usually, the laws of energy conservation and continuity as well as many other specific laws or principles in physics, chemistry, biology and mathematics provide adequate sources to build mathematical equations, including differential or difference equations (deterministic or stochastic) and other algebraic expressions. However this approach may be suitable only for studying relatively simple systems. For a complex system such as a spider mite predator-prey-plant system, this method is not applicable to many aspects of the system where the biological information is uncertain or unknown. Because of this, the theory and technique of system identification has been developed into a very attractive and active research field. System identification is an appropriate approach for studying a complex system, because it is mainly based on observations of the system. Zadeh (1962) defined system identification as an approach, which seeks an
equivalent system (model) for the observed system from a
class of systems (models) based only on the observations of
that system. There are four major steps in the process of
system identification: 1) test design, 2) structural
determination of the model, 3) parameter estimation, and 4)
validation of the model (See Fig. 1). In step 4),
validation of a best model means that if the model has the
same input as the observed system, the difference (error)
between outputs from the observed system and the model will
be minimized. In system identification, this minimization
can be achieved by either changing the values of the
parameters within the model or changing the structure of the
model in an optimal direction by various techniques.

In the literature of modeling spider mite predator-prey-
plant system, several authors have proposed mathematical
models which are generally deterministic and the classic
predator-prey demography such as density dependent predation
(functional response and numerical response) (Nicholson and
Bailey, 1935; Holling, 1959) is the main framework for
building the model. Analytics was a dominant method used to
describe the interactions of components within a predator-
prey-plant system, and information on life history,
predation, and density and food (host plant and prey)
quality-dependent migration was essential for writing
mathematical equations. Several assumptions were also made
as the system was hard to analyze. If reasonable
assumptions are made by the modelers, and the parameters in
the model have physical meaning and can be understood
independently of one another, the result of the analytic
method is usually theoretically consistent with biological
realities (Bernstein, 1985; Nachman, 1987a). Using the
analytic approach, the output error between real systems and
the model can also be reduced by changing the values of the
parameters within the model; however the best way to
determine parameter values is generally unknown (especially
when there are many parameters in the model). This kind of
"blindness" in parameter estimation existed in the analytic
approach. Pearl et al. (1989) proposed a sophisticated
arthropod predator-prey-plant model in which both analytic
approach and systems identification were used, by which they
have developed simulation-based parameter estimation in a
multi-dimensional setting. The parameter estimation
technique has three components: a criterion, a searching
technique and a way to incorporate existing knowledge.
Applying this technique, minimized criterion was achieved by
computations (Horn et al., 1991, unpublished). This present
research represents the most recent development of applying
systems approach to a stochastic spider mite management
model. Application of system identification in spider mite
management models is a turning point which indicates that we
have entered into a new powerful phase in the development of
modeling the spider mite management system.
Fig. 1. The major procedures of system identification (based on Zadeh, 1962).
Test design → Input/output data → Parameter estimation → Validation

Yes: Final model

No: Principles of natural science → Model structure → Parameter estimation → Validation → Is model accepted?

Fig. 1.
1.5.2 Simulation models and control models

Two kinds of models can be used for description of a system. A simulation model (also called descriptive model, see Shoemaker, 1973a) is used only for describing the interactions among state variables of the system, and a control model is used not only for describing the interactions among state variables but also inputs of the system. For instance, a simulation model can be developed for a spider mite predator-prey-plant system by writing several differential equations (or difference equations) for the changes of the mite population densities and the leaf damage index (or the area of edible leaf surface) which are defined as state variables. By these equations we can simulate the population dynamics on a computer from any initial values. If we want to describe a spider mite control system, it is necessary to develop a control model, because only a control model can tell us directly in which way the system responds to its inputs without "trial and error" simulation. Biological control by release of predators and chemical control by application of pesticide are inputs of a pest management system. It is very important to know the responses of the system to any particular input in order to find the best control strategy. It is usually impossible to test the response of a spider mite system to a large number of different inputs by an
experiment-based approach. An analytic approach can be used to determine the interactions between state variables and inputs of a spider mite-plant system, but it may be very difficult because of the uncertainty of the system. In this case, system identification is an appropriate method to build a control model based on input/output observations. In chapter 5, I apply this approach to build a fuzzy model of a spider mite control system. Since a difficulty exists in building control models, no control model has been proposed for spider mite management although several authors have proposed optimization models for spider mite management (Dover et al., 1979; Havelka and Kindlmann, 1984; Horn et al., 1991; Rabbinge and Hoy, 1980; Nakao et al., 1987; Pearl et al., 1989). The models used by these authors are generally simulation models, by which an optimal control strategy can be obtained only from computer simulated experiments and only a powerful computer can complete this task. Horn and others (Horn et al., 1991, unpublished) have planned to apply a simulation-based approach to search for an optimal control strategy by a supercomputer, Cray Y-MP/864. From the above discussion, the shortcoming of applying a simulation model to control problems without a supercomputer is obvious. I anticipate that more systems theories and techniques such as system identification and optimal control or stochastic optimal control will be introduced into such research during the near future.
1.6 DEVELOPING OPTIMALITY OF SPIDER MITE MANAGEMENT SYSTEM IN MODERN AGRICULTURAL PRACTICES

1.6.1 Mathematical model

A control model which is used to describe a spider mite management system generally has two kinds of equations: state equation and observation equation. The state equation describes the most important interacting factors in the system such as populations of predator and prey, as well as the edible leaf area of the host plant. Since the amount of damage to the host (crop) plant and the susceptibility to control treatments (biological and chemical) depend upon the age of the 2SSM individuals, and the predation capacity of predators, and the migration of both predator and prey depend upon the ages of individuals within these two species, it is necessary to know not only adult populations but also the distributions into age classes. In a detailed model (Horn et al., 1991; Pearl et al., 1989) both predator and prey populations were partitioned into four categories: egg, nymph, adult male and adult female. For instance, in a mxn-plant greenhouse system (plants grow in m rows and n columns), the changes of population densities of predator and prey and the edible leaf surface need to be described on each plant; therefore the system has mxnx9 important interacting factors which form a state vector X. The state
equation also describes the interactions between state variables and inputs. If the control methods are release of predator and application of acaricide, then they form a control vector $U$. Environmental and demographic stochasticity also can be introduced into the state equation. In doing so, the equation has the general form:

$$X_{t+1} = f(X_t, U, t) + v_t$$  \hspace{1cm} (1.1)$$

where $v_t$ is a stochastic process.

In view of the observations from spider mite management system, observations such as relative population densities (population densities on a small portion of the total leaf surface) and leaf damage index (Hussey and Parr, 1963) are appropriate for a commercial greenhouse system. The relations of observations to population densities can be described by an observation equation:

$$Y_t = g(X_t, t) + w_t$$ \hspace{1cm} (1.2)$$

where $Y_t$ is the observation vector and $w_t$ usually is a Gaussian process which represents the observation error. For simplicity, associated conditions of Eqs. 1.1 and 1.2 are omitted.
1.6.2 Method for optimization

Spider mite management in greenhouse crops is usually a control problem over a finite time interval (the duration of a growing season). The purpose of optimal management is to find the best control strategy from a given model (eqs. 1.1 and 1.2). The criterion function is the means by which the quality of all possible strategies can be judged. An economic criterion should be developed that will allow us to minimize the total costs of the control and loss of crop damage. To estimate these two economic functions, production scale experiments need to be conducted. As mentioned earlier, Hussey and Parr (1963) estimated the indirect measurement for the crop loss, when the average leaf damage index of cucumber plants does not exceed a certain level, there will be no economic loss on cucumber production. More study needs to be done to develop an economic criterion (such as cost of control, spider mite population size and leaf damage index with respect to net weight and cosmetic value of the crop) in order to use dynamic programing and other optimal techniques for optimality of the spider mite management system. However, the optimality of a general nonlinear stochastic control system (described by Eqs. 1.1 and 1.2) has not been yet solved, although the optimal control theory of linear stochastic system (when $f$ and $g$ are linear functions) was
completed more than twenty years ago (Astrom, 1970; Fuller, 1970).

1.7 SCOPE OF STUDY

It is clear from the above discussion that a great deal of research has been stimulated by the economic importance of 2SSM. Using a stochastic stimulation technique to modeling predator-prey interaction and developing optimal pest management in greenhouses is a recent development. The study presented here reflects recent achievements in the course of developing a stochastic model. In Chapter 2, the main research objective was to carry out experimental validation of the model through intensive demographic censuses of predator and prey populations on lima bean plants. The parameter estimation focused on the most sensitive ones, such as maturation time, reproduction rate, predation rate and migration rate associated with the effects of environmental factors. In Chapter 3 I discuss the death process and reproduction of a population under starvation. The death process is simulated by Monte-Carlo procedures. The proposed death process can be incorporated into a model by which the dynamics of a migrating population can be described more realistically. In Chapter 4 I investigate the effect of different host plants, Lima bean and cucumber on the life history parameters in the model,
which will provide information to convert the current laboratory Lima bean system into a model for commercial cucumber system. In Chapter 5 I discuss an alternative approach: fuzzy analysis to modeling of predator-prey interactions and optimality of pest control problems on cucumbers in a greenhouse.
CHAPTER II
EXPERIMENTAL VALIDATION OF A PREDATOR-PREY
STOCHASTIC MODEL ON LIMA BEANS

2.1 INTRODUCTION

As discussed earlier, applications of stochastic modeling to spider mite predator-prey-plant systems is a recent development. Two stochastic models of spider mite systems have been published recently, one by Nachman (1987a), and one by Pearl et al. (1989). The model developed by Pearl et al. is complex and has already gained some success in describing the realities of a spider mite predator-prey system. This model is still undergoing experimental validation and parameter refinement.

Pearl's stochastic model (Pearl et al., 1989; Horn et al., 1991) was designed to simulate and predict the development and interaction of predator and prey populations located on plants growing in a row. Within the model, 10 state variables (number of eggs, nymphs, adult males and adult females of each species, amount of active pesticide, and edible leaf surface area) are tracked on each plant; two

"The model is designated "Pearl's" for convenience; the model has been developed through the joint effort of Pearl, Bartoszynski and Horn."
additional processes, temperature and humidity, are integrated into parameters which are temperature and humidity dependent (such as maturation rate, egg laying rate, etc.). The pesticide decay function is exponential; growth of the edible leaf area is governed by a logistic differential equation and transitions between different stages are assigned as probabilistic events. The maturation time of egg or nymph is assumed to be a linear function of the average temperature and humidity and is characterized by a mean and a variance. The sex ratio of both species was 1:2 (male:female) in the original version of the model. A ten-dimensional Markov process is used to determine the occurrence of the other demographic events (death, predation and migration between the times of egg hatching, nymph maturing or pesticide/predator release) within the system. Each stochastic event has an assumption of event intensity based on an understanding of biology. The event intensity of prey egg death is a linear combination of natural death and predation by predator nymphs, adult males and adult females. The event intensity of predator egg death is caused by natural factors only. The event intensity of prey nymph death is a linear function of natural causes, starvation, pesticide effects and predation by predator nymphs and adults. The event intensity of predator nymph death is a linear function of natural causes, starvation and pesticide effects. The event intensity of adult death is
analogous to that of the nymph death in each species (except that predator nymphs do not feed on prey adult females). In regard to prey dispersal, only the adult is able to disperse; however with regard to predators, all mobile stages are able to disperse. The event intensity of prey dispersal rate is proportional to competition for edible leaf area. The event intensity of predator dispersal rate depends on the number of prey per total leaf surface. For dispersal event intensities, a success rate is assigned for each stage in both species. Finally, the event intensity of egg laying is a linear function of temperature and humidity, and decreases with starvation.

The mathematical description of the 12 processes discussed above forms the earlier version of the stochastic model which was programmed (by D. K. Pearl) on a Pyramid 90X computer. Initial simulations used parameters from published literature on various spider mite-plant systems or from preliminary estimates (Kallander, 1989) when literature values were unavailable (Table 1). Based on the simulations, a sensitivity analysis was conducted; the results showed that an economic criterion of the system was highly sensitive to small changes in maturation times and oviposition rates. This suggested that the study should be focused on estimation of these parameters and to account for the environmental stochasticity associated with changing temperature and humidity.
Table 1. Parameters for initial simulations based on Pearl's stochastic model. (All values are rates per mite per day, at 25°C, in various systems).

<table>
<thead>
<tr>
<th>Parameters</th>
<th>2SSM</th>
<th>PPE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Egg mortality</td>
<td></td>
<td></td>
</tr>
<tr>
<td>natural death</td>
<td>.011 (Sabelis, 1981)</td>
<td>&lt;.001 (Shaw, 1984)</td>
</tr>
<tr>
<td>predation</td>
<td>.02 (Liang, 1968)</td>
<td></td>
</tr>
<tr>
<td>Nymph mortality</td>
<td></td>
<td></td>
</tr>
<tr>
<td>natural death</td>
<td>.006 (Sabelis, 1981)</td>
<td>&lt;.001 (Shaw, 1984)</td>
</tr>
<tr>
<td>by pesticide</td>
<td>.065</td>
<td>0 (resistant)</td>
</tr>
<tr>
<td>predation</td>
<td>.04 (Bravenboer and Dosse, 1962)</td>
<td></td>
</tr>
<tr>
<td>Adult mortality</td>
<td></td>
<td></td>
</tr>
<tr>
<td>natural death</td>
<td>.028 (Sabelis, 1981)</td>
<td>.033 (Liang, 1968)</td>
</tr>
<tr>
<td>by pesticide</td>
<td>.065</td>
<td></td>
</tr>
<tr>
<td>predation</td>
<td>.05 (by adult predation)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>.024 (by immature predation)</td>
<td></td>
</tr>
<tr>
<td>Oviposition</td>
<td>2.5 (Sabelis, 1981)</td>
<td>2.5 (Liang, 1968)</td>
</tr>
<tr>
<td>Emigration</td>
<td>.001 (Nachman, 1987a)</td>
<td>.01 (Nachman, 1987a)</td>
</tr>
<tr>
<td>Maturation (days)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>egg</td>
<td>4 (Sabelis, 1981)</td>
<td>3 (Liang, 1968)</td>
</tr>
<tr>
<td>nymph</td>
<td>6 (Sabelis, 1981)</td>
<td>5 (Liang, 1968)</td>
</tr>
</tbody>
</table>

(after Pearl et al., 1989)
Most parameters used in Pearl's original model (Pearl et al., 1989) were adapted from different biological systems under a variety of environmental conditions. The important parameters such as maturation and oviposition rates therefore needed to be estimated. In accomplishing this, the model computer program has been converted into a Cray X-MP/24 supercomputer (the new version of program contains a vectorilized feature and computation is carried out in a parallel fashion) to speed the simulation. Use of the supercomputer makes it feasible to estimate system parameters in a multidimensional setting by simulation-based techniques.

2.2 VALIDATION OF THE MODEL ON A SINGLE PLANT

2.2.1 Introduction

To estimate parameters precisely for the preceding model, an intensive demographic survey of predator and prey populations was conducted. Lima bean, *Phaseolus limensis* L. was chosen as host plant of 2SSM, because it has a relatively small size that is helpful for censusing and for conducting experiments. Two mite species, PPE and 2SSM comprise of a predator-prey system is ideal for testing the model, since both species can be reared either in a greenhouse or a laboratory (Sabelis, 1981). PPE has been
widely used for control of greenhouse spider mites, and the
demography of both species have been extensively studied
(See Chapter 1). Using this predator-prey-plant system,
relatively accurate information on demographic events in a
single plant system can be achieved through censuses. This
information is essential for an accurate estimation of
important biological parameters in the model such as
reproduction, development time and predation rates. The
effects of physical factors (such as temperature and
relative humidity) on these parameters were also considered
by examining effect of temperature in five small scale
experiments with different temperatures from June 13 to
October 27, 1990.

