THERMAL BIOLOGY OF THE COLORADO POTATO BEETLE (<u>LEPTINOTARSA</u> <u>DECEMLINEATA</u>

(SAY) (COLEOPTERA: CHRYSOMELIDAE)), WITH APPLICATION TO PEST MANAGEMENT

DECISION MAKING

BY

DEREK JON LACTIN

A thesis

Submitted to the Faculty of Graduate Studies

in Partial Fulfilment of the requirements

for the Degree of

DOCTOR OF PHILOSOPHY

IN THE

DEPARTMENT OF ENTOMOLOGY

University of Manitoba,

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Religion
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Economics
    General 0501
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    Commerce-Business 0505
    Finance 0508
    History 0509
    Labor 0510
    Theory 0511
Folklore 0358
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Gerontology 0351
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Ancient 0579
Medieval 0581
Modern 0582
Black 0328
African 0331
Asia, Australia and Oceania 0332
Canadian 0334
European 0335
Latin American 0336
Middle Eastern 0333
United States 0337
History of Science 0585
Law 0398
Political Science
    General 0615
    International Law and
        Relations 0616
    Public Administration 0617
Recreation 0814
Social Work 0452
Sociology
    General 0626
    Criminology and Penology ... 0627
    Demography 0938
    Ethnic and Racial Studies 0631
    Individual and Family
        Studies 0628
    Industrial and Labor
        Relations 0629
    Public and Social Welfare 0630
    Social Structure and
        Development 0700
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Transportation 0709
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    General 0306
    Anatomy 0287
    Biostatistics 0308
    Botany 0309
    Cell 0379
    Ecology 0329
    Entomology 0353
    Genetics 0369
    Limnology 0793
    Microbiology 0410
    Molecular 0307
    Neuroscience 0317
    Oceanography 0416
    Physiology 0433
    Radiation 0821
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Biophysics
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Physical Geography 0368
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    Audiology 0300
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    Dentistry 0567
    Education 0350
    Hospital Management 0769
    Human Development 0758
    Immunology 0982
    Medicine and Surgery 0564
    Mental Health 0347
    Nursing 0569
    Nutrition 0570
    Obstetrics and Gynecology .. 0380
    Occupational Health and
        Therapy 0354
    Ophthalmology 0381
    Pathology 0571
    Pharmacology 0419
    Pharmacy 0572
    Physical Therapy 0382
    Public Health 0573
    Radiology 0574
    Recreation 0575

Speech Pathology 0460
Toxicology 0383
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Computer Science 0984

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    Aerospace 0538
    Agricultural 0539
    Automotive 0540
    Biomedical 0541
    Chemical 0542
    Civil 0543
    Electronics and Electrical 0544
    Heat and Thermodynamics ... 0348
    Hydraulic 0545
    Industrial 0546
    Marine 0547
    Materials Science 0794
    Mechanical 0548
    Metallurgy 0743
    Mining 0551
    Nuclear 0552
    Packaging 0549
    Petroleum 0765
    Sanitary and Municipal 0554
    System Science 0790
Geotechnology 0428
Operations Research 0796
Plastics Technology 0795
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Art 0273
Collèges communautaires 0275
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Évaluation 0288
Finances 0277
Formation des enseignants 0530
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Lecture 0535
Mathématiques 0280
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Orientation et consultation 0519
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Programmes d'études et
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Psychologie 0525
Sciences 0714
Sciences sociales 0534
Sociologie de l'éducation 0340
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Langues
   Généralités 0679
   Anciennes 0289
   Linguistique 0290
   Modernes 0291
Littérature
   Généralités 0401
   Anciennes 0294
   Comparée 0295
   Mediévale 0297
   Moderne 0298
   Africaine 0316
   Américaine 0591
   Anglaise 0593
   Asiatique 0305
   Canadienne (Anglaise) 0352
   Canadienne (Française) 0355
   Germanique 0311
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   Généralités 0318
   Clergé 0319
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   Histoire des religions 0320
   Philosophie de la religion 0322
Théologie 0469

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   Archéologie 0324
   Culturelle 0326
   Physique 0327
Droit 0398
Économie
   Généralités 0501
   Commerce-Affaires 0505
   Économie agricole 0503
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   Finances 0508
   Histoire 0509
   Théorie 0511
Études américaines 0323
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Études féministes 0453
Folklore 0358
Géographie 0366
Gérontologie 0351
Gestion des affaires
   Généralités 0310
   Administration 0454
   Banques 0770
   Comptabilité 0272
   Marketing 0338
Histoire
   Histoire générale 0578