2.2.2 Methods and materials

Sixteen two-week old Lima bean plants (P. limensis L.)
were used for each of five single plant experiments. Each
plant was limited to its first five leaves and additional
growth trimmed. Plants grew individually in small plastic
pots, pots were placed in pans (81cmx31cmx2.5cm) filled with
water and covered by organdy cages (80cmx30cmx30cm) to
prevent mite escape. The single plant systems were located
in an environmental chamber (Conviron E30) and in each
experiment temperatures were controlled at five constant
levels: 20°C, 22.5°C, 25°C, 27.5°C and 30°C respectively
(relative humidity 80±10%).

In each experiment, two 2SSM adult females were transferred from a laboratory stock culture onto each of 16 plants. Soon after all mite stages were present (nine to 17 days after 2SSM introduction), the number of females on each plant was adjusted to 20. Two mated PPE females were then transferred from a laboratory culture (originally obtained from Koppert, Ltd., The Netherlands) and released onto each of eight test plants. The eight control plants did not receive predatory mites.

At one-day intervals following initial introduction of the 2SSM, eggs, nymphs, and both sexes of adults were censused for four to five days. The census for both species was continued at three-day intervals thereafter conducted with the aid of a stereo microscope and tape recorder. The total and infested areas of plant leaves were also measured. The demographic study on the control plants was ended when one complete life cycle of 2SSM was attained; the demographic study on the treated plants was terminated when a complete life cycle of PPE was attained.

2.2.3 Results and discussion

The simulation-based parameter estimation has been successful in estimating many parameters in the model (Horn et al., 1991), in which a criterion was minimized with a
high probability through searching. These simulations were conducted on a supercomputer, Cray Y-MP/864, programmed by J-F Maa. The estimates of most important parameters are shown in Table 2. Figs. 2 and 3 show the simulation-based fit to single plant experiment data of 2SSM and PPE populations at 25°C respectively. Fig. 4 shows the fit to 2SSM female data at different temperatures. The estimates of maturation time and oviposition rate at different temperatures provided information to improve the predictive ability of the model in different environmental conditions. As effect of temperature was added, the parameters became functions of temperature instead of constants. These functions were derived by linear and nonlinear regressions and incorporated into the model which currently reflects the effect of temperature on development and reproduction of both mite species and on plant growth. Figs. 2-4 all show a good match between experimental and simulated data. The stochastic model fits not only the average numbers of the populations but also captures the inherent dynamic variability within the populations.
Table 2. Results of the single plant experiments: some important parameter estimates in Pearl's model by a simulation-based estimation based on the data from single plant systems.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Temperature (°C)</th>
<th>2SSM</th>
<th>PPE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maturation time</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(eggs)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>20</td>
<td>5.16</td>
<td>2.8</td>
<td></td>
</tr>
<tr>
<td>22.5</td>
<td>3.73</td>
<td>2.65</td>
<td></td>
</tr>
<tr>
<td>25</td>
<td>2.8</td>
<td>1.91</td>
<td></td>
</tr>
<tr>
<td>27.5</td>
<td>3.06</td>
<td>1.86</td>
<td></td>
</tr>
<tr>
<td>30</td>
<td>2.77</td>
<td>2.5</td>
<td></td>
</tr>
<tr>
<td>(nymphs)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>20</td>
<td>5.78</td>
<td>2.81</td>
<td></td>
</tr>
<tr>
<td>22.5</td>
<td>5.15</td>
<td>2.06</td>
<td></td>
</tr>
<tr>
<td>25</td>
<td>5.38</td>
<td>2.43</td>
<td></td>
</tr>
<tr>
<td>27.5</td>
<td>4.32</td>
<td>1.71</td>
<td></td>
</tr>
<tr>
<td>30</td>
<td>4.30</td>
<td>1.5</td>
<td></td>
</tr>
<tr>
<td>Egg laying rate</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(l/day)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>20</td>
<td>4.08</td>
<td>2.35</td>
<td></td>
</tr>
<tr>
<td>22.5</td>
<td>5.5</td>
<td>3.22</td>
<td></td>
</tr>
<tr>
<td>25</td>
<td>6.14</td>
<td>4.05</td>
<td></td>
</tr>
<tr>
<td>27.5</td>
<td>6.99</td>
<td>4.5</td>
<td></td>
</tr>
<tr>
<td>30</td>
<td>7.38</td>
<td>3.5</td>
<td></td>
</tr>
<tr>
<td>Predation¹</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(g/day, g)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>a₂, rₐ₂</td>
<td>.066, 1.184</td>
<td></td>
<td></td>
</tr>
<tr>
<td>a₃, rₐ₃</td>
<td>.167, 1.269</td>
<td></td>
<td></td>
</tr>
<tr>
<td>a₄, rₐ₄</td>
<td>.352, .382</td>
<td></td>
<td></td>
</tr>
<tr>
<td>b₃, rₐ₃</td>
<td>.052, 1.26</td>
<td></td>
<td></td>
</tr>
<tr>
<td>b₄, rₐ₄</td>
<td>.187, 1.74</td>
<td></td>
<td></td>
</tr>
<tr>
<td>b₅, rₐ₅</td>
<td>.293, .675</td>
<td></td>
<td></td>
</tr>
<tr>
<td>g₃, rₐ₃</td>
<td>.0238, 1.21</td>
<td></td>
<td></td>
</tr>
<tr>
<td>g₄, rₐ₄</td>
<td>.024, .96</td>
<td></td>
<td></td>
</tr>
<tr>
<td>g₅, rₐ₅</td>
<td>.055, .327</td>
<td></td>
<td></td>
</tr>
<tr>
<td>s₄, rₐ₄</td>
<td>.5, 2.83</td>
<td></td>
<td></td>
</tr>
<tr>
<td>s₅, rₛ₅</td>
<td>.117, .075</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sex ratio</td>
<td>.37: .663</td>
<td>.28:.72</td>
<td></td>
</tr>
<tr>
<td>Plant growth rate</td>
<td>25</td>
<td>.3218</td>
<td></td>
</tr>
<tr>
<td>(l/day)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Prey feeding rate</td>
<td>25</td>
<td>.3569</td>
<td></td>
</tr>
</tbody>
</table>

¹ The meaning of the predation parameters is explained in Appendices A and B. (from Horn et al., 1991, unpublished).
Fig. 2. Simulation-based fit to the single plant experiments: populations of 2SSM on each plant at 25°C. Sample output from 16 simulations with comparison of the experimental data. Asterisk: outlier (from Horn et al., 1991, unpublished).
Fig. 2.
Fig. 3. Simulation-based fit to the single plant experiments: populations of PPE on each plant at 25°C. Sample output from 8 simulations with comparison of the experimental data. Asterisk: out-lier (from Horn et al., 1991, unpublished).
Fig. 3.
Fig. 4. Simulation-based fit to the single plant experiments: population of 2SSM females on each plant at different temperatures. Sample output from 16 simulations with comparison of the experimental data. Asterisk: out-lier (from Horn et al., 1991, unpublished).
Fig. 4.
2.3 VALIDATION OF THE MODEL ON A FOUR-PLANT SYSTEM

2.3.1 Introduction

In single plant experiments with emphasis on estimation of important life history parameters of both mite species, the interplant dispersal and the death processes of a population during migration was neglected. In this section I discuss estimation of dispersal parameters and validation of the refined model which was improved with data on starvation and gut filling processes of both species (data are shown in Chapter 3). These processes and related death processes have been mathematically described and estimated by a maximum likelihood estimation (Horn et al., 1991, unpublished). The importance of these processes for a migrating population is obvious; my investigation of death process of a population during its dispersal (under starvation) will be detailed in Chapter 3. An experiment on a four-plant system conducted to estimate the dispersal-related parameters, also served as independent validation of the life history parameter estimates derived from single plant experiments.

2.3.2 Methods and materials

An experiment was conducted on 2-week old Lima bean (P.
limensis L.) plants in linear arrays of four plants each from Oct. 30 to Dec. 27, 1990. Plants grew singly in small plastic pots; each plant was limited to five leaves and additional leaves were trimmed. Plants in each array were connected by plastic "bridges" (18cmx2cm) to direct the interplant dispersal of mites. Each array was placed in a pan (81cmx31cmx2.5cm) filled with water and isolated within a plastic and organdy cage (80cmx30cmx30xcm). There were eight replications in the experiment. All four-plant arrays were situated in a controlled environment chamber at 25°C and relative humidity 75±5%.

Three 2SSM adult females from a stock culture were released onto the third plant of each array. After 14 days plants were infested to varying degrees and were classed into eight groups of different damage levels. In each of eight groups four plants were used to re-construct an array connected by plastic "bridges", the order of a plant in the array was selected randomly. So, the 2SSM on each array had a randomized distribution with a particular population level. On the same day four PPE adult females from a laboratory culture were released onto the third plant in each caged array. At 1-3 day intervals following initial release of 2SSM, eggs, nymphs, and both sexes of adults were censused. The experiment was terminated on day 28.
Table 3. Results of the four-plant experiment: migration related parameter\(^2\) estimates in Pearl's model by a simulation-based estimation based on the data from 4-plant systems.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Unit</th>
<th>2SSM Estimate</th>
<th>PPE Estimate</th>
</tr>
</thead>
<tbody>
<tr>
<td>(h_N^<em>, r_h^</em>)</td>
<td>g/day, g</td>
<td>.01, 62.5</td>
<td>.03</td>
</tr>
<tr>
<td>(P(\text{death/mig.})) (nymph)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(h_n(h_n), r_{h^<em>n}(r_{h</em>n}))</td>
<td>g/day, g</td>
<td>.006, 26.53</td>
<td>.17, 76.1</td>
</tr>
<tr>
<td>(P(\text{death/mig.})) (male)</td>
<td></td>
<td>.0053</td>
<td>.051</td>
</tr>
<tr>
<td>(h_u(h_u), r_{h^<em>u}(r_{h</em>u}))</td>
<td>g/day, g</td>
<td>.011, 11.51</td>
<td>.201, 79.2</td>
</tr>
<tr>
<td>(P(\text{death/mig.})) (female)</td>
<td></td>
<td>.0123</td>
<td>.06</td>
</tr>
</tbody>
</table>

\(^2\) See Appendices A and B, for the meaning of migration parameters (from Horn et al., 1991, unpublished).
2.2.3 Results and discussion

The simulation-based parameter estimation was employed to refine the migration parameters and the probabilities of death during migration. Migration related death processes were incorporated in the new version of the model. The parameter estimates are shown in Table 3. Figs. 5 and 6 give 2SSM population dynamics (egg and female) in a four-plant system with the comparisons of experimental data and simulated data from the new version model. Both experiment and simulation were replicated eight times; in addition to means, variations are also described in the figures.

As we can see from Fig. 5, on day 1 and day 6 the distribution of simulated and experimental output match almost exactly one day into the initial infestation. By day 11 a small infestation has begun on neighboring plants, the distribution of egg population was still evident in the simulation. By day 14 substantial infestations occur on neighboring plants and population distributions in simulated and experimental data appear nearly identical. Fig. 6 shows the spatial and temporal distribution of the 2SSM female population; the simulated and experimental data also match with respect to population levels and variations in development and migration. The time of migration was identical (day 8), and subsequent development of migrated population on the neighboring plants are also similar.
Fig. 5. Simulation-based fit to the 4-plant experiment: spatial and temporal distribution of the 2SSM egg population following initial release of 2 females at day 0 on plant 3. Sample output from 16 simulations. Asterisk: out-lier (from Horn et al., 1991, unpublished).
Fig. 5.
Fig. 6. Simulation-based fit to the 4-plant experiment: spatial and temporal distribution of the 2SSM female population following initial release of 2 females at day 0 on plant 3. Sample output from 16 simulations. Asterisk: outlier (Horn et al., 1991, unpublished).
Fig. 6.
Data for males and nymphs are not presented but these both show an equal quality of fit. However, PPE data did not fit so well -- dispersal in a four-plant system may be too rapid to detect during the census interval.
CHAPTER III

DEATH, SURVIVAL AND REPRODUCTION OF Phytoseiulus persimilis AND Tetranynchus urticae UNDER STARVATION

3.1 INTRODUCTION

In a greenhouse acarine predator-prey-plant system, starvation of a mite population may occur in three different situations: migration, local crash of a prey population and local extermination of a host population. During long distance dispersal, PPE and 2SSM migrate from one plant to others and spread out on greenhouse plants by crawling on the greenhouse structure, soil surface or the plastic covering between plants. 2SSM also "balloons" via silk or air movement. Migrating populations of both species have been considered as "wandering populations", and prey or host location has been assumed to be a matter of chance (Putman, 1962; Mori and Chant, 1966b; Rabbinge, 1976). However this hypothesis has been rejected by several researchers who demonstrate that phytoseiids can perceive kairomones produced by their spider mite prey in the process of prey
location (Hislop et al., 1978; Hoy and Smilanick, 1981; Sabelis and Van de Baan, 1983; Sabelis et al. 1984a, b; Sabelis and Dicke, 1985). Whether or not prey mites response to similar cues to find a new food source has not been studied. Therefore, it can be expected that when the predator and prey populations move far beyond food resources (emitters of chemicals), chances for successful food location must be very low and migrating populations die of starvation.

Extinction is not the only fate of mite populations suffering starvation in a greenhouse unless the situation is extremely detrimental to them. Generally, individual mites can survive for some time and females can even produce eggs during several days of food deprivation. Starved females are able to recover once a new food resource is available and subsequently can oviposit as effectively as they did before starvation (Sabelis, 1981; Blommers and van Arendonk, 1979). Weight loss is one of the common characters of starved mites. Sabelis (1981) reported that after egg deposition had ceased within a day (counted from the beginning of starvation), the weight of PPE females decreased steadily, but much more slowly and approached dry weight.

Temperature and relative humidity are two important survival factors. High temperature causes dehydration of mites and high humidity or the presence of water enables prolonged survival. Hamamura et al. (1978) found that when
food was depleted, PPE females died within a few days. At lower temperatures they survived longer periods of starvation, e.g. 5-10 days at 20°C to more than a month at 5-10°C. When water was available, PPE females lived 1-4 weeks instead of a few days (Mori and Chant, 1966a). In greenhouses, water spraying occurs frequently and it may be expected that mites are able to prolong life by drinking water.

Among predators, cannibalism may also provide means to survive under starvation. Dosse (1958) first reported cannibalism in PPE. The extent of cannibalism he reported was relatively high: 12 hours of food deprivation at T = 20°C induced cannibalism of eggs; longer periods led to feeding on larval and nymph stages. Cannibalism does not always persist from population to population; from my own observations, cannibalism never occurred even under extremely negative conditions including absence of food and water for 7 days.

Tetranychid food resources, as a mean of survival for the Phytoseiidae, have been investigated by many researchers. PPE seems to be a specialized predator of Tetranychidae and shows no tendency to reproduce on other types of food, such as pollen, honey etc. (McMurtry et al., 1970; Dosse, 1958; Chant, 1961a; Ashihara et al., 1978). Mori and Chant (1966b) found that the addition of nutritive substances such as sucrose, glucose pollen, honey and fish
meals of various kinds to the drinking water did not significantly increase longevity compared to the effect of drinking water alone. Ashihara et al. (1978) also found that PPE did not reproduce on honey or pollen (strawberry, castor and red pine), but mean adult longevity was increased to 45 days by nutritional substances such as fresh honey or a 10% sucrose solution, as compared to 12 days with only water available. However, Liang (1968) found that strawberry pollen did not promote longevity or development of PPE.