Ancienne 0579
Médiévale 0581
Moderne 0582
Histoire des noirs 0328
Africaine 0331
Canadienne 0334
États-Unis 0337
Européenne 0335
Moyen-orientale 0333
Latino-américaine 0336
Asie, Australie et Océanie 0332
Histoire des sciences 0585
Loisirs 0814
Planification urbaine et
   régionale 0999
Science politique
   Généralités 0615
   Administration publique 0617
   Droit et relations
      internationales 0616
Sociologie
   Généralités 0626
   Aide et bien-être social 0630
   Criminologie et
      établissements
      pénitentiaires 0627
   Démographie 0938
   Études de l'individu et
      de la famille 0628
   Études des relations
      interethniques et
      des relations raciales 0631
   Structure et développement
      social 0700
   Théorie et méthodes. 0344
   Travail et relations
      industrielles 0629
Transports 0709
Travail social 0452

SCIENCES ET INGÉNIERIE

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Agriculture
   Généralités 0473
   Agronomie. 0285
   Alimentation et technologie
      alimentaire 0359
   Culture 0479
   Élevage et alimentation 0475
   Exploitation des péturages 0777
   Pathologie animale 0476
   Pathologie végétale 0480
   Physiologie végétale 0817
   Sylviculture et faune 0478
   Technologie du bois 0746
Biologie
   Généralités 0306
   Anatomie 0287
   Biologie (Statistiques) 0308
   Biologie moléculaire 0307
   Botanique 0309
   Cellule 0379
   Écologie 0329
   Entomologie 0353
   Génétique 0369
   Limnologie 0793
   Microbiologie 0410
   Neurologie 0317
   Océanographie 0416
   Physiologie 0433
   Radiation 0821
   Science vétérinaire 0778
   Zoologie 0472
Biophysique
   Généralités 0786
   Medicale 0760

SCIENCES DE LA TERRE
Biogéochimie 0425
Géochimie 0996
Géodésie 0370
Géographie physique 0368

Géologie 0372
Géophysique 0373
Hydrologie 0388
Minéralogie 0411
Océanographie physique 0415
Paléobotanique 0345
Paléoécologie 0426
Paléontologie 0418
Paléozoologie 0985
Palynologie 0427

SCIENCES DE LA SANTÉ ET DE L'ENVIRONNEMENT
Économie domestique 0386
Sciences de l'environnement 0768
Sciences de la santé
   Généralités 0566
   Administration des hipitaux ..0769
   Alimentation et nutrition 0570
   Audiologie 0300
   Chimiothérapie 0992
   Dentisterie 0567
   Développement humain 0758
   Enseignement 0350
   Immunologie 0982
   Loisirs 0575
   Médecine du travail et
      thérapie 0354
   Médecine et chirurgie 0564
   Obstétrique et gynécologie ...0380
   Ophtalmologie 0381
   Orthophonie 0460
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   Pharmacie 0572
   Pharmacologie 0419
   Physiothérapie 0382
   Radiologie 0574
   Santé mentale 0347
   Santé publique 0573
   Soins infirmiers 0569
   Toxicologie 0383

SCIENCES PHYSIQUES
Sciences Pures
Chimie
   Généralités 0485
   Biochimie 487
   Chimie agricole 0749
   Chimie analytique 0486
   Chimie minérale 0488
   Chimie nucléaire 0738
   Chimie organique 0490
   Chimie pharmaceutique 0491
   Physique 0494
   PolymÇres 0495
   Radiation 0754
Mathématiques 0405
Physique
   Généralités 0605
   Acoustique 0986
   Astronomie et
      astrophysique 0606
   Electronique et électricité 0607
   Fluides et plasma 0759
   Météorologie 0608
   Optique 0752
   Particules (Physique
      nucléaire) 0798
   Physique atomique 0748
   Physique de l'état solide 0611
   Physique moléculaire 0609
   Physique nucléaire 0610
   Radiation 0756
Statistiques 0463

Sciences Appliqués Et Technologie
Informatique 0984
Ingénierie
   Généralités 0537
   Agricole 0539
   Automobile 0540