In a greenhouse mite and plant system, predator and prey populations are composed of many sub-populations which may be under different types of biotic and abiotic conditions ranging from the unfavorable to favorable (as discussed above). The population dynamics of the whole system depend on the integrated dynamics of all subpopulations. For a better understanding of population dynamics, therefore, the abnormal dynamics of a sub-population with an unfavorable condition should be considered as important as the normal dynamics of a sub-population with a favorable condition. In this chapter, I discuss the abnormal death processes and reproduction of PPE and 2SSM.
3.2 STOCHASTIC MODELS OF DEATH PROCESSES DURING STARVATION

3.2.1 Introduction

Without hosts for a period of time, a mite population will undergo an unusual death process (Sabelis, 1981) which is more dynamic and complex than the process of natural death. This unusual death process may occur within a migrating mite population during long-range dispersal, because food sources are seldom available for the mites when they are far away from their hosts, especially in a greenhouse. Study of death processes of populations during their migrations in acarine predator-prey systems has already shown the importance of understanding population interactions and spatial distributions (Nachman, 1987a, b; Pearl et al., 1989; Horn et al., 1991). Previous studies have shown that the death processes of a mite population during starvation is not only affected by the food assimilation and digestion efficiency of individuals but is also influenced by various environmental factors, especially temperature and relative humidity (references cited in Section 3.1).

In this section I focus on modeling the death processes of a mite population during starvation. First, I claim that the important property of a death process is not deterministic but stochastic, due to the combination of
demographic stochasticity of the population and environmental stochasticity surrounding it. Therefore, stochastic analysis is appropriate for the study of death processes. My procedure involved two steps: 1) estimating mean death rate of a population through nonlinear and linear regressions and 2) generating a Poisson death model which contains an estimated death rate by Monte-Carlo simulations.

3.2.2 Data collection

Four experiments were conducted to observe the occurrence of death in PPE and 2SSM populations under starvation. The data from these experiments can be used for estimating the death rate of a starved population. 

Experiment 1 Observations of death in a starved PPE female population

One hundred well-fed mated young PPE females (originally obtained from Koppert Ltd., Netherlands) were transferred to 10 Petri dishes, 10 mites per dish. A fresh Lima bean (*P. limensis* (L.) leaf (average area = 24cm²) was placed upper surface down on a piece of damp filter paper in each dish. A hole (radius = 1cm) was made on the bottom of the dish to allow air exchange through the paper. The dishes were closed to prevent escape of mites and maintained in a controlled environment chamber at: T=25°C, RH=75±15% and photophase D:L=12:12. Survivors were counted daily from
12 to 20 Feburary, 1990.

**Experiment 2**  Observations of death in a starved 2SSM female population

One hundred well-fed mated young 2SSM females were transferred from a laboratory culture to 10 empty Petri dishes, 10 mites per dish. Dishes were placed directly on a piece of damp filter paper on the dish bottom. Other procedures and experimental conditions were the same as those in Experiment 1. Survivors were counted daily from 2 to 11 April, 1990.

**Experiment 3**  Observations of death in a starved PPE male population

Twenty four well-fed young PPE males were taken from a culture and each put into 24 small empty vials (volume = 1.08 cm$^3$), closed with damp cotton. Vials were placed on a damp towel in a larger container and loosely closed to retain moisture. Temperature was maintained at 25±3°C, RH 75±15%. Survivors were counted daily from 20 to 26 April, 1990.

**Experiment 4**  Observations of death in a starved 2SSM male population

Forty well-fed young 2SSM males were transferred from a stock culture to 20 small empty vials (volume = 1.08 cm$^3$). Each vial contained 2 mites. Other procedures and experimental conditions were the same as those in Experiment 3. Survivors were counted daily from 12 to 20 April, 1990.
The survival data of the starved populations from experiments 1-4 were shown in Tables 4 and 5.
Table 4. Survivors of PPE and 2SSM adult females during starvation at T = 25°C, RH = 75±15% and L:D = 12:12 with 10 replications.

<table>
<thead>
<tr>
<th>Days of starvation</th>
<th>PPE females</th>
<th>2SSM females</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>SD (s\textsubscript{10})</td>
</tr>
<tr>
<td>0</td>
<td>10.0</td>
<td>.00</td>
</tr>
<tr>
<td>1</td>
<td>8.7</td>
<td>1.10</td>
</tr>
<tr>
<td>2</td>
<td>7.1</td>
<td>1.76</td>
</tr>
<tr>
<td>3</td>
<td>5.4</td>
<td>1.62</td>
</tr>
<tr>
<td>4</td>
<td>2.6</td>
<td>1.74</td>
</tr>
<tr>
<td>5</td>
<td>1.1</td>
<td>1.51</td>
</tr>
<tr>
<td>6</td>
<td>.7</td>
<td>1.00</td>
</tr>
<tr>
<td>7</td>
<td>.2</td>
<td>.40</td>
</tr>
<tr>
<td>8</td>
<td>.0</td>
<td>.00</td>
</tr>
</tbody>
</table>
Table 5. Survivors of PPE and 2SSM adult males during starvation at $T = 25^\circ C$, RH = 75±15% and L:D = 12:12 with no replications.

<table>
<thead>
<tr>
<th>Days of starvation</th>
<th>PPE males Survivors</th>
<th>2SSM males Survivors</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>24</td>
<td>40</td>
</tr>
<tr>
<td>1</td>
<td>21</td>
<td>37</td>
</tr>
<tr>
<td>2</td>
<td>16</td>
<td>32</td>
</tr>
<tr>
<td>3</td>
<td>12</td>
<td>26</td>
</tr>
<tr>
<td>4</td>
<td>9</td>
<td>18</td>
</tr>
<tr>
<td>5</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>6</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>7</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>
3.2.3 Estimation of mean death rate of a population

To simulate a death process of a starved population, first we need to estimate the population mean death rate which can be derived from a survivorship function $S(t)$. A logistic model was used to simulate $S(t)$ for PPE females and both sexes of 2SSM. The model has the general form of the following equation:

$$\frac{dS(t)}{dt} = rS(t)(1 - S(t)/S_m)$$

$$S(0) = S_0$$

(3.1)

where $r$ ($r < 0$) is the decreasing rate of survivorship, $S_m$ ($S_m = 1$) is the maximum survivorship, and $S_0$ is the initial survivorship of the population (for mathematical convenience, we assume that $S_0$ is less than 1, but it can be very close to 1).

Equation (3.1) has an analytic solution, such that

$$S(t) = \frac{\exp(b_0 + b_1 t)}{1 + \exp(b_0 + b_1 t)}$$

(3.2)

where $b_0 = \ln \frac{S_0}{1 - S_0}$, $b_1 = r$, and $t$ is time.
Based on the above discussion, we know that $b_0$ is a quantity which expresses the ratio of the initial number of survivors and deaths, and $b_1$ is the decreasing rate of survivorship of the population under starvation. Therefore, we can define $b_0$ as a gut content coefficient; and $b_1$ as food digestion rate of the population.

From equation (3.2), the mean number of deaths at $t$ can be written as

$$D(t) = \frac{n}{1 + \exp(b_0 + b_1 t)} \tag{3.3}$$

where $n$ is the initial size of the population. Therefore, the mean death rate is

$$\frac{dD(t)}{dt} = \frac{-n b_1 \exp(b_0 + b_1 t)}{[1 + \exp(b_0 + b_1 t)]^2} \tag{3.4}$$

In addition to a logistic model (3.2), a linear model was also used for the survivorship of PPE males, since the data showed a close linear relationship between survivorship and time. In the linear model, death rate was estimated as a constant. In the nonlinear regressions, parameters $b_0$ and $b_1$ were estimated by a modified Gauss-Newton algorithm to ensure convergence (Table 6).
Table 6. Estimations of gut content coefficient \( (b_o) \), food digestion rate \( (b_1) \) and mean death rate \( (D'(t)) \) of both sexes of PPE and 2SSM by regressions based on data shown in Tables 4 and 5. All rates are measured per mite per hour.

<table>
<thead>
<tr>
<th>Species</th>
<th>Sex</th>
<th>( b_o )</th>
<th>( b_1 )</th>
<th>( D'(t) )</th>
</tr>
</thead>
<tbody>
<tr>
<td>PPE</td>
<td>F</td>
<td>2.94</td>
<td>-0.043</td>
<td>( 0.43 \exp(2.94 - 0.043t) ) [1 + \exp(2.94 - 0.043t) ]^2</td>
</tr>
<tr>
<td></td>
<td>M</td>
<td>-</td>
<td>-</td>
<td>0.18</td>
</tr>
<tr>
<td>2SSM</td>
<td>F</td>
<td>3.96</td>
<td>-0.053</td>
<td>( 0.53 \exp(3.96 - 0.053t) ) [1 + \exp(3.96 - 0.053t) ]^2</td>
</tr>
<tr>
<td></td>
<td>M</td>
<td>4.70</td>
<td>-0.054</td>
<td>( 2.16 \exp(4.70 - 0.054t) ) [1 + \exp(4.70 - 0.054t) ]^2</td>
</tr>
</tbody>
</table>
3.2.4 Poisson death process

A death process can be modelled as a Poisson process since the number of deaths occurring during a time interval \((t, t+dt]\) is a binomial random variable with a parameter of mean death rate \(x\ dt\) (Chesson, 1978), and when \(dt\) is small, the binomial approximates to a Poisson with mean death rate \(x\ dt\) (Nachman, 1987a). The probability of \(i\) individuals dying during interval \((t, t + dt]\) is thus obtained as

\[
p_t(i) = (\text{mean death rate} \times dt)^i \times \exp(- \text{mean death rate} \times dt) / i!
\]

(3.5)

The actual number of deaths occurring during \((t, t + dt]\) is denoted \(I\). It can be derived by Monte-Carlo simulations as the smallest integer value of \(I\) that satisfies the condition

\[
\sum_{i=0}^{1} p_t(i) \geq R
\]

(3.6)

where \(R\) is a random number between 0 and 1 (drawn by the computer from a uniform distribution).

In all simulations, \(dt\) is chosen as .1 hour; thus the death events are tracked every .1 hour.
Fig. 7. Logistic and linear regressions for the survivorships of PPE during a period of starvation. Simulation: solid circles with dotted lines for females and a solid line for males; experimental data: open circles with solid lines for females and open circles for males.
Survivorship of PPE females

Survivorship of PPE males

S(t) = 1.017 - .18 t
R = 99.2%

Fig. 7.
Fig. 8. Logistic regressions for the survivorships of 2SSM during a period of starvation. Simulation: solid circles with dotted lines; experimental data: open circles with solid lines.
Fig. 8.
Fig. 9. Sample output from 10 simulations with comparison of the experimental data (from experiments 1 and 3 of this chapter). Data are mean survivors of each PPE population during starvation; bars are ± SD. Simulation: solid circles; experimental data: open circles.
Fig. 9.
Fig. 10. Sample output from 10 simulations with comparison of the experimental data (from experiments 2 and 4 of this chapter). Data are mean survivors of each 2SSM population during starvation; bars are ± SD. Simulation: solid circles; experimental data: open circles.
Fig. 10.
3.2.5 Results

The nonlinear and linear regressions are shown in Figs. 7 and 8. The sum of square errors (SSEs) are .011, .025 and .076 for the data of PPE females, 2SSM females and males respectively. Estimated gut content coefficients, food digestion rates and mean death rates of both species and sexes are given in Table 6. Sample output of 10 simulations of the Poisson death processes for both species and sexes were obtained and shown with comparisons to experimental data in Figs. 9 and 10.

3.2.6 Discussion

The results of nonlinear regressions show that the PPE female has a lower gut content coefficient and food digestion rate than her female prey, and the 2SSM female has lower values of these two parameters than the 2SSM male. (From my observations, 2SSM females are able to produce eggs for a few days after starvation, which may explain why females have lower values of gut content coefficients than males, because this reproduction was not considered when we estimated parameters.) Equation (3.4) shows that the mean death rates are not only related to gut content and food digestion rate but also to the initial size of the population. This is not surprising, because the mean death
rate is measured for a particular population through a survivorship function (in which the initial population size is involved).

Monte-Carlo simulations show that the stochastic model behaves in a way that coincides with our experimental data. We describe death processes by a sequence of death rates which are influenced by the combination of demographic and environmental stochasticity, i.e. randomized gut content, food digestion rate, temperature and relative humidity.

Use of stochastic processes to model animal demographic events is uncommon, and the application of a stochastic model to mite death processes during starvation is a novel approach. It provides a valuable tool for further study of arthropod predator-prey interactions, especially in the investigation of migration and spatial distribution of mite populations.

3.3 GUT CONTENT OF Phytoseiulus persimilis

3.3.1 Introduction

The food content of the gut and the food digestion rate may be the main indicators for describing the death processes of a starving population. In section 3.2 I used an indirect method to investigate the abnormal death processes of PPE and 2SSM populations based on a logistic
negative growth model of survivorship in a population suffering starvation. In that case, two coefficients, initial gut content and food digestion rate reflect real biological values to a limited extent. Mite gut content and food digestion processes have been well documented by many researchers. Mitchell (1973) reported weight increase of an initially hungry predator (2 day starvation at $T = 20^\circ C$) before feeding and after feeding until satiation on a certain prey stage. This weight increase was an approximation of the maximum gut content of the predator feeding on that particular prey stage. In other experiments ingestion (inverse of digestion) was measured in relation to feeding time by measuring predator weight before feeding and after a predetermined feeding interval. A more precise method (Fransz, 1974) used $^{32}$P-labeled prey, in which the spider mites were labeled by feeding for 12 hours on a bean leaf treated previously with a $^{32}$P solution (1mCi) for a day. Radioactive eggs were obtained from radioactive females. The labeled prey was offered to an unlabeled female predator, being starved for 2 days at $T = 20^\circ C$. The changes of ingestion can be tested through $^{32}$P in the gut of predator (here it assumed the amount of radioactivity in the predator was proportional to its food content). Sabelis (1981) developed a ingestion model of predator as follows:

$$I_f = (1 - \exp(-rrfi*ft)) \times \min(sdg, fcp)$$  
(3.7)
where $ft$ = feeding time, $I$ = ingested food, $if$ = ingestable food content of the prey per predator, $rrfi$ = relative rate of food ingestion, $sdg$ = satiation deficit of the gut, and $fcp$ = ingestable food content of the prey. The model shows that the amount of food consumed is determined by either the available space in the gut or the food content of the prey, depending on which one is less. Sabelis (1981) also carried out a detailed experiment to measure the rate of gut emptying at three different temperatures; the amount of food required to satiate the predator after different periods of starvation was weighed. His results showed that the gut is emptied in an exponential fashion.

The goal of my research in this section was to provide some useful information on maximum gut content and food digestion rate for further understanding of the mechanism of abnormal death processes of predator populations in a harsh habitat.

3.3.2 Materials and methods

Experiments were conducted from April 24 to June 16, 1990 with the following procedures:

Prey egg preparation

One or two young 2SSM adult females were transferred to an experimental habitat — a portion of fresh lima bean ($P. \text{ limensis}$ (L.)) leaf, its under surface is upward and placed
atop damp cotton in a plastic container. Four holes (radius = .05cm) were made on the top of the container to allow air exchange and avoid excessive moisture on the leaf surface that could have negative effect on egg production of 2SSM. The experimental habitat was set up in an environment chamber with controlled temperature at 25°C. Within 24 hours, mites were expected to lay about 10 to 15 eggs grouped in a small patch with expanded webbing structure, simulating the microhabitat on the leaf surface. As soon as the mites laid more than 10 eggs, adult females were removed from the container. I then counted the eggs and put the egg mass into a refrigerator at T = 4°C to slow down further development of eggs.

**Food deprivation of adult predator**

Young PPE adult females and adult males were randomly taken from a laboratory culture and confined in small vials which contained only fresh lima bean leaf portions and were closed with damp cotton. With this design a water drop could be condensed on the inside surface of vials (volume = 1.08 cm³) and maintained continuously for about 2 days at T = 25°C in the chamber. Both females and males were deprived of food for different periods: 2, 4, 8, 16, 36 and 48 hours.
Fig. 11. Weight increase (before and after three-hour feeding) of a PPE adult and number of 2SSM eggs consumed (during three-hour feeding) by a PPE adult after differing starvation periods; bars are ± SD. Weight increase: solid circles with solid lines; eggs eaten: open circles with dashed lines.
Fig. 11.
Procedure

After completion of starvation treatments, mites were weighed individually on an automatic "CHAN 25" electrobalance, and released on the previously prepared 2SSM egg masses, with a single PPE to each egg mass. The number of prey eggs consumed by a single predator was counted at various time periods: 0.5, 1.0, 1.5, 2.0 and 3.0 hours. After 3 hours' feeding, the satiated PPE were re-weighed. In a few cases, a PPE female laid an egg during feeding; then both the mite and egg were weighed together.

3.3.3 Results and discussion

Changes of weight increase (before and after three-hour feeding) of a predator and changes of number of prey eggs consumed by a single predator after differing starvation periods are shown in Fig. 11. These results indicate that weight increases of PPE females are an exponential function of starvation period (at least for the initial period), in agreement with Sabelis' (1981) results. Mean of eggs eaten by a single PPE female corresponds to her weight increase except in two groups starved for 16 and 36 hours. In these two groups that mean was much lower than expected, and implies the added weight is partly due to water consumption. Fig. 11 also shows no close relationship between mean male weight increase and starvation period (water consumption
observed). This suggests that ingestion and digestion by males may be independent of the starvation period. The relationship between weight increases of PPE females and starvation period is useful for study of 'gut-filling' and 'gut-decaying' processes which were previously incorporated into Pearl's model (Horn et al., 1991, unpublished).

3.4 REPRODUCTION OF *Phytoseiulus persimilis* and *Tetranychus urticae* DURING STARVATION

3.4.1 Introduction

Reproduction is one of the most important components of mite population dynamics. Under normal conditions, the rates of food ingestion of predator and prey females increase drastically soon after mating. Sabelis (1981) and Sabelis and Dicke (1985) reported total egg biomass that can be produced by a PPE female per day is equivalent to the biomass of the female herself: at 30°C a young female produced 5 eggs of 4.5 g each per day, equaling her live weight. Eveleigh and Chant (1981) found that PPE needed at least 5 prey protonymphs per day for basic maintenance and an additional 6 prey protonymphs per day for each egg produced. These studies show the importance of food to the reproductive biology of females. In this section I discuss how reproductive ability is affected by starvation.
3.4.2 Materials and methods

The following experiments were conducted from April 12 to 27, 1990. Young mated females of both species were randomly chosen from laboratory cultures. Materials and procedures are as described in Subsection 3.2.3; with T=25°C, 75 ± 15%RH and photophase D:L = 12:12.

3.4.3 Results and discussion

Results of reproduction of both species during a period of starvation are shown in Table 7. The reproduction dynamics of PPE was taking place much faster than that of the 2SSM. (Reproduction ended one day earlier than that of the prey) Reproductive activity of both predator and prey was described by Sabelis and Dicke (1985). They pointed out that the weight of PPE females is approximately equal to that of 2SSM females (ca. 22 g), but this predator produces eggs that weigh 4.5 times more than those of 2SSM (ca. 1 g). Thus it appears that PPE females invest relatively more biomass in producing large eggs than in producing a large number of eggs. My calculations based on data shown in Table 7 (assume the weight of a 2SSM egg is 1 g) show the average total egg biomass produced by a single PPE female after food deprivation is 1.04 g which is much lower than that (6.01 g) produced by 2SSM.
Table 7. Mean number of eggs laid by single PPE and 2SSM females after differing starvation periods. T=25°C, RH=75 ± 15% and photophase D:L=12:12.

<table>
<thead>
<tr>
<th>Days of starvation</th>
<th>PPE mean</th>
<th>PPE variance</th>
<th>n</th>
<th>2SSM mean</th>
<th>2SSM variance</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>0 - 1/6</td>
<td>.565</td>
<td>.648</td>
<td>23</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>1/6 - 1</td>
<td>.478</td>
<td>.651</td>
<td>23</td>
<td>4.56³</td>
<td>1.878</td>
<td>20</td>
</tr>
<tr>
<td>1 - 2</td>
<td>0</td>
<td>0</td>
<td>23</td>
<td>1.15</td>
<td>1.062</td>
<td>20</td>
</tr>
<tr>
<td>2 - 3</td>
<td>0</td>
<td>0</td>
<td>23</td>
<td>.3</td>
<td>.781</td>
<td>20</td>
</tr>
<tr>
<td>3 - 4</td>
<td>0</td>
<td>0</td>
<td>23</td>
<td>0</td>
<td>0</td>
<td>20</td>
</tr>
</tbody>
</table>

³Eggs laid by a prey female during the time period: 0-1 day.
Thurling (1980) found that PPE eggs had higher metabolic rates than 2SSM eggs and suggested that this probably reflects the shorter incubation period of predator eggs, which may result from eggs' being laid in a more advanced stage of development than those of the prey (or maybe they simply develop faster). This implies that more energy is needed for ovigensis by predator females than by prey females. Therefore, as food supply is cut off, the reproductive activity will end more quickly for PPE females.
CHAPTER IV
PRELIMINARY STUDY FOR EXTENSION OF A STOCHASTIC
MODEL FROM LABORATORY LIMA BEANS TO
COMMERCIAL GREENHOUSE CUCUMBERS

4.1 INTRODUCTION

In Chapter 2, I discussed validation of Pearl's stochastic model (Pearl et al., 1989; Horn et al., 1991; Horn et al., 1991, unpublished) on Lima bean (P. limensis L.) plants. With subsequent refinements, the model now contains re-estimated parameters and newly identified starvation processes. The model now fits well to our data of predator and prey populations on a row of four Lima bean plants. Since the goal of this simulation model is to develop an optimal pest management system for commercial production of greenhouse cucumber (Cucumis sativus L.), I conducted several comparative experiments on Lima beans and cucumbers to determine values of some important parameters for a cucumber model based on known parameters in the Lima bean model. As pointed out previously, maturation and reproduction parameters of both mite species and predation parameters of the predatory mite are among the most
important concerns.

4.2 MATURATION AND REPRODUCTION PARAMETERS OF THE PREY, *Tetranychus urticae*, FEEDING ON LIMA BEANS AND CUCUMBERS

4.2.1 Introduction

Effects of different host plants on development and reproduction of the 2SSM have been investigated for many years. It is evident that the suitability of plants for settling and food of the 2SSM varies between and within plant taxa. Crooker (1985) pointed out that differences in development, reproduction, longevity and population development of mites on different plants are common. These differences may be associated with impediments to feeding such as plant texture and vestiture, nutritional value of the plant, host physiology, or the favorability of the micro-environment. Numerous reports demonstrate the effects of host plants on the developmental time of immature mites and egg laying rates for several tetranychid species (Puttaswamy, 1980, 1981; Van de Vrie et al., 1972; Jeppson et al., 1975). The "life types" (physical structure of a mite colony on a leaf of its host) of spider mites was intensively investigated from the aspect of their webbing systems which range from simple to complex (Saito, 1983).
The life type of spider mites is closely related to the host type, and the pattern of webbing is largely determined by morphological features of a host plant (Saito, 1985). In addition, the energy allocated to web production influences the oviposition rate, as was suggested by Gerson and Aronowitz (1981). Through observations of surfaces of Lima bean and cucumber leaves, I found that trichomes of cucumber leaves are much denser than those of Lima beans. Also, Lima beans and cucumbers differ chemically. For that reason I conducted a comparative study for examining the differences between the maturation and reproduction parameters of 2SSM in the model.

4.2.2 Materials and methods

Reproduction experiments

Several small scale experiments were conducted from Nov. 5 to 20, 1991. Leaf discs (radius=1.4cm) were randomly taken from 3-week old Lima bean and cucumber plants, and placed upper surface down on damp cotton. A 2SSM adult female selected at random from a stock culture (cucumber or Lima bean) was introduced onto each disc (cucumber or Lima bean) and placed in an environmental chamber programmed 12:12 photophase. Temperature was maintained at either 25°C or 30°C (in separate experiments) and relative humidity kept at 85±15%.
On leaf discs, 2SSM adult females were allowed to lay eggs for 3 days and eggs on each disc were then counted.

Development experiments

Experiments were conducted from Nov. 21 to Dec. 2, 1991. The same procedure was used to prepare leaf discs as that in reproduction experiments above, as was temperature, lighting and humidity. One 2SSM adult female from a stock culture (cucumber or Lima bean) was placed on each leaf disc (cucumber or Lima bean). Females were removed after 1-day oviposition, and mite development was then observed at 12-hour intervals until all individuals had completed development.

4.2.3 Results and discussion

The oviposition rates of the 2SSM feeding on Lima bean and cucumber leaf discs are shown in Table 8. Oviposition rates of females feeding on cucumber leaf discs were much lower than those on Lima bean discs (t-test, P-value < .0001 in both cases). I also found the average distance between eggs laid on cucumber discs are much greater than that on Lima beans although large variations existed. Applying Saito's theory of "life types" (Saito, 1983, 1985), I observed a complicated webbing (CWu) system on cucumber leaf discs, and a little webbing (LWc) system on Lima bean. These observations indicated that the morphological
<table>
<thead>
<tr>
<th>n</th>
<th>Host plant</th>
<th>Temperature (°C)</th>
<th>Oviposition rate (X)</th>
<th>variance $s_n^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>26</td>
<td>Lima bean</td>
<td>25</td>
<td>9.63</td>
<td>3.76</td>
</tr>
<tr>
<td>31</td>
<td>Lima bean</td>
<td>30</td>
<td>15.45</td>
<td>3.96</td>
</tr>
<tr>
<td>29</td>
<td>cucumber</td>
<td>25</td>
<td>7.78</td>
<td>2.77</td>
</tr>
<tr>
<td>27</td>
<td>cucumber</td>
<td>30</td>
<td>11.11</td>
<td>2.39</td>
</tr>
</tbody>
</table>

All differences in oviposition rate are significant.
characters of cucumber leaf may influence the rate of oviposition. In addition to this, the chemical constituents of the leaf cells probably also play a major role in influencing the oviposition rate (Breukel and Post, 1959; Van de Vrie et al., 1972).

The maturation time of 2SSM eggs, nymphs and both sexes of adults feeding on both host plant leaf discs at 25°C and 30°C is shown in Tables 9 and 10. The maturation time of each stage on each host plant is shorter consistently at 30°C than 25°C. The maturation times at both temperatures are shorter on Lima bean than that on cucumber (t-test, P-value is small) except for maturation time of male nymphs at 25°C (t-test, P-value is large). This result suggests that the estimated maturation and reproduction parameters in the Lima bean model need to be increased somewhat for a cucumber model. Under similar ambient conditions, slower population dynamics of 2SSM would be expected in a cucumber system. The result also shows relatively small variances in maturation time, caused by a large interval between two observations (12 hours).

Mite development was not observed individually in these experiments, and egg maturation time was not recorded for each individual, but a mean maturation time was calculated for a group of eggs on a leaf disc. Furthermore, the maturation time of nymphs on the disc was determined
Table 9. Maturation time of 2SSM feeding on 2 different leaf discs at temperature T = 25°C, L:D = 12:12 and RH = 80±15%.

<table>
<thead>
<tr>
<th>n</th>
<th>Stage</th>
<th>Host plant</th>
<th>Number of days</th>
<th>Variance s²n²</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Max.</td>
<td>Min.</td>
</tr>
<tr>
<td>187</td>
<td>eggs</td>
<td>Lima bean</td>
<td>5</td>
<td>2.71</td>
</tr>
<tr>
<td>147</td>
<td></td>
<td>cucumber</td>
<td>5</td>
<td>2.71</td>
</tr>
<tr>
<td>41</td>
<td>nymphs(m)</td>
<td>Lima bean</td>
<td>5.18</td>
<td>3.21</td>
</tr>
<tr>
<td>31</td>
<td></td>
<td>cucumber</td>
<td>5.25</td>
<td>3.06</td>
</tr>
<tr>
<td>138</td>
<td>nymphs(f)</td>
<td>Lima bean</td>
<td>6.22</td>
<td>4.43</td>
</tr>
<tr>
<td>108</td>
<td></td>
<td>cucumber</td>
<td>6.21</td>
<td>4.5</td>
</tr>
</tbody>
</table>

All differences in maturation time are significant except that of male nymphs.
Table 10. Maturation time of 2SSM feeding on 2 different leaf discs at temperature $T = 30^\circ C$, $L:D = 12:12$ and $RH = 80\pm 15\%$.

<table>
<thead>
<tr>
<th>n</th>
<th>Stage</th>
<th>Host plant</th>
<th>Number of days Max.</th>
<th>Min.</th>
<th>Mean</th>
<th>Variance $s^2_n$</th>
</tr>
</thead>
<tbody>
<tr>
<td>190</td>
<td>eggs</td>
<td>Lima bean</td>
<td>3</td>
<td>2</td>
<td>2.42</td>
<td>.12</td>
</tr>
<tr>
<td>126</td>
<td>eggs</td>
<td>cucumber</td>
<td>4</td>
<td>2</td>
<td>2.62</td>
<td>.13</td>
</tr>
<tr>
<td>48</td>
<td>nymphs(m)</td>
<td>Lima bean</td>
<td>4</td>
<td>2.4</td>
<td>3.04</td>
<td>.32</td>
</tr>
<tr>
<td>26</td>
<td>nymphs(m)</td>
<td>cucumber</td>
<td>4.71</td>
<td>2.94</td>
<td>3.41</td>
<td>.36</td>
</tr>
<tr>
<td>115</td>
<td>nymphs(f)</td>
<td>Lima bean</td>
<td>4.82</td>
<td>2.86</td>
<td>3.57</td>
<td>.46</td>
</tr>
<tr>
<td>85</td>
<td>nymphs(f)</td>
<td>cucumber</td>
<td>5.5</td>
<td>3.12</td>
<td>4.45</td>
<td>.54</td>
</tr>
</tbody>
</table>

All differences in maturation time are significant.
individually based on the mean maturation time of eggs. Thus, the experimental design and data handling may have introduced measurement errors into the results. However, with this design, a webbing structure and associated "life types" of spider mites could be observed on each leaf disc, which was more realistic than having a single mite live alone on each leaf disc.

4.3 PREDATION, MATURATION AND REPRODUCTION PARAMETERS OF THE PREDATOR, Phytoseiulus persimilis ON LIMA BEANS AND CUCUMBERS

4.3.1 Introduction

PPE, 2SSM and its host plant form a three trophic level food pyramid in which PPE is on the top. Even though PPE is thus trophically distant, I thought the morphological characters and nutritional value of the host plant might affect the predator function, reproduction and maturation. Therefore in this section I discuss predation and oviposition rates of PPE females feeding on 2SSM eggs on Lima and cucumber leaves, and I also report another comparative study for detecting differences between maturation parameters in Lima bean and cucumber models. I anticipate that these efforts will help development of a cucumber model.
4.3.2 Materials and methods

**Predation and reproduction experiment**

Laboratory cultures of PPE used in this experiment was originally obtained from Koppert Ltd., The Netherlands.

Twenty-five freshly laid 2SSM eggs (from mothers previously fed on Lima bean and cucumber leaves respectively) were placed on each Lima bean and cucumber leaf disc (radius=1.4cm) to serve as food for the predators. All leaf discs were placed upper surface down on damp cotton. A PPE adult female taken at random from the culture (with Lima bean or cucumber) was allowed to feed on 2SSM eggs for three days on each leaf disc (Lima bean or cucumber), and all discs were then kept in an environment chamber with controlled temperature \( T = 25^\circ C, \quad RH = 80\pm15\% \) and \( L:D = 12:12 \).