Biomédicale 0541
Chaleur et ther
   modynamique 0348
Conditionnement
   (Emballage) 0549
Génie aérospatial 0538
Génie chimique 0542
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Génie électronique et
   électrique 0544
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   (Technologie) 0795
Recherche opérationnelle 0796
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PSYCHOLOGIE
Généralités 0621
Personnalité 0625
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Psychologie clinique 0622
Psychologie du comportement ...0384
Psychologie du développement ..0620
Psychologie expérimentale 0623
Psychologie industrielle 0624
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THERMAL BIOLOGY OF THE COLORADO POTATO BEETLE (LEPTINOTARSA DECEMLINEATA (SAY)

(COLEOPTERA: CHRYSOMELIDAE)), WITH APPLICATION TO PEST

MANAGEMENT DECISION MAKING

BY

DEREK JON LACTIN

A Thesis submitted to the Faculty of Graduate Studies of the University of Manitoba in partial fulfillment of the requirements of the degree of

DOCTOR OF PHILOSOPHY

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ABSTRACT

Thermal Biology of the Colorado Potato Beetle (<u>Leptinotarsa</u> <u>decemlineata</u>
(Say) (Coleoptera: Chrysomelidae)), with Application to Pest Management
Decision Making.

By

Derek Jon Lactin

Major Advisor: Dr. N. J. Holliday

Temperature-dependence of larval Colorado potato beetle development
and feeding were investigated under temperature and insolation regimes
ranging from constant to relatively natural.

At constant temperatures, feeding in short-term trials continued at
temperatures which are lethal in long-term trials. Developmental rates in
long-term constant temperature trials agreed with published values.

Under field conditions, larval microhabitat choice was quantified
under combinations of temperature and insolation. A possible solar
heating effect on body temperature was inferred.

Under natural conditions, larval feeding was measured by confining
larvae with leaflets in small cages, and larval development was measured
by following cohorts through their ontogeny.

Models were assembled which estimate larval feeding and development
under field conditions. In both the feeding and development models,
predictions agreed best with observations if microhabitat choice and
inferred effects of solar heating on body temperature were considered.
The feeding model predicts feeding well. The best developmental rate
model consistently underestimates measured development by ≈9%; the bias

probably occurs because constant-temperature rate functions do not apply well to variable conditions.

The development and feeding models were further tested, using Colorado potato beetle phenology and damage data from populations on caged potato plants. The development model consistently overestimated numbers of third instars and underestimated numbers of fourths; plausible but non-exclusive explanations include model error and sampling bias against smaller instars. The feeding model was tested by converting daily population estimates from the development model into feeding estimates, summing these over the season, and comparing estimated total feeding to the difference between leaf area of infested and uninfested plants at harvest. This difference exceeds estimated total feeding; the disagreement increases with infestation intensity. The difference may result from reduction in photosynthetic area feeding back to reduce plant growth rate, or to bias observed in the development model.

Yield and population change data from the cage studies were used to estimate economic-injury levels for Colorado potato beetles on 'Russet Burbank' potato plants in southern Manitoba.

ACKNOWLEDGMENTS

DEDICATION

This thesis

is dedicated

to the memory

of the marriage

that it destroyed

TABLE OF CONTENTS

LIST OF TABLES

LIST OF TABLES, Cont'd

LIST OF TABLES, Cont'd

LIST OF FIGURES

LIST OF FIGURES, Cont'd

LIST OF FIGURES, Cont'd

LIST OF FIGURES, Cont'd

LIST OF APPENDICES

SECTION I. GENERAL INTRODUCTION

Section I. Chapter A)

BACKGROUND AND THESIS ORGANIZATION

1) The problem

Production of potatoes (Solanum tuberosum L. Solanaceae) is a major industry in Southern Manitoba. In 1979, ≈ 15000 ha. were planted to potatoes in this region; gross receipts accounted for $ 22.5 million. Processing potatoes, primarily cv. 'Russet Burbank', accounted for over 75% of planted area and over 77% of receipts (Manitoba agriculture 1981). Gross receipts from potato production in Manitoba were $36 million in 1985 and $38 million in 1986 (Agriculture Canada 1986).

The Colorado potato beetle (Leptinotarsa decemlineata (Say) (Coleoptera: Chrysomelidae) is a major pest of potatoes in Manitoba. Uncontrolled infestations of this pest can completely defoliate fields (Senanayake 1987; Ferro et al. 1983), and smaller infestations can cause economic damage. Economically, control measures are justifiable only if their cost is recovered as reduced yield loss (Stern et al. 1959). Normally, this is assumed to occur at a fixed population density, the economic injury level. This value varies according to growing conditions. Consequently, an economic injury level estimate derived in one area is probably not applicable to other areas. Similarly, the economic injury level differs among cultivars under identical conditions.