Each disc was observed daily. The number of 2SSM eggs eaten was recorded for each individual PPE female and a fresh supply of 25 eggs was provided for each PPE female daily while the old eggs were removed. Discs containing PPE adult females were observed daily for egg laying and prey consumption for three days.

**Development experiments**

Experiments were conducted from Jan. 2 to 25, 1992. Leaf discs (radius=1.4cm) of 3-week old Lima bean and cucumber were placed upper surface down on damp cotton. A
2SSM colony (from Lima bean or cucumber) was placed on each disc (Lima bean or cucumber) to serve as food for the predators. PPE adult females taken at random from a culture (Lima bean or cucumber) were introduced onto discs and allowed to oviposit on those discs (all eggs were laid during a 6-hour period). The discs were then kept in an environment chamber in which the temperature was controlled at 25°C, RH = 80±15% and L:D = 12:12.

The maturation time of PPE eggs, adults of both sexes for each disc was recorded at 12-hour intervals until the predators had completed development.

4.3.3 Results and discussion

The number of 2SSM eggs consumed and eggs laid by a PPE female daily are dependent on whether she is in her pre-ovipositional period, is ovipositing, or has ceased to oviposit. Since we do not classify different stages of PPE adult females in Pearl's stochastic model, the predation and reproduction parameters obtained here only represent average rates. In controlled laboratory conditions: at temperature varying from 15°C to 28°C, RH=80±15% and L:D=15.5:8.5, Liang (1968) found that ovipositing PPE females ate an average of 14.3 2SSM eggs per day; during the pre-ovipositional and post-ovipositional periods they consumed only 1/2 and 1/3 of that respectively.
Sixteen mated PPE adult females consumed an average of 15.31 2SSM eggs on Lima bean leaf discs and 13.88 eggs on cucumber leaf discs, with a standard deviation 2.56 and 2.74 respectively (Table 11). The oviposition rates of these females are also shown in Table 11. T-tests showed that there was no significant difference in the predation (0.5 < P-value < 0.1) and oviposition rates (P-value is large) between the PPE on Lima beans and the PPE on cucumbers. Results of this comparative study suggest that PPE predation and reproduction parameters in the Lima bean model may not need to be changed for a cucumber model. There was no indication that the observed morphological differences between Lima bean and cucumber leaves could affect these two parameters.
Table 11. Predation and oviposition rates of PPE adult females feeding on 2SSM eggs at T = 25°C, L:D = 12:12 and RH = 80±15%.

<table>
<thead>
<tr>
<th>Host plant</th>
<th>Predation rate (/day)</th>
<th>Standard deviation</th>
<th>Oviposition rate (/day)</th>
<th>Standard deviation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lima bean</td>
<td>15.31</td>
<td>2.18</td>
<td>2.20</td>
<td>0.97</td>
</tr>
<tr>
<td>Cucumber</td>
<td>13.87</td>
<td>2.52</td>
<td>2.36</td>
<td>1.15</td>
</tr>
</tbody>
</table>
Table 12. Maturation time of PPE feeding on 2SSM at $T = 25^\circ C$, $L:D = 12:12$ and $RH = 80\pm 15\%$.

<table>
<thead>
<tr>
<th>PPE stage &amp; sex</th>
<th>n</th>
<th>Host plant</th>
<th>Number of days</th>
<th>Standard deviation</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Min.</td>
<td>Max.</td>
</tr>
<tr>
<td>Eggs</td>
<td>36</td>
<td>Lima bean</td>
<td>2.13</td>
<td>2.63</td>
</tr>
<tr>
<td></td>
<td>35</td>
<td>Cucumber</td>
<td>1.88</td>
<td>3.63</td>
</tr>
<tr>
<td>Adults (M)</td>
<td>14</td>
<td>Lima bean</td>
<td>5.13</td>
<td>5.63</td>
</tr>
<tr>
<td></td>
<td>13</td>
<td>Cucumber</td>
<td>4.63</td>
<td>5.88</td>
</tr>
<tr>
<td>Adults (F)</td>
<td>22</td>
<td>Lima bean</td>
<td>4.63</td>
<td>5.63</td>
</tr>
<tr>
<td></td>
<td>22</td>
<td>Cucumber</td>
<td>5.13</td>
<td>6.38</td>
</tr>
</tbody>
</table>
The average maturation time of incubation for the PPE eggs was 2.40±0.25 days on Lima beans and 2.42±0.32 days on cucumbers; the average maturation time of the PPE adults (male) was 5.23±0.21 days on Lima beans and 5.28±0.44 days on cucumbers; the average maturation time of the PPE adults (female) was 5.44±0.34 days on Lima beans and 5.55±0.31 days on cucumbers respectively (Table 12).

Applying t-tests, I found that there was no significant difference between the maturation times of the PPE feeding on the 2SSM on Lima beans and cucumbers. The results of this comparative study suggest that all the maturation parameters in the Lima bean model are adaptable to a cucumber model.

Ragusa (1965) found developmental time for PPE females from egg through the pre-ovipositional period to vary from five to 12 days at a temperature oscillating between 25 and 28°C. Dosse (1985) reported a maturation time from egg to maturity of 11.9 days for PPE at a temperature range of 10 to 25°C. Liang (1968) found a developmental time of 7.5 days at a temperature range of 15 to 28°C. The corresponding periods for PPE adults in this study varied from 5.23 to 5.55 days under a constant temperature of 25°C. This is considerably shorter than the above findings because of the effect of temperature. Dosse (1958) also reported the developmental time for PPE to be 4.5 days at a constant temperature of 25°C. Thus, the developmental time
in my experiments is close to Dosse's finding.

In conclusion, the result of this chapter shows that the maturation and reproduction parameters of 2SSM should be reduced for a cucumber model compared to the parameters in the Lima bean model. Populations of 2SSM grow more slowly on cucumbers than on Lima beans. However, the population dynamics of PPE is not directly affected by these two host plants; in other words, the predation, maturation and reproduction parameters of the predator in the Lima bean model can be used for a cucumber model.
CHAPTER V
AN ALTERNATIVE APPROACH TO MODELING AND
OPTIMALITY OF SPIDER MITE MANAGEMENT

5.1 INTRODUCTION

As discussed in Chapter 1, because of the economical importance of spider mite management, there have been many efforts to establish mathematical models for spider mite systems during the last two decades. The models which have been most widely used in spider mite management are based on simulation techniques (Rabbinge and Hoy, 1980; Shaw, 1984; Sabelis et al., 1988; Nachman, 1987a, b, 1988; Pearl et al., 1989; Horn et al., 1991). Because of the advances of modern computer science and computational techniques, simulations are very useful in describing dynamics of agricultural ecosystems. In addressing management questions, however, simulation models may have some disadvantages, since the outcomes of a range of potential management strategies must be specified for comparison where the simulation model is calculated. It is usually costly to find an optimal strategy from many alternatives by simulation alone (Shoemaker and Onstad, 1983). The main function of a
simulation model is to describe the interaction of components within a system, while the purpose of a control model is to find the best way (by applying systems theory) to manage the system.

In an attempt to optimize pest management, Watt (1964) first developed a simulation model to find the best policy to control a pest population. A more theoretical approach called dynamic programming (Bellman and Kalaba, 1960; Bellman, 1967; 1975) with its applications in agricultural pest management has been discussed by Shoemaker (1973b, c). And Havelka and Kindlmann (1984) developed a deterministic control model to estimate optimal release of predator and prey to control the 2SSM on greenhouse cucumbers; this was a preliminary step to optimal mite management for a complex mite/cucumber system. Uncertainty and complexity of the spider mite/plant ecosystem are extremely challenging to modelers and management decision makers, even under greenhouse conditions. A large number of biological, physiological, and behavioral uncertainties are involved, and a stochastic environment affects the degree of management policy. In order to seek a workable solution to the problem, artificial assumptions (even though most retain reality with their simplicity) are frequently used in current modeling and optimization research. So far, the full, accurate, detailed description of a real ecosystem is restricted by lack of knowledge.
As an alternative approach, the notion of a fuzzy control system, introduced by Zadeh (1975), presented a very attractive alternative tool for handling and modeling the nonprobabilistic form of uncertainty (Gupta et al., 1977; Dubois and Prade, 1980; Pedrycz, 1983, 1984). Fuzzy systems analysis emphasizes the relationship between input and output of a system which is considered a black box, i.e. the internal structure and interaction of the components within the system are ignored because of uncertainty. Further, in a fuzzy control model, verbal expressions are used to describe the dynamics of the controlled state variables (assuming they can be observed from output); the states and inputs are measured by certain grades (ranged from low to high, for example) instead of numbers. It is clear that the verbal grades such as low and high are fuzzy concepts, so they are defined as fuzzy sets in fuzzy analysis. A fuzzy set has no meaning unless it has certain relation with real numbers. This relation is usually called a membership function (Zadeh, 1975; 1978) which can be determined by different ways. One of the reliable methods to evaluate a membership function of a fuzzy set is called "expert meeting". For example, by this way we can determine a membership function of fuzzy set "young man" which is related to a possible human age (ranged from 0 to 100 years old), since the membership of age X years old lies between 0 and 100 is the proportion of votes from those experts being
in favour of "age X is young". A membership function is also a possibility distribution of a fuzzy set. It should be noted that the possibility distribution does not always have a property of "sum into unit" like the probability distribution does. In this chapter I introduce fuzzy modeling and optimality of spider mite control on a single cucumber plant system.

5.2  A FUZZY BIOLOGICAL CONTROL MODEL OF *Tetranychus urticae*

5.2.1 Introduction

Fuzzy control models have been widely used in industrial control systems. However, this may be the first attempt to develop such models for a agricultural pest control system. In this section I introduce a linguistic model for a spider mite control system. An experiment was conducted on cucumber plants in a greenhouse, in which ten 2SSM adult females were first introduced on each cucumber plant and the population controlled by manipulating PPE. In this fuzzy control model, mite population densities are conceptually expressed as low, medium-, medium+ and high, and the quantity of control is expressed as negative, zero and positive (remove predator, do nothing and release predator). Construction of a fuzzy control model is based on the input and output data of the system. Two kinds of fuzzy logic:
"max-min" and "max-prod" compositions are used to identify the linguistic relations between the input and output. The spider mite control system can be described by a group of sentences: \{if \ldots \text{then} \ldots\}, instead of mathematical equations. I also conducted sensitivity analysis for the proposed model to determine its robustness to changes of the membership functions (relative to state and control variables).

5.2.2 Materials and methods

Data collection

Cucumbers (\textit{C. sativus} L.) were planted 10 Aug., 1989 in a 120 m\textsuperscript{2} greenhouse compartment. The temperature was controlled at 25\textdegree{} to 30\textdegree{}C and relative humidity at 70 \pm 10\%. 2SSM and PPE adults were censused and manipulated on each of six plants chosen from among eighty plants. On 27 Aug., 1989, ten 2SSM adult females selected randomly from a laboratory culture were placed on the 8th leaf (from the base) of each plant, which averaged twelve leaves. Six days later, two PPE adult females (originally obtained from Koppert Ltd., The Netherlands) were introduced on the same leaf of each plant. Adult mites on each plant were counted every three days, and control was affected by removing 1-4 predators (-control), doing nothing (0-control) and releasing 1-3 predators (+control) to each of the six plants.
Table 13. Census of mean population densities of 2SSM and PPE adults with control of predator on a single cucumber plant (mite numbers are rounded to the nearest integers).

<table>
<thead>
<tr>
<th>Day</th>
<th>2SSM</th>
<th>PPE</th>
<th>Control</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>10</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>3</td>
<td>57</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>6</td>
<td>108</td>
<td>2</td>
<td>+2</td>
</tr>
<tr>
<td>9</td>
<td>197</td>
<td>11</td>
<td>0</td>
</tr>
<tr>
<td>12</td>
<td>82</td>
<td>15</td>
<td>-1</td>
</tr>
<tr>
<td>15</td>
<td>41</td>
<td>9</td>
<td>0</td>
</tr>
<tr>
<td>18</td>
<td>104</td>
<td>23</td>
<td>+3</td>
</tr>
<tr>
<td>21</td>
<td>146</td>
<td>30</td>
<td>-2</td>
</tr>
<tr>
<td>24</td>
<td>17</td>
<td>5</td>
<td>-3</td>
</tr>
<tr>
<td>27</td>
<td>40</td>
<td>8</td>
<td>+1</td>
</tr>
<tr>
<td>30</td>
<td>130</td>
<td>13</td>
<td>0</td>
</tr>
<tr>
<td>33</td>
<td>203</td>
<td>18</td>
<td>-4</td>
</tr>
<tr>
<td>36</td>
<td>172</td>
<td>17</td>
<td>-3</td>
</tr>
<tr>
<td>39</td>
<td>62</td>
<td>7</td>
<td>0</td>
</tr>
<tr>
<td>42</td>
<td>24</td>
<td>13</td>
<td>+2</td>
</tr>
<tr>
<td>45</td>
<td>0</td>
<td>0</td>
<td>/</td>
</tr>
</tbody>
</table>
Mite populations were exterminated by day 45. The system input (control) and output (population densities) were recorded on each sampling day (Table 13).

5.2.3 State and control variables of mite/cucumber system

In the mite/cucumber control model, population densities of prey and predator $X_t$ and $Y_t$ are two states which were mapped into four fuzzy sets as follows: $x_i$ and $y_i$, $i = 1, 2, 3, 4$, denote Low(L), Medium-(M-), Medium+(M+) and High(H) densities of prey and predator respectively. Also, three fuzzy sets $u_i$, $i = 1, 2, 3$, are used to express -control, 0-control and +control. The mapping between actual data and conceptual set is done by a membership function (Zadeh, 1975, 1978). Obviously, all fuzzy sets used here are conceptual and arbitrary; the selection depends on individual's experience in handling data. In general, the more sets are chosen, the more accurate results will be, but at the expense of increasing computation time and usage of computer memory space. To illustrate the concept of a fuzzy restriction and the determination of membership function, let us consider a simple example, say "The prey population density is low." in which low is a fuzzy subset of a range of prey population density $X \in [0, 203]$ and characterized by the membership function $m_{low}(x) = 1 - L(x; a, b)$, where $x$ is the numerical prey population density and
L-function is defined by $L(x; a, b) = 0$, for $x < a$; $(x - a)/(b - a)$ for $a \leq x \leq b$; $1$ for $x > b$. Here, parameters $a = 30$ and $b = 100$ is a choice based on an concept that if prey population density is low, it should lie within a range $[0, 100]$; if the population density is absolutely low, it should lie within $[0, 30]$. These two figures chosen only for cucumber plants. Plant size and leaf area are two major factors closely related to the selection of $a$ and $b$. Fig. 12 shows the fuzzy set and the relationship between the actual data and their memberships with different sets. For instance, value $x_{21} = 146$ is mapped into $L$ and $M-$ with possibility $0$, $M+$ with possibility $0.68$ and $H$ with possibility $0.72$ by the membership function in Fig. 12.

This can be written as $\mathbf{M}(x_{21}) = (L/0, M-/0, M+/0.68, H/0.72)$, and figures in the right side of the equation is called the fuzzy data of $x_{21}$, denoted as $x_{21} = (0, 0, 0.68, 0.72)$. The fuzzy data of the mite/cucumber control system are shown in Table 14. All the conceptual state variables formed a fuzzy state space $\mathbf{E} = \mathbf{E}(e_1, e_2, ..., e_{16})$ (Fig. 13) and all the inputs formed an admissible control space $\mathbf{U} = \mathbf{U}(u_1, u_2, u_3)$. 
Fig. 12. Fuzzy 0-1 mappings: the relationship between a) number of PPE operated and its membership with different fuzzy control sets: $u_1$-negative control, $u_2$-zero control, and $u_3$-positive control; b) 2SSM population density and its membership with different fuzzy sets: $x_1$-low density, $x_2$-medium density, $x_3$-medium+ density, and $x_4$-high density; c) PPE population density and its membership with different fuzzy sets: $y_1$-low density, $y_2$-medium-density, $y_3$-medium+ density and $y_4$-high density.
Table 14. Conceptual data of adult population densities and control for the mite/cucumber system. The data were obtained by fuzzy 0-1 mappings, which are defined in Fig. 12.

<table>
<thead>
<tr>
<th>Day</th>
<th>2SSM x_1</th>
<th>x_2</th>
<th>x_3</th>
<th>x_4</th>
<th>PPE Y_1</th>
<th>Y_2</th>
<th>Y_3</th>
<th>Y_4</th>
<th>Control u_1</th>
<th>u_2</th>
<th>u_3</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>1.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>1.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.25</td>
<td>1.0</td>
<td>0.25</td>
</tr>
<tr>
<td>3</td>
<td>0.61</td>
<td>0.62</td>
<td>0.0</td>
<td>0.0</td>
<td>1.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.25</td>
<td>1.0</td>
<td>0.25</td>
</tr>
<tr>
<td>6</td>
<td>0.0</td>
<td>0.53</td>
<td>0.56</td>
<td>0.0</td>
<td>0.92</td>
<td>0.08</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.25</td>
<td>0.86</td>
</tr>
<tr>
<td>9</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>1.0</td>
<td>0.17</td>
<td>0.83</td>
<td>0.0</td>
<td>0.0</td>
<td>0.25</td>
<td>1.0</td>
<td>0.25</td>
</tr>
<tr>
<td>12</td>
<td>0.26</td>
<td>0.97</td>
<td>0.04</td>
<td>0.0</td>
<td>0.0</td>
<td>0.78</td>
<td>0.29</td>
<td>0.0</td>
<td>0.5</td>
<td>0.8</td>
<td>0.0</td>
</tr>
<tr>
<td>15</td>
<td>0.84</td>
<td>0.35</td>
<td>0.0</td>
<td>0.0</td>
<td>0.33</td>
<td>0.67</td>
<td>0.0</td>
<td>0.0</td>
<td>0.25</td>
<td>1.0</td>
<td>0.25</td>
</tr>
<tr>
<td>18</td>
<td>0.0</td>
<td>0.6</td>
<td>0.48</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.7</td>
<td>0.4</td>
<td>0.0</td>
<td>0.0</td>
<td>1.0</td>
</tr>
<tr>
<td>21</td>
<td>0.0</td>
<td>0.0</td>
<td>0.68</td>
<td>0.72</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>1.0</td>
<td>0.75</td>
<td>0.4</td>
<td>0.0</td>
</tr>
<tr>
<td>24</td>
<td>1.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.67</td>
<td>0.33</td>
<td>0.0</td>
<td>0.0</td>
<td>1.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>27</td>
<td>0.86</td>
<td>0.33</td>
<td>0.0</td>
<td>0.0</td>
<td>0.42</td>
<td>0.58</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.75</td>
<td>0.57</td>
</tr>
<tr>
<td>30</td>
<td>0.0</td>
<td>0.17</td>
<td>1.0</td>
<td>0.4</td>
<td>0.0</td>
<td>1.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.25</td>
<td>1.0</td>
<td>0.25</td>
</tr>
<tr>
<td>33</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>1.0</td>
<td>0.0</td>
<td>0.44</td>
<td>0.71</td>
<td>0.0</td>
<td>1.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>36</td>
<td>0.0</td>
<td>0.0</td>
<td>0.16</td>
<td>1.0</td>
<td>0.0</td>
<td>0.56</td>
<td>0.57</td>
<td>0.0</td>
<td>1.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>39</td>
<td>0.54</td>
<td>0.7</td>
<td>0.0</td>
<td>0.0</td>
<td>0.5</td>
<td>0.5</td>
<td>0.0</td>
<td>0.0</td>
<td>0.25</td>
<td>1.0</td>
<td>0.25</td>
</tr>
<tr>
<td>42</td>
<td>1.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>1.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.25</td>
<td>0.25</td>
</tr>
<tr>
<td>45</td>
<td>1.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>1.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>/</td>
<td>/</td>
<td>/</td>
</tr>
</tbody>
</table>
Fig. 13. Conceptual paired state variables of PPE and 2SSM in the mite/cucumber system after taking fuzzy mappings on the experimental data.
<table>
<thead>
<tr>
<th></th>
<th>L</th>
<th>M⁻</th>
<th>M⁺</th>
<th>H</th>
</tr>
</thead>
<tbody>
<tr>
<td>L</td>
<td>$e_1$</td>
<td>$e_2$</td>
<td>$e_3$</td>
<td>$e_4$</td>
</tr>
<tr>
<td>M⁻</td>
<td>$e_5$</td>
<td>$e_6$</td>
<td>$e_7$</td>
<td>$e_8$</td>
</tr>
<tr>
<td>M⁺</td>
<td>$e_9$</td>
<td>$e_{10}$</td>
<td>$e_{11}$</td>
<td>$e_{12}$</td>
</tr>
<tr>
<td>H</td>
<td>$e_{13}$</td>
<td>$e_{14}$</td>
<td>$e_{15}$</td>
<td>$e_{16}$</td>
</tr>
</tbody>
</table>

**Fig. 13.**
5.2.4 Fuzzy biological control model

Construction of a fuzzy control model is based on the input/output data \((U_t/X_t, Y_t, X_{t+1}, Y_{t+1})\) (Table 12), which are linked by fuzzy relations \(R_1\) and \(R_2\) such that

\[
X_{t+1} = X_t \circ Y_t \circ U_t \circ R_1 \\
Y_{t+1} = X_t \circ Y_t \circ U_t \circ R_2
\]  
(5.3)

where \(\circ\) is a fuzzy operator, \(X_t\) and \(Y_t\) are population densities of prey and predator and \(U_t\) is a control at time \(t:\)

\[
X_t = (x(1,t), x(2,t), x(3,t), x(4,t)), \quad Y_t = (y(1,t), y(2,t), y(3,t), y(4,t))\) and \(U_t = (u(1,t), u(2,t), u(3,t))\),

and the components of the vectors are memberships with certain conceptual sets. In my study, two different operators are used to describe the system; using them, Eq. 5.3 can be written in detail:

"Max-min" type:

\[
x(i_4,t+1) = \max_{1 \leq i_1 \leq 3} \min_{1 \leq i_2 \leq 4} \min_{1 \leq i_3 \leq 4} \{u(i_1,t), x(i_2,t), y(i_3,t), r(1,i_1,i_2,i_3,i_4)\}
\]
(5.4)

\[
y(i_4,t+1) = \max_{1 \leq i_1 \leq 3} \min_{1 \leq i_2 \leq 4} \min_{1 \leq i_3 \leq 4} \{u(i_1,t), x(i_2,t), y(i_3,t), r(2,i_1,i_2,i_3,i_4)\}
\]
(5.5)
"Max-prod" type:

$$x(i_4, t+1) = \max_{1 \leq i_1 \leq 3, 1 \leq i_2 \leq 4, 1 \leq i_3 \leq 4} (u(i_1, t)x(i_2, t)y(i_3, t)r(1, i_1i_2i_3i_4)) \quad (5.6)$$

$$y(i_4, t+1) = \max_{1 \leq i_1 \leq 3, 1 \leq i_2 \leq 4, 1 \leq i_3 \leq 4} (u(i_1, t)x(i_2, t)y(i_3, t)r(2, i_1i_2i_3i_4)) \quad (5.7)$$

where $i_4=1,4$, $R_1 = [r(1, i_1i_2i_3i_4)]$ and $R_2 = [r(2, i_1i_2i_3i_4)]$.

For fuzzy models (5.4)-(5.5), (5.6)-(5.7) and a collection of conceptual input/output data $(U(k)/X(k), Y(k), X(k+1), Y(k+1))$, $k = 1, 15$ (the time interval is three days), my purpose is to identify the linguistic relations $R_1$ and $R_2$ which best fit the data. The performance functions are sum of square errors between $U(t)oX(t)oY(t)oR_1/R_2$ and respectively $X(t+1)/Y(t+1)$ (see Appendix C).

5.2.5 Results

The spider mite/cucumber system was identified by using the conceptual input-output data and the estimation started with $r(1, i_1i_2i_3i_4) = r(2, i_1i_2i_3i_4) = 0$, $i_1 = 1,3$, $i_2$, $i_3$, $i_4 = 1,4$. The performance functions for every step of iteration are given in Fig. 14. Applying "max-prod" composition, the relations of linguistic system are given by the matrices in Table 15 and 16.
Fig. 14. The performance functions Q1 (for X variable) and Q2 (for Y variable) against the number of iterations for the "max-prod" structure of the mite/cucumber control system. Q₁: solid line with open circles; Q₂: dashed line with solid circles.
Table 15. The possibility matrices of the mite/cucumber control system with respect to the transition between current state and predicted 2SSM state driven by different controls.

<table>
<thead>
<tr>
<th>Y</th>
<th>L</th>
<th>M-</th>
<th>M+</th>
<th>H</th>
</tr>
</thead>
<tbody>
<tr>
<td>L</td>
<td>.65</td>
<td>.22</td>
<td>.02</td>
<td>0</td>
</tr>
<tr>
<td>M-</td>
<td>.04</td>
<td>.2</td>
<td>.06</td>
<td>0</td>
</tr>
<tr>
<td>M+</td>
<td>0</td>
<td>.03</td>
<td>.03</td>
<td>.26</td>
</tr>
<tr>
<td>H</td>
<td>.01</td>
<td>.32</td>
<td>.13</td>
<td>.58</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Y</th>
<th>L</th>
<th>M-</th>
<th>M+</th>
<th>H</th>
</tr>
</thead>
<tbody>
<tr>
<td>L</td>
<td>.04</td>
<td>.03</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>M-</td>
<td>.05</td>
<td>.01</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>M+</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>H</td>
<td>0</td>
<td>.04</td>
<td>.1</td>
<td>0</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Y</th>
<th>L</th>
<th>M-</th>
<th>M+</th>
<th>H</th>
</tr>
</thead>
<tbody>
<tr>
<td>L</td>
<td>.44</td>
<td>.2</td>
<td>.03</td>
<td>0</td>
</tr>
<tr>
<td>M-</td>
<td>.17</td>
<td>.7</td>
<td>.09</td>
<td>0</td>
</tr>
<tr>
<td>M+</td>
<td>0</td>
<td>.01</td>
<td>.04</td>
<td>0</td>
</tr>
<tr>
<td>H</td>
<td>.02</td>
<td>.19</td>
<td>.14</td>
<td>0</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Y</th>
<th>L</th>
<th>M-</th>
<th>M+</th>
<th>H</th>
</tr>
</thead>
<tbody>
<tr>
<td>L</td>
<td>.29</td>
<td>.58</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>M-</td>
<td>.25</td>
<td>.11</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>M+</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>H</td>
<td>0</td>
<td>.03</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Y</th>
<th>L</th>
<th>M-</th>
<th>M+</th>
<th>H</th>
</tr>
</thead>
<tbody>
<tr>
<td>L</td>
<td>.11</td>
<td>.03</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>M-</td>
<td>.04</td>
<td>.04</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>M+</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>H</td>
<td>.01</td>
<td>.03</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

Note: u_i,L, u_i,M-, u_i,H, u_i,M+ represent the transition states driven by different controls.
Table 15 (Continued)

<table>
<thead>
<tr>
<th></th>
<th>L</th>
<th>M-</th>
<th>M+</th>
<th>H</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>.16</td>
<td>.08</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>.18</td>
<td>.07</td>
<td>.23</td>
<td>.05</td>
</tr>
<tr>
<td></td>
<td>0</td>
<td>0</td>
<td>.06</td>
<td>.06</td>
</tr>
<tr>
<td></td>
<td>0</td>
<td>0</td>
<td>.06</td>
<td>.14</td>
</tr>
<tr>
<td></td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>.04</td>
<td>.23</td>
<td>.49</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>.06</td>
<td>.06</td>
<td>.14</td>
<td>.05</td>
</tr>
<tr>
<td></td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

\( u_3, M^+ \) 0 0 0 0 \( u_3, H \)
Table 16. The possibility matrices of the mite/cucumber control system with respect to the transition between current state and predicted PPE state driven by different controls.

<table>
<thead>
<tr>
<th></th>
<th>L</th>
<th>M-</th>
<th>M+</th>
<th>H</th>
<th>L</th>
<th>M-</th>
<th>M+</th>
<th>H</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>.46</td>
<td>.09</td>
<td>.01</td>
<td>0</td>
<td>.5</td>
<td>.02</td>
<td>.01</td>
<td>0</td>
</tr>
<tr>
<td>M-</td>
<td>.07</td>
<td>.06</td>
<td>.02</td>
<td>0</td>
<td>.05</td>
<td>.2</td>
<td>.05</td>
<td>0</td>
</tr>
<tr>
<td>M+</td>
<td>0</td>
<td>.03</td>
<td>.02</td>
<td>.17</td>
<td>0</td>
<td>.08</td>
<td>.03</td>
<td>.08</td>
</tr>
<tr>
<td>H</td>
<td>.13</td>
<td>.28</td>
<td>.51</td>
<td>u1,L</td>
<td>.02</td>
<td>.42</td>
<td>.64</td>
<td>.25</td>
</tr>
<tr>
<td></td>
<td>.02</td>
<td>.04</td>
<td>0</td>
<td>0</td>
<td>.01</td>
<td>.03</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>M-</td>
<td>.01</td>
<td>.04</td>
<td>0</td>
<td>0</td>
<td>.01</td>
<td>.01</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>M+</td>
<td>0</td>
<td>.09</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>H</td>
<td>.01</td>
<td>.19</td>
<td>.39</td>
<td>0</td>
<td>u1,M+</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>.99</td>
<td>.15</td>
<td>.01</td>
<td>0</td>
<td>.11</td>
<td>.57</td>
<td>.02</td>
<td>0</td>
</tr>
<tr>
<td>M-</td>
<td>.3</td>
<td>.18</td>
<td>.04</td>
<td>0</td>
<td>.24</td>
<td>.79</td>
<td>.08</td>
<td>0</td>
</tr>
<tr>
<td>M+</td>
<td>.01</td>
<td>.01</td>
<td>0</td>
<td>.01</td>
<td>.05</td>
<td>.39</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>H</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>.01</td>
<td>u2,L</td>
<td>.01</td>
<td>.72</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>.01</td>
<td>.43</td>
<td>0</td>
<td>0</td>
<td>.01</td>
<td>.25</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>M-</td>
<td>.03</td>
<td>.12</td>
<td>0</td>
<td>0</td>
<td>.02</td>
<td>.04</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>M+</td>
<td>0</td>
<td>.62</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>H</td>
<td>0</td>
<td>.31</td>
<td>0</td>
<td>0</td>
<td>u2,M+</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>.2</td>
<td>.88</td>
<td>0</td>
<td>0</td>
<td>.14</td>
<td>.14</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>M-</td>
<td>.11</td>
<td>.03</td>
<td>0</td>
<td>0</td>
<td>.58</td>
<td>.11</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>M+</td>
<td>.04</td>
<td>.01</td>
<td>.01</td>
<td>0</td>
<td>.18</td>
<td>.02</td>
<td>.01</td>
<td>0</td>
</tr>
<tr>
<td>H</td>
<td>0</td>
<td>.04</td>
<td>.04</td>
<td>0</td>
<td>u3,L</td>
<td>.02</td>
<td>.12</td>
<td>.04</td>
</tr>
</tbody>
</table>
Table 16 (Continued)

<table>
<thead>
<tr>
<th></th>
<th>.02</th>
<th>.05</th>
<th>0</th>
<th>0</th>
<th>.01</th>
<th>.03</th>
<th>0</th>
<th>0</th>
</tr>
</thead>
<tbody>
<tr>
<td>M-</td>
<td>.01</td>
<td>.02</td>
<td>0</td>
<td>0</td>
<td>.01</td>
<td>.01</td>
<td>.21</td>
<td>.12</td>
</tr>
<tr>
<td>M+</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>.17</td>
<td>.09</td>
</tr>
<tr>
<td>H</td>
<td>.01</td>
<td>.03</td>
<td>0</td>
<td>0</td>
<td>u₃,M⁺</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>
Table 17*. Comparison of a verbal mite/cucumber control system and a simulation of its fuzzy control model.