The economic injury level of Colorado potato beetles on Russet Burbank potatoes is not known with certainty in Manitoba, so potato producers' control decisions are not as well informed as they could be. In 1988, assuming a single annual application (B. Geisel, pers. comm. 1988) of registered chemicals at recommended rates (Kolach and McCullough 1992. Colorado potato beetle control in Manitoba were near $500,000 (N.J.

(N.J. Holliday, pers. comm. 1989). Clearly, any improvement in the accuracy of producers' control assessments could save a considerable amount of money. Thus, the ultimate objective of this thesis is to define an economic injury level for Colorado potato beetles on 'Russet Burbank' potatoes in Southern Manitoba.

Although economic injury levels are frequently stated as numbers per plant, this approach overlooks the dynamic nature of both the pest infestation and the ability of the plant to respond to it. Validated models of both processes would allow this simplification to be abandonned.

Insects are poikilothermic, which implies that some aspects of their physiology and behavior are dependent on ambient temperature. This dependency can be exploited to develop predictive models of insect phenology and, in the case of pest species, their damage potential. Approaches to developing such models fall along a gradient of complexity. Simplest is to compare responses of cohorts of insects reared under various constant temperatures, but the utility of such data in predicting behaviour under fluctuating temperature regimes is unclear (Hagstrum and Milliken 1991). Consequently, numerous authors have measured insect development rates under regularly varying temperature regimes (references in Hagstrum and Milliken 1991), but such regimes remain somewhat artificial in being predictable.

The next level of sophistication is to measure insect behaviour under conditions of naturally varying temperature. This type of study is complicated by microenvironmental heterogeneity and the capacity of the insects to move among microhabitats. Therefore, to be successful, the range of microhabitats available to the insect must be characterized, and

the impact of microhabitat choice by the insects must be determined. Combined, these data allow a relatively definitive determination of the temperature regime experienced by insects in the field. Feeding and developmental rates can then be related directly to this temperature regime.

2) Statement of objectives

My objectives in this study are to contribute to the understanding of the reactions of Colorado potato beetles to temperature, and to apply this understanding to pest management decision making. This obective will be attained by first quantifying the temperature-dependence of Colorado potato beetle behavior, feeding and development under controlled conditions, and then under variable field conditions. I will then assemble this information into mechanistic models of infestation and damage. Ultimately, I will attempt to apply these models to the decision making process in management of this pest.

3) Thesis organization

The thesis is organized as follows.

In Section I, Chapter B, the literature on economic injury level concept, on the biology of Colorado potato beetles and potato plants, and on the interaction of the two species, is summarized.

The section of the thesis which presents experimental results is divided into three sections (II - IV) as follows.

Section II consists of two chapters, which are devoted to characterising the feeding and developmental rates, respectively, of Colorado potato beetle larvae under constant temperatures in growth chambers. These studies repeat published studies, which were obtained

using larvae from various geographic locations. The repetition was deemed
necessary because of a suggestion (Tauber et al. 1988) that local strains
may differ in their thermal responses. Information obtained in these
studies is fundamental to later simulations.

Section III is divided into four chapters and deals with thermal
biology of Colorado potato beetles under field conditions. In Chapter A,
the materials and methods used throughout the section are summarized and
empirical relationships are derived by which temperature and insolation
within microclimates available to Colorado potato beetle larvae may be
estimated from macroclimatic data.

In Section III, Chapter B, the larval behavioral response to
combinations of insolation and ambient temperature is characterized.
Given this information, the distribution of larvae among microclimates may
be estimated using meteorological data.

In Section III, Chapters C and D, rates of larval feeding and
development, respectively, are measured under field conditions. In both
chapters, models are derived by which feeding and development under field
conditions may be estimated from theoretical insolation, and hourly
macroclimate data on temperature and cloud cover. Different versions of
these models include or ignore the effects of insolative heating and
behavioral thermoregulation, on larval body temperature. The measured
values of feeding and development are compared to predictions made by the
model versions.

Section IV deals with aspects of economic thermal biology of
Colorado potato beetles in Southern Manitoba. This section includes
methods and information required to validate the models of feeding and

development which were derived in Section III, and to derive economic injury levels of Colorado potato beetles on 'Russet Burbank' potatoes in southern Manitoba. In Chapter A, a method is described by which fresh mass of leaflets on potato plants may be estimated rapidly, and in Chapter B, the calibration of the mass estimate to an area estimate is explored. In Chapter C, populations of Colorado potato beetle larvae and adults are manipulated on caged plants, and the resulting data are used to test the models of feeding and development which were derived in Section III, and to derive economic injury level estimates.

Section V is a general discussion, in which the broader context of the results of the preceding sections is explored, contributions to knowledge are summarized, and possible avenues for further research are noted. Section VI contains references and appendices.

Section I.   Chapter B)

LITERATURE REVIEW

1) THE ECONOMIC INJURY LEVEL

1.1 Introduction

"Crop production" is a system of applied ecology by which humans ameliorate local environmental conditions to favor production of valued tissues by certain plant species (Geier and Clarke 1979). Conditions are simultaneously ameliorated for numerous other species, some of which (pests) may cause reduction in the yield value of these tissues. This review pertains specifically to insect pests.

Crop production is also a business, and the economic losses attributable to pests must be mitigated. The requirement of profitability dictates that all production decisions, including those of pest management, must be evaluated in terms of monetary costs and benefits. Pest control measures are economically justifiable only if benefit is expected to exceed cost; this statement is the foundation of the economic-injury level concept (Stern et al. 1959).

The literature on the theory and practice of integrated pest management has been discussed from various aspects in several excellent reviews (e.g. Bardner and Fletcher 1974; Mumford and Norton 1984; Pedigo et al. 1986). Only the most pertinent information is detailed here.

1.2 Economic injury level formulations

Evaluation of the economic impact of pests on crops is not a trivial undertaking. Direct pest effects (injury) may or may not (Pierce 1934) translate ultimately into yield loss (damage). Generally, the relationship between injury and damage is nonlinear; in the idealized case, it is logistic. Factors which determine the shape of this curve

include: plant tolerance of, or compensation for, limited injury; pest competition for favored sites at high infestation levels; and the intensity and timing of infestation relative to plant phenology. Bardner and Fletcher (1974) discuss these and other factors in detail.

The inherent nonlinearity of the relationship of injury to damage complicates assessment of the costs and benefits of specific pest management actions. Several approaches to this assessment have been postulated. Mumford and Norton (1984) recognized four general categories.

1.2.1 **The decision theory approach** is based on game theory (e.g. Luce and Raiffa 1957). All management choices (including inaction) are evaluated. The expected cost of any choice is its initial cost (e.g. labor and insecticides) plus the weighted sum of the costs of all possible consequences of that choice (i.e. yield loss), where the weight is the probability of occurrence. The best choice is that with the lowest expected cost. This approach requires detailed knowledge of the costs and probabilities of all possible outcomes. This is not always feasible; in fact, costs and probabilities may be spatiotemporally variable.

1.2.2 **The behavioral decision theory approach** (Mumford 1981) is a more subjective version of the previous approach, which is used when data are incomplete. The personal experiences of the producer or extension agent substitute for data. Thus, decisions are based more on individual perceptions of the problem, than on the real problem (Mumford 1981). This intuitive approach is better than a "standard operating procedure," such as fixed-schedule, or "insurance" spraying, but probably should be used only until data become available.

The decision-theory and behavioral decision-theory approaches are both probabilistic: the mean actual outcome approaches the expected value only after numerous trials. If the producer's goal is to maximize immediate profits, these approaches seem inappropriate.

1.2.3 **The marginal analysis approach** (Headley 1972, 1973) is a concept from economics. The producer attempts to maximize the difference 'benefit minus cost'. The assumptions are that gross revenue is an asymptotic increasing function of production costs and that the cost of removing X% of the pests from the population is an increasing exponential function of X. (This approach would be equally applicable where revenue and control cost have other relationships to X.) By fine-tuning insecticide application rate, the insect population should be reduced to the point that the difference between the two functions (i.e. benefit - cost) is greatest.

This is a deterministic approach which requires detailed knowledge of the mortality response of the pest population to a range of pesticide concentrations in the field, and of the relationship between yield and production costs, including the response of yield to pest infestation if insecticides are not used. In fact, both relationships are stochastic functions of growing conditions; this reality reduces the feasibility of the approach. This approach has a further defect: the assumption that insect mortality can be precisely tuned by adjusting the concentration at which pesticides are applied. This is invalid: pesticides are applied at a narrow range of rates (Kolach and McCullough 1992). This approach is theoretically rigorous "at the expense of biological and practical reality" (Mumford and Norton 1984).