<table>
<thead>
<tr>
<th>Day</th>
<th>Observation</th>
<th>Simulation</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2SSM PPE Control</td>
<td>2SSM PPE Control</td>
</tr>
<tr>
<td>0</td>
<td>L L 0</td>
<td>L L 0</td>
</tr>
<tr>
<td>3</td>
<td>M- L 0</td>
<td>M- L 0</td>
</tr>
<tr>
<td>6</td>
<td>M+ L +</td>
<td>M+ L +</td>
</tr>
<tr>
<td>9</td>
<td>H M- 0</td>
<td>H M- 0</td>
</tr>
<tr>
<td>12</td>
<td>M- M- 0</td>
<td>M- M- 0</td>
</tr>
<tr>
<td>15</td>
<td>L M- 0</td>
<td>L M- 0</td>
</tr>
<tr>
<td>18</td>
<td>M- M+ +</td>
<td>M+ M- +</td>
</tr>
<tr>
<td>21</td>
<td>H H -</td>
<td>H M- -</td>
</tr>
<tr>
<td>24</td>
<td>L L -</td>
<td>M- M- -</td>
</tr>
<tr>
<td>27</td>
<td>L M- 0</td>
<td>L M- 0</td>
</tr>
<tr>
<td>30</td>
<td>M+ M- 0</td>
<td>M+ M- 0</td>
</tr>
<tr>
<td>33</td>
<td>H M+ -</td>
<td>H M+ -</td>
</tr>
<tr>
<td>36</td>
<td>H M+ -</td>
<td>H M- -</td>
</tr>
<tr>
<td>39</td>
<td>M- L(or M-) 0</td>
<td>M- M- 0</td>
</tr>
<tr>
<td>42</td>
<td>L M- +</td>
<td>L M- +</td>
</tr>
<tr>
<td>45</td>
<td>L L /</td>
<td>M+ L /</td>
</tr>
</tbody>
</table>

*Both observation and simulation can be derived directly from Tables 14, 15 and 16 by "principle of maximum possibility", for example, if \( U(k) = (0.5, 0.8, 0) \), then \( U(k) \) is zero control.
Since I found the "max-prod" composition is more accurate than "max-min" to this particular system. I used it as my identification approach. From Tables 15 and 16, the linguistic expression of the system has the general form: "If 2SSM population density is $x_k$, $1 \leq k \leq 4$, PPE population density is $y_k$, $1 \leq k \leq 4$ and control is $u_k$, $1 \leq k \leq 3$ at the present time, then the 2SSM population density will be $x_k$ with possibility $p_k$, $1 \leq k \leq 4$ and the PPE population density will be $y_k$ with possibility $q_k$, $1 \leq k \leq 4$, in three days." For example, if 2SSM and PPE population densities are low and control is zero now, then in three days the 2SSM population density will be low with possibility 0.44, medium- with possibility 0.66, medium+ with possibility 0.29 and high with possibility 0.02, and the PPE population density will be low with possibility 0.99, medium- with possibility 0.11, medium+ with possibility 0.01 and high with possibility 0.01 (see underlined components of matrices $R_1$ and $R_2$). A comparison of the verbal system and its simulation is shown in Table 17.

5.2.6 Sensitivity analysis

As discussed in subsection 5.2.3 the fuzzy model of spider mite/cucumber biological control system was built on membership functions of fuzzy sets relative to state and control variables which are quite arbitrary. In order to
have a meaningful model, I study the robustness (or inversely, sensitivity) of the model to changes of the membership functions as follows:

1). Increasing by 10% the value of memberships (not in excess of 1) for the data of 2SSM and PPE population densities and control respectively. Calculating the maximum changes of elements within matrices R1 and R2.

2). Increasing by 10% the value of memberships (not in excess of 1) for the data of 2SSM and PPE population densities and control simultaneously. Calculating the maximum changes of elements within matrices R1 and R2.

Results from step 1 (see Table 18) show that the relation matrices R1 and R2 are less sensitive to membership functions of the 2SSM population density and more sensitive to membership functions of control. Results from step 2 show a large combined effects on the elements of R1 and R2; the maximum change of elements within R1 and R2 is .4218 and .3884 respectively.
Table 18. Effects of increasing 10% of membership functions on changes in the elements of R1 and R2.

<table>
<thead>
<tr>
<th>System variables</th>
<th>The maximum changes in the elements of R1</th>
<th>R2</th>
</tr>
</thead>
<tbody>
<tr>
<td>X</td>
<td>.0797</td>
<td>.0692</td>
</tr>
<tr>
<td>Y</td>
<td>.1122</td>
<td>.1061</td>
</tr>
<tr>
<td>U</td>
<td>.2292</td>
<td>.1476</td>
</tr>
</tbody>
</table>
5.2.7 Discussion

The model discussed in this section provides a fuzzy linkage between input and output without regard to any inner relation of the system, which is always complex, a detailed model could involve as many as several hundred parameters (Pearl et al., 1989; Horn et al., 1991). The sensitivity analysis for this model is also necessary to detect the effects of membership functions on the predictability of the model; the results show that membership functions for control variables should be designed carefully. The attempt in this section may be a stepping stone towards an complex greenhouse pest control system design and management. To reach this goal, the single plant fuzzy model should be expanded to a mxn plant system. Interplant migration of both predator and prey mites should be considered and described by fuzzy rules. In addition to this, a stochastic fuzzy process need to be involved in describing interplant migrations of mites to simulate the spatial variations of mite population.

In the present study, I assume that the system output \((X(t+1), Y(t+1))\) merely depends on \((X(t), Y(t), U(t))\), and is not affected by any historical system variables. However, in some other cases, historical effects on the current output may be important. An advantage of the fuzzy model is due to its special structure; it is easy to be
translated into computer software, it needs less calculation and less memory space in a computer. I expect that a fuzzy mite control system will be easy for growers access and only visual sampling will be necessary for pest management since the basic variables of the system are not actual numbers but their conceptual meanings.

5.3 OPTIMAL USE OF *P. persimilis* FOR BIOLOGICAL CONTROL OF *T. urticae* ON GREENHOUSE CUCUMBERS BASED ON A HYPOTHETICAL ECONOMIC CRITERION

5.3.1 Introduction

In this section I investigate an application of dynamic programming to optimal biological control of a greenhouse spider mite/cucumber system. Based on a fuzzy biocontrol model developed in section 5.2, I introduce a N-stage decision process based on a hypothetic criterion of control cost and crop loss caused by spider mites for the system to judge the optimality of the biological control employed.

5.3.2 State transition of the fuzzy biological control model

From the previous study we know that there are 16 fuzzy states (see Fig. 13) of paired population densities (*X_t, Y_t*)
in the model: \( e_1 = LL, e_2 = LM^-, \ldots, e_{16} = HH \), which formed a fuzzy state space \( E \). By Table 13 and 14, we have transition relations of the state variables in space \( E \) under all admissible controls (Fig. 15). Working from Table 15 and 16, I use the maximum possibility principle to determine state transition from one to another. For example, if current state is \( e_1(LL) \), and input is \(-\) control then the predicted 2SSM and PPE states should be \((L/0.65, M^-/0.32, M^+/0.04, H/0)\) and \((L/0.46, M^-/0.5, M^+/0.02, H/0.01)\), respectively, therefore the most likely paired state should be \( e_2(LM^-) \); with possibility 0.5 \((\min(0.65, 0.5))\); if input is \(0\)-control then the most likely paired state should be \( e_5(M-L) \) with possibility 0.66; finally, if input is \(+\) control rather than the above two then the predicted state of 2SSM should be \((L/0.11, M^-/0.16, M^+/0.16, H/0.04)\), and therefore, paired state is unpredictable by the model. Fig. 15 shows the transitions for all the predictable states in space \( E \), the transitions with possibilities less than 0.1 are omitted. From Fig. 14, it is important to know that many states in space \( E \) may never be reached no matter how the admissible control is employed.
Fig. 15. Control rules of mite/cucumber system which is represented by fuzzy biocontrol model (5.3). Under these rules: a) -control, b) 0-control and c) +control, a state may be driven to another by an admissible control. If a series of admissible controls are employed, a state may be moved to another through multiple transitions, which can be also determined by such rules. *: an uncontrollable variable.
a) Under -control with fuzzy mean: -2 (see Appendix C)

b) Under 0-control with fuzzy mean: 0 (see Appendix C)

c) Under +control with fuzzy mean +3 (see appendix C)
5.3.3 Optimal problem of mite/cucumber biological control system

The purpose of optimization for the mite/cucumber biological control system is to specify the best timing and the best amount of PPE manipulated over a growing season. A hypothetic economical criterion (for a minimal cost) was used for evaluating the quality of control policy, by which all the contributing factors were converted into common units of dollars and cents. The crop loss can be estimated in dollars and the control policies each have a cost for application and materials. On a production scale, the estimation of economical criterion is feasible. No work has been done by myself for this small scale system.

Let $g_0[e(1)]$ be the minimum cost incurred in the growing season with $N = 15$ stages (plants averaging 12 leaves at stage 1) when the state variable at stage 1 is $e(1)$. Then

$$g_0[e(1)] = \min \{ \sum_{i=1}^{N} l[e(i+1)] + c[u(i)] \}$$

$$u(1), \ldots, u(N)$$

$$+ l[e(1)] \quad (5.8)$$

where $l[e(i)]$ is the loss of cucumber damage caused by the 2SSM at stage $i$ and $c[u(i)]$ is the cost of implementing the control decision.
Fig. 16. A N-stage decision process of the mite /cucumber control system (N = 15). Where $l(i) = l[e(i)], i = 1, \ldots, N$, is crop loss at stage $i$, $e(i)$ is in space $E$ and $u(i)$ is in $U$. 
Fig. 16.
Table 19. A hypothetic cost of control and loss of cucumber damage caused by the 2SSM for 30 cucumber plants.

<table>
<thead>
<tr>
<th>Control employed</th>
<th>Control cost $</th>
<th>Mite's state $</th>
<th>Crop loss $</th>
</tr>
</thead>
<tbody>
<tr>
<td>-control ($u_1$)</td>
<td>10</td>
<td>$e_1, e_2$</td>
<td>0</td>
</tr>
<tr>
<td>0-control ($u_2$)</td>
<td>0</td>
<td>$e_5$</td>
<td>1</td>
</tr>
<tr>
<td>+control ($u_3$)</td>
<td>5</td>
<td>$e_6$</td>
<td>0.8</td>
</tr>
<tr>
<td>/</td>
<td>/</td>
<td>$e_9$</td>
<td>5</td>
</tr>
<tr>
<td>/</td>
<td>/</td>
<td>$e_{10}$</td>
<td>4.8</td>
</tr>
<tr>
<td>/</td>
<td>/</td>
<td>$e_{14}$</td>
<td>10</td>
</tr>
<tr>
<td>/</td>
<td>/</td>
<td>$e_{15}$</td>
<td>9.8</td>
</tr>
</tbody>
</table>
If we consider the control model and economical criterion together we have a N-stage decision process which will be used for optimization (Fig. 16). The economical criterion of our mite/cucumber system is hypothesized in dollars and cents; they are figures for convenience, and no actual measurement has been done for this system (Table 19). Based on the above discussion, the optimal control problem of the mite/cucumber system can be addressed as: "During a growing season of a cucumber plant, for a predetermined 15 control stages (45 days), how can we find an optimal policy from the admissible alternatives to drive an initial state \( e(1) \) to \( e(15) \) and to minimize the criterion?" This has been solved by use of dynamic programming.

5.3.4 Dynamic programming: Bellman's principle of optimality

Bellman's optimality principle is stated as follows: "An optimal policy has the property that whatever the initial state and initial decision are, the remaining decisions must constitute an optimal policy with regard to the state resulting from the first decision" (Bellman, 1967).

Related to our economical criterion, there is a backwards algorithm available which is derived based on Bellman's optimality principle:
\[ g_N[e(1)] = \min \left( l[e(N+1)] + c[u(N)] + g_{N-1}[e(1)] \right) \]
\[ u(N) \]

\[ g_{N-1}[e(1)] = \min \left( l[e(N)] + c[u(N-1)] + g_{N-2}[e(1)] \right) \]
\[ u(N-1) \]

\[ \ldots \ldots \] (5.9)

\[ g_2[e(1)] = \min \left( l[e(3)] + c[u(2)] + g_1[e(1)] \right) \]
\[ u(2) \]

\[ g_1[e(1)] = \min \left( l[e(1)] + l[e(2)] + c[u(1)] \right) \]
\[ u(1) \]

Instead of using eq. (5.8), which cannot be used directly for complex systems, we calculate it backwards by algorithm (5.9) which has been proved to be very efficient to solve optimality problems.

5.3.5 Results and discussion

For a predetermined 15 control stages and an economical criterion (5.8) (Table 19), algorithm (5.9) was computed for various initial states. The optimal strategies, associated optimal state trajectories and minimized economical criterion were obtained (Table 20). The results reveal
several important facets of the biocontrol system:

1) There exist multiple optimal strategies that will provide flexible choices for practical use.

2) The optimal state trajectories exhibit fluctuating dynamics which is a desired property of a stabilized prey-predator system (Nachman, 1987b, 1988).

3) Within a 45 day biological control period, control starting at $e_1$, $e_6$ or $e_{14}$ resulted a lower cost and loss compared to others; therefore these are good starting states to initiate the biological control.

The advantages of optimization methods for the mite/cucumber biological control system can be illustrated by considering the number of simulations that would have been normally required to obtain the best strategies present in Table 20. To determine the best strategies by a fuzzy simulation model it would be necessary to compute $4 \times 4 \times 3^{15}$ (number of 2SSM state x number of PPE state x number of alternatives$^{stage}$) times, which is larger than $2 \times 10^8$. Compared to this, the best strategies derived from the fuzzy control model only requires to calculate $2 + 1 + 1 + 8 \times 15 = 124$ times. There are two reasons for the huge reduction of computation: 1) the relationship between state variables and control alternatives is specified in the control model that results in avoidance of unnecessary simulations, and 2) the algorithm tremendously reduces the computation.
Table 20. Minimized goal function $g_0[e(1)]$ of control cost and cucumber loss caused by the 2SSM in the mite/cucumber control system during 45 days.

<table>
<thead>
<tr>
<th>$e(1)$</th>
<th>$g_0[e(1)]$</th>
<th>Optimal strategy</th>
<th>Optimal trajectory</th>
</tr>
</thead>
<tbody>
<tr>
<td>$e_1$</td>
<td>92.6</td>
<td>1) 0+00++0000-0000</td>
<td>$e_1$-5-14-6-2-9-14-6-2-10-15-14-6-2-10-15</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1) 000-00++00++000</td>
<td>$e_1$-6-2-10-15-14-6-2-9-14-6-2-9-14-6-2-10</td>
</tr>
<tr>
<td>$e_6$</td>
<td>92.6</td>
<td>2) 0++0000-00++000</td>
<td>$e_6$-2-9-14-6-2-10-15-14-6-2-9-14-6-2-10</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3) 0++00++0000-000</td>
<td>$e_6$-2-9-14-6-2-9-14-6-2-10-15-14-6-2-10</td>
</tr>
<tr>
<td>$e_9$</td>
<td>93.0</td>
<td>1) 00++00++00++000</td>
<td>$e_9$-14-6-2-9-14-6-2-9-14-6-2-9-14-6-2-10</td>
</tr>
</tbody>
</table>
As mentioned earlier, an economical criterion should be estimated before doing any optimization. Temporal homogeneity of a criterion does not always exist in agricultural ecosystems. Loss of crop due to damage by pests could vary during season, so the loss should be expressed as $l[e(i), i]$ instead of $l[e(i)]$ in many systems.
GENERAL DISCUSSION AND CONCLUSIONS

The studies conducted were motivated by an interest in developing an optimal pest management program for greenhouse cucumber systems. Optimality has not yet become a familiar concept for most entomologists, although optimization with its applications in agricultural ecosystems has been investigated by many researchers (e.g. Watt, 1964; Shoemaker 1973a, b, c; Rovinsky and Shoemaker, 1981; Shoemaker and Onstad, 1983). Since the occasional outbreaks of the two-spotted spider mites in many agricultural systems, contemporary spider mite management systems have moved toward increased reliance on integrating biological and chemical control (Horn, 1988; Huffaker and Rabb, 1984; Metcalf and Luckmann, 1982). The common control strategy applied in conventional integrated pest management systems is to prevent the pest population from exceeding a maximum acceptable level which is called the economic injury level (EIL). The practical meaning of IPM is to restrict the overuse of chemical pesticides and to have economically and ecologically sound pest management. In contrast to conventional integrated pest management, in an optimization
approach there is no EIL but an economic criterion (cost of control and loss of damage), and a control or simulation model of the system is required to find the best control strategy which minimizes the economic criterion.

I began my studies by experimentally validating the early version of a stochastic arthropod predator-prey-plant model (Pearl et al., 1989). This model was originally validated with a small scale laboratory Lima bean system composed of four 5-leaf plants grown in a linear row. The strategy we used involved development of a relatively simple model, in which both the sizes of plants and the dimension of the plant universe were simplified. The model was designed to have flexibility for expansion into a production scale system. Therefore, the simulation time was largely reduced during the early testing period. In the early version of the model, most parameters were obtained either from published literature or from early experiments by Kallander (1989). The development of this model is designed to serve as a testing base for optimal spider mite management in greenhouse cultural systems. Following the sensitivity analysis on this model, I conducted a series of laboratory experiments using Lima bean plants to provide demographic information of predator and prey populations on a single plant system and a 4-plant system (Chapter 2).
Through these experiments, the most important parameters in the model such as reproduction rate, maturation time, migration rate and predation coefficients were refined by simulation-based estimations. An extensive census was conducted to reduce the sampling error and eventually to increase the accuracy of the parameter estimates. After this procedure, the refined model has an unique ability to reflect the inherent dynamics of populations both in mean and variance. The outcomes of experimental and simulation data correspond well with each other.

A further refinement of the preceding model will be to incorporate a death process into a population during its long distant dispersal. Since both predator and prey mites are relatively small compared to host plants and greenhouse structures, these mites may take several days to move randomly through greenhouse structures from one plant to others. This suggests that the death processes of a migrating population are important to the population dynamics. In Chapter 3 I discussed that deaths occurring within a starved population during its migration are drastic compare to the normal death. Based on this fact, I applied Monte-Carlo simulations to generate a number of Poisson processes to mimic the death events for each species and each sex. These randomized death events can be incorporated into the model; during long distance dispersal these death
events continually take place within a population until all remaining individuals have found a new food source or die. The ability of both species to recover from starvation, the reproductive capacity of starved females and the effect on their progeny were observed in related studies. The results suggested that both mite species have the ability to resume their normal life as soon as food source is available to them; therefore, it is unnecessary to incorporate any additional treatment into the model for survivors of migrating populations. Stochastic processes adequately described death processes with respect to demographic and environmental stochasticity within migrating mite populations.

After the refinement of the parameters and incorporation of several stochastic gut content and food decay processes into the model (Horn et al., 1991, Horn et al., 1991, unpublished), a detailed stochastic predator-prey-plant model has been developed which has the ability to dynamically mimic the complexities of environmental realities. The proposed stochastic model has been able to follow the system changes which are governed by a probabilistic structure rather than a pre-determined course. The model follows the changes (both mean and variance) of nymphs and adults of both predator and prey populations on Lima bean plants grown in a linear row, the growth and
infestation of the plants, and the temperature and humidity of the surrounding environment. The next goal of this modeling research is to investigate the optimal strategy of integrating biological and chemical control efforts on greenhouse spider mite populations attacking cucumber plants. Therefore, our modeling technology needs to be transferred to a practical production system involving the growth of cucumbers in a commercial sized greenhouse. This will require detailed modeling of the 2SSM and cucumber plant interaction and further refinement of some parameter estimates of mite demographics which may change in such an expanded system. For this purpose, in Chapter 4, I conducted several comparative experiments under identical environmental conditions to detect changes of some important demographic parameters of two mite species grown on cucumber leaves. These comparative studies indicated that important demographic parameters such as maturation time and reproduction rate for the 2SSM population should be re-estimated by simulations searching along a negative gradient, and anticipated that the population dynamics for 2SSM feeding on cucumbers is slower than that on Lima beans. This study also indicated that the important demographic parameters for PPE in the Lima bean model can be used for a cucumber system.
The studies presented in Chapters 2-4 reflect my participation in experimental validation of a rather sophisticated predator-prey-plant model. This model is still under development. The subsequent objectives of this work are to assess the level of miticide resistance in the 2SSM population, to develop an economic criterion by carrying out a production scale experiment on cucumber plants, to use computer simulation to find the optimal pest management strategy, to test the efficacy of this strategy by a production scale experiment and finally, to develop a PC supported decision package.

The last chapter (Chapter 5) of my research is rather independent of the others. In it I have presented an alternative approach, a so-called fuzzy systems analysis (Zadeh, 1975, 1978) to modeling and optimality of a spider mite/cucumber management system. I developed a control model for the system rather than a simulation model. In this model, verbal expressions are used to describe the population dynamics. Further, I have also investigated an application of dynamic programming to optimal biological control of spider mites on greenhouse cucumbers. However, the optimal control strategy was derived only for a hypothetic economic criterion which needs to be developed by a production scale experiment. Furthermore, the proposed fuzzy model needs to be expanded to a mxn-plant universe in
a greenhouse, and inter-plant dispersal of mite populations should be involved. The research in Chapter 5 provided a framework for applying fuzzy modeling and fuzzy decision technology to a complicated spider mite management system, although the methodology in this study needs to be further developed. The advantage of fuzzy systems analysis is obvious: the model is simple, the cost of research is low, less sampling information is necessary for the control and the associated PC linguistic decision package can be readily accepted and used by growers.
SUMMARY

This study reports the experimental validation of a general simulation-based stochastic model which has been programmed to produce fast, realistic simulations of the development and interaction of populations of predator and prey, including prey (pest) infestation of crop plants.

To develop this predator-prey-plant model I conducted several extensive demographic studies on populations of *Tetranynchus urticae* Koch and its predator *Phytoseiulus persimilis* Athias-Henriot growing on Lima bean plants in a controlled environmental chamber with various temperatures. Eggs, nymphs and adults of both species were censused on a single plant system and a 4-plant system. Following the sensitivity analysis on the original version of the model, my experiments refined the most important parameters in the model, such as reproduction, development, dispersal and predation. Based on my census data, the stochastic model has been refined several times by using a simulation-based estimation technique. (It was proposed and programmed by my colleagues in the Statistics Department, The Ohio State University.)
A stochastic death process of a starved population was incorporated into the model to mimic deaths occurring in a migrating population within the spider mite predator-prey-plant system. For this purpose, I undertook a series of starvation experiments. I found that the death processes of a migrating population of both species and sexes can be described by Poisson processes which are characterized by mean death rate functions (including a constant) of the populations.

Comparative studies of plant/mite interactions were conducted on Lima beans and cucumbers to provide information necessary to transfer modeling technology from a laboratory Lima bean system to a commercial greenhouse cucumber system. Through these studies, I found that under identical conditions the population dynamics of the prey mites on cucumber was slower than that on Lima beans, because reproduction and development were lower on cucumbers compared to Lima beans. The results suggest that refinement of demographic parameter estimates of the spider mites should be negatively directed. The results also suggest that the predation, reproduction and maturation parameters of the predator mite in the Lima bean system can be directly adapted to a cucumber system.

To simulate the complex predator-prey-plant system and further to find the optimal management strategy, I applied
fuzzy system analysis to a greenhouse cucumber/mite system in which a linguistic biological control model was proposed to describe the system. Optimal control strategies were also proposed for various pest situations under a hypothetic economic criterion by applying Bellman's principle of optimality.
LIST OF REFERENCES


145


APPENDICES

A. LIST OF REFERRED PARAMETERS

\( a_2 \) - Predation rate of PPE nymphs feeding on the 2SSM eggs.
\( a_3 \) - Predation rate of PPE males feeding on the 2SSM eggs.
\( a_4 \) - Predation rate of PPE females feeding on the 2SSM eggs.
\( b_0 \) - Ratio of initial survivors and deaths in a population.
\( b_1 \) - Decreasing rate of a survivorship function.
\( b_3 \) - Predation rate of PPE nymphs feeding on the 2SSM nymphs.
\( b_4 \) - Predation rate of PPE males feeding on the 2SSM nymphs.
\( b_5 \) - Predation rate of PPE females feeding on the 2SSM nymphs.
\( D^*_m \) - Gut-content function of PPE males at time t.
\( D^*_n \) - Gut-content function of PPE nymphs at time t.
\( D^*_w \) - Gut-content function of PPE females at time t.
\( E \) - Number of 2SSM eggs at time t.
\( g_3 \) - Predation rate of PPE nymphs feeding on the 2SSM males.
$g_4$ - Predation rate of PPE males feeding on the 2SSM males.
$g_5$ - Predation rate of PPE females feeding on the 2SSM males.
$h_m$ - Migration rate of 2SSM males.
$h_m^*$ - Migration rate of PPE males.
$h_n^*$ - Migration rate of PPE nymphs.
$h_u$ - Migration rate of 2SSM females.
$h_u^*$ - Migration rate of PPE females.
$M$ - Number of 2SSM males at time $t$.
$M^*$ - Number of PPE males at time $t$.
n - Initial size of a starved population.
$N$ - Number of 2SSM nymphs at time $t$.
$N^*$ - Number of PPE nymphs at time $t$.
r - Decreasing rate of a survivorship function ($r=b_o$).
$R$ - Random number between 0 and 1.
$r_{a2}$ - Predation related nutritional constant of PPE nymphs feeding on the 2SSM eggs.
$r_{a3}$ - Predation related nutritional constant of PPE males feeding on the 2SSM eggs.
$r_{b4}$ - Predation related nutritional constant of PPE females feeding on the 2SSM eggs.
$r_{b3}$ - Predation related nutritional constant of PPE nymphs feeding on the 2SSM nymphs.
$r_{b4}$ - Predation related nutritional constant of PPE males feeding on the 2SSM nymphs.
$r_{b5}$ - Predation related nutritional constant of PPE females
feeding on the 2SSM nymphs.

- Migration related nutritional constant of 2SSM males.

- Migration related nutritional constant of PPE males.

- Migration related nutritional constant of PPE nymphs.

- Migration related nutritional constant of 2SSM females.

- Migration related nutritional constant of PPE females.

- Predation related nutritional constant of PPE nymphs feeding on the 2SSM males.

- Predation related nutritional constant of PPE males feeding on the 2SSM males.

- Predation related nutritional constant of PPE females feeding on the 2SSM males.

- Predation related nutritional constant of PPE females feeding on the 2SSM females.

- Predation related nutritional constant of PPE males feeding on the 2SSM females.

- Predation related nutritional constant of PPE females feeding on the 2SSM females.

- Edible leaf surface at time t.

- Predation rate of PPE males feeding on the 2SSM females.

- Predation rate of PPE females feeding on the 2SSM females.

- Maximum survivorship \((S_m=1)\) of a starved population.

- Initial survivorship of a starved population.

- Number of 2SSM females at time t.

- Number of PPE females at time t.
$w_0$ - Weight of a 2SSM egg.

$w_1$ - Weight of a 2SSM nymph.

$w_2$ - Weight of a 2SSM male.

$w_3$ - Weight of a 2SSM female.

B. FORMULAE RELATIVE TO CHAPTER II

Predation intensities in Pearl's model:

Predation intensity of PPE on the 2SSM eggs:

$$a_2 N^*/(D^*_M + r_{a_2}) + a_3 M^*/(D^*_M + r_{a_3}) + a_4 W^*/(D^*_W + r_{a_4}) \quad (B.1)$$

Predation intensity of PPE on the 2SSM nymphs:

$$b_3 N^*/(D^*_M + r_{b_3}) + b_4 M^*/(D^*_M + r_{b_4}) + b_5 W^*/(D^*_W + r_{b_5}) \quad (B.2)$$

Predation intensity of PPE on the 2SSM adult males:

$$g_3 N^*/(D^*_M + r_{g_3}) + g_4 M^*/(D^*_M + r_{g_4}) + g_5 W^*/(D^*_W + r_{g_5}) \quad (B.3)$$

Predation intensity of PPE on the 2SSM adult females:

$$s_4 M^*/(D^*_M + r_{s_4}) + s_5 W^*/(D^*_W + r_{s_5}) \quad (B.4)$$

Migration intensities in Pearl's model:

Migration intensity of 2SSM adult males:

$$h_m (w_1 N + w_2 M + w_3 W)/(S + r_{hm}) \quad (B.5)$$
Migration intensity of 2SSM adult females:

\[ h_u(w_1N + w_2M + w_3N)/(S + r_{hw}) \]  \hspace{1cm} (B.6)

Migration intensity of PPE nymphs:

\[ h_u^*/(w_0E + w_1N + r_{hw}) \]  \hspace{1cm} (B.7)

Migration intensity of PPE adult males:

\[ h_u^*/(w_0E + w_1N + w_2M + w_3N + r_{hw}) \]  \hspace{1cm} (B.8)

Migration intensity of PPE adult females:

\[ h_u^*/(w_0E + w_1N + w_2M + w_3N + r_{hw}) \]  \hspace{1cm} (B.9)

C. FORMULAE RELATIVE TO CHAPTER V

The performance functions \( Q_1 \) and \( Q_2 \) in fuzzy control model:

\[ Q_1 = \sum_{i=0}^{15} \left\{ \max_{1 \leq i_1 \leq 3, 1 \leq i_2 \leq 4, 1 \leq i_3 \leq 4} \min[u(i_1, t), x(i_2, t), y(i_3, t), r(1, i_1, i_2, i_3, i_4)] - x(i_4, t+1)^2 \right\} \]  \hspace{1cm} (C.1)

\[ Q_2 = \sum_{i=0}^{15} \left\{ \max_{1 \leq i_1 \leq 3, 1 \leq i_2 \leq 4, 1 \leq i_3 \leq 4} \min[u(i_1, t), x(i_2, t), y(i_3, t), r(2, i_1, i_2, i_3, i_4)] - y(i_4, t+1)^2 \right\} \]  \hspace{1cm} (C.2)

where integers \( i_1 - i_4 \) are orders of the fuzzy sets, and \( t \) is the number of observations. Performance functions (C.1) and (C.2) are sums of square error of model predictions in fuzzy
Let $M_f(n)$ be a membership function which is also a 0-1 mapping from a real set $R: (n; a \leq n \leq b)$ to a fuzzy set $f$, the fuzzy mean of $f$ is then defined as

$$n_f = \frac{\int_a^b nM_f(n)dn}{\int_a^b M_f(n)dn} \quad (C.3)$$