1.2.4 The gain threshold approach (Edwards and Heath 1964; Stone and Pedigo 1972) suggests simply that pesticides be applied when benefit equals or exceeds cost. Benefit per hectare is calculated from the value of harvested produce, the population of the pest, the relationship between pest density and yield reduction, and the proportion of pests killed by pesticide application (Pedigo et al. 1986). Cost per hectare is the sum of pesticide costs and application costs. The economic injury level is the pest density which reduces yield value by a proportion equal to the ratio of control costs to yield value (Stone and Pedigo 1972). This approach merely specifies the minimum pest population at which benefit exceeds cost; it does not maximize net revenue.

The simplicity of this concept is illusory. The most basic problem is that forecasting proportionate reduction in yield value requires knowledge of yield value at harvest; most likely an educated guess is used. A similar difficulty is that yield reduction is a stochastic function of numerous interacting meteorological, biological, and agronomic variables.

Clearly, none of these methods of quantifying the cost:benefit relationship in pest management is perfect, but the gain threshold approach appears to be the best available compromise between economic rigor and biological realism. It will be adopted as the starting point for the following dissertation.

1.3 Economic injury level application

Estimation of the economic injury level is only the first step in the decision making process. The next step involves defining an "economic threshold" i.e. a pest population slightly smaller that the economic

injury level, such that farmers have time to mobilize their resources before the economic injury level is surpassed (Stern et al. 1959). Application of this concept involves predicting whether the pest population will surpass the economic threshold in the foreseeable future. This requirement dictates development of some sort of predictive model of the pest phenology. While such models come in many forms (Coulson and Saunders 1987), the most realistic and hence most reliable, are those founded on detailed information about the biology of the pest.

In this thesis, I examine the possibility of forecasting feeding injury by Colorado potato beetles (Leptinotarsa decemlineata (Say) (Coleoptera: Chrysomelidae)) on potato plants (Solanum tuberosum L. (Solanaceae)), by synthesizing data on temperature-dependent feeding and development with information on thermoregulatory behavior. The following section is a review of literature relevant to these goals.

2) THE COLORADO POTATO BEETLE - POTATO INTERACTION

2.1 INTRODUCTION

The current association of Colorado potato beetles (Leptinotarsa decemlineata (Say) (Coleoptera: Chrysomelidae)) and cultivated potatoes (Solanum tuberosum L. (Solanaceae)) is due to human intervention. The potato originated and was first domesticated in the Andes. The crop was introduced to Europe after the Spanish conquest of the Inca empire, and from Europe into North America in the 18th century (Hurst 1975). Colorado potato beetles probably originated in what is now northern Mexico (Tower 1906) or the south central Great Plains of what is now the U.S.A. (Neck 1983). The Colorado potato beetle originally fed on the leaves of solanaceous herbs, primarily S. rostratum Dunal, which is a widely-

distributed annual weed (Bassett and Munro 1986). The geographic range of Colorado potato beetles may have expanded northward along Spanish caravan routes (Tower 1906); that of the potato unquestionably expanded as a consequence of European settlement of the Great Plains. When this human movement resulted in range overlap of potatoes and Colorado potato beetles in the mid-1800s, Colorado potato beetles switched to the new host and spread quickly through potato growing areas (Hurst 1975). The Colorado potato beetle is now the most important defoliating pest of potatoes in most of the world (Ewing 1981), including Manitoba (Cole 1951).

2.2 COLORADO POTATO BEETLE BIOLOGY

2.2.1 **Life history.** Colorado potato beetle life history varies geographically, but there are certain constant traits. In Canada, adults overwinter and emerge in spring at about the time of potato emergence (Gibson et al. 1925). After feeding and mating the females deposit masses of ≈ 30 eggs, generally on the underside of host leaflets (Gibson et al. 1925; Harcourt 1963, 1964, 1971). Each female can produce up to 3000 eggs (Peferoen et al. 1981). There are four larval instars and a pupal stage. First instars move to the terminal leaflets of a young leaf. Larvae usually spend their entire feeding life on one plant, but may move among adjacent plants if the leaves touch (Gibson et al. 1925). Pupation occurs in the soil, near the base of the host plant. Adults emerge after a temperature-dependent duration and may oviposit. Depending on the length of the growing season, one to three generations may be completed (Hurst 1975). Canadian populations are usually univoltine (Gibson et al. 1925).

2.2.2 **Mortality factors.** Harcourt (1971) conducted a 10-year study of factors affecting undisturbed Colorado potato beetle populations in

Eastern Ontario. Key mortality factors (sensu Morris 1959) differed among life stages. For eggs, the key factor was cannibalism by larvae; for larvae younger than the middle of the second instar, it was rainfall; for older larvae, it was starvation after defoliation of the field; and for pupae, it was parasitization by Myiopharus doryphorae (Riley) (Diptera: Tachinidae). Although not a mortality factor, emigration was the key factor which affected adult numbers. Mortality of eggs and early larvae was density-independent. Starvation of late larvae was directly density-dependent. Pupal mortality was inversely density-dependent. Adult emigration was directly density-dependent, but overcompensating; over 95% of adults usually left if any did.

Overall, in this study, starvation of late larvae and emigration of adults were the key factors in the dynamics of these populations (Harcourt 1971), but both occurred only after the field was defoliated. In well managed crops, these factors are not important because no producer would allow defoliation to reach this extent. Hence, in agronomically realistic situations, no directly density-dependent mortality factors exist; that this species has attained pest status is therefore not surprising.

2.2.3 **Thermal biology.** Thermal biology is a subdiscipline which deals with organismal responses to temperature. Here I focus on the temperature effects on feeding, development, and behavior.

2.2.3.1 Feeding. Studies of temperature dependent feeding rates of immature phytophagous insects are uncommon in the literature. I have located only four studies in which rates of all instars are compared at a series of constant temperatures (Colorado potato beetle: Logan et al. 1985; Ferro et al. 1985; soybean looper, Pseudoplusia includens

[Lepidoptera: Noctuidae]: Kogan and Cope 1974; Trichilo and Mack 1989).
In all cases, feeding rate (area units)·(time unit)$^{-1}$ was obtained by
measuring total leaf consumption by the instar and dividing by the
stadium. Rates so calculated were temperature-dependent, but the results
provided no guidance in circumstances where temperatures briefly exceed
values which are lethal in long-term exposure.

Several groups have measured feeding rates of Colorado potato
beetles under laboratory conditions. Gibson et al. (1925) reared larvae
at a single temperature; Tamaki and Butt (1978) did so under varying
temperatures, but gave no details of thermal regime. Neither of these
studies show how temperature affects leaf consumption rate.

Ferro et al. (1985) reared all Colorado potato beetle feeding
instars at a range of constant temperatures (12 to 33°C) and a 16L:8D diel
cycle on excised bouquets of leaflets (cv. 'Superior'). Feeding response
to temperature differed among instars. In the 1st instar, total leaf
consumption was relatively independent of temperature; in instars 2 and 3
it increased over the range of temperatures, and for both 4th instars and
adults it peaked at 24°C. Because the 3rd and 4th instars and adults do
most of the feeding, maximum lifetime leaf consumption occurred at 24°C.

Logan et al. (1985) reared Colorado potato beetle larvae on excised
potato leaflets of unspecified cultivar at a range of constant
temperatures (15° - 33°C) and a 14L:10D diel cycle. In the 1st instar,
leaf consumption was highest between 19 and 23°C; that of the 2nd instar
peaked between 17 and 25°C, with an additional peak at 33°. Total leaf
consumption by both 3rd and 4th instars peaked at 23°C. Total lifetime
leaf consumption also peaked at 23°C. These authors did not test adults.

Ferro <u>et</u> <u>al</u>. (1985) and Logan <u>et</u> <u>al</u>. (1985) detected different relationships between temperature and leaf consumption in the 1st and 2nd instars; in both studies, measurement noise was large compared with the estimate, and may have obscured the true trend. This difficulty is of little consequence, because these instars consume only a small proportion of the total consumed over their lifetime. Their estimates of leaf consumption by larger instars and of lifetime leaf consumption agree well. Total larval leaf consumption is maximum at 23° to 24°C.

2.2.3.2 <u>Development</u> Development of Colorado potato beetle under laboratory conditions has been well studied (Walgenbach and Wyman 1984; Ferro <u>et</u> <u>al</u>. 1985; Logan <u>et</u> <u>al</u>. 1985; Groden and Casagrande 1986; Tauber <u>et</u> <u>al</u>. 1988). The results of the studies agree qualitatively. In all cases, development occurs only within a temperature range of $\approx$ 15° to 33°C and is maximal near 29°C, but there are some differences in the exact shape of the function relating developmental rate and temperature. Tauber <u>et</u> <u>al</u>. 1988 suggested that developmental rates of Colorado potato beetles from different geographic areas may differ, but their data did not show significant differences between populations; nonetheless, this possibility should be acknowledged.

In all studies, the development rate varied with temperature. Thus, the change in age-structure of a population of Colorado potato beetles may be predicted from temperature data, given sufficient data on temperature responses of the population under consideration. Descriptions of temperature-dependent development in this document use the non-linear model introduced by Logan <u>et</u> <u>al</u>. (1976). The choice of model was based on the following considerations. Linear and logistic models were rejected

based on inspection of the data and the consensus (e.g. Lamb and Gerber 1985) that they are inadequate. Five reasonable non-linear developmental rate models remained.

Harcourt and Yee (1982) proposed a cubic polynomial, which fits reasonably well at medium temperatures and approximates the developmental rate drop at high temperatures, but at low temperatures this model predicts a sharp (and infinite) increase in developmental rate, which is unreasonable.

Stinner et al. (1974) proposed a two-phase model, which uses a logistic model for temperatures up to that (T_{max}) at which development is maximal, then inverts the logistic relationship at higher temperatures. The curve fits data poorly at temperatures greater than T_{max}. A further problem is that the operator must intervene in the curve-fitting process to judge T_{max} by inspection of data plots. This subjective process is undesirable, particularly when data may be sparse near this temperature.

Sharpe and DeMichele (1977) proposed a model with a purported physiological basis. Lamb et al. (1984) seriously questioned the validity of the model's premises and suggested that the model fits well simply because it has six parameters.

Taylor (1981) proposed using a normal curve to describe the response, where the curve is scaled by multiplying the normal function by a factor sufficient to raise the maximum value to the observed maximum developmental rate. This model is unable to account for the asymmetry of the developmental response. Lamb and Gerber (1985) suggested fitting separate half-normal curves to the data above and below T_{max}. The following objections caused me to not use this model. First, at least

four data points are needed to estimate the curve above T_{max}. This requirement is frequently difficult to fulfil because of the narrow temperature range above T_{max} in which survival is possible, and because T_{max} is seldom known sufficiently well in advance to guide selection of appropriate temperatures for experimentation. Second, the nonlinear method of fitting separate curves with matched asymptotes requires intervention in the choice of T_{max}. As noted for the Stinner model, this subjective approach is undesirable.

The Logan model (Logan et al. 1976) has several comparative advantages. It has only four, yet consistently produces a curve which fits data well. Most importantly, all data contribute to estimation of the portion of the curve above T_{max}. Thus, the ability to estimate this section of the curve does not require several points in this region. I judged this model to be most appropriate for the present study.

2.2.4 **Thermoregulation.** Despite a large knowledge base regarding insect thermoregulation, most of this information pertains to endothermy in flying adults (Heinrich 1981; May 1979). May (1981, 1982) is the only source of information regarding Colorado potato beetle thermoregulation. He determined that adults and late instar larvae maintain body temperature (T_b) above ambient temperature (T_a) during daytime, and derived multiple regression equations which enable estimation of T_b from T_a, insolation, wind speed and relative humidity. Insolation is the strongest determinant of T_b elevation. While constituting an important first step in characterizing Colorado potato beetle thermoregulation, this study was essentially a cross-sectional survey of Colorado potato beetle distributions under given conditions. A longitudinal study of the change

in population distribution in response to changes in meteorological variables would clarify whether these changes can be predicted in the short term. This aspect of the dynamics of the behavioral thermoregulatory response is very important in field population models.

2.2.5 Application of constant-temperature data to variable-temperature conditions.

Numerous groups have compared developmental rates of immature insects under constant and varying temperatures; results have been mixed, for two main reasons. First, compared to developmental rates at constant temperatures, variable temperatures have been variously observed to reduce developmental rate (e.g. Siddiqui and Barlow 1973; Hagstrum and Leach 1973), to increase developmental rate (e.g. Messenger 1964; Hagstrum and Leach 1973), or to have no effect (e.g. Welbers 1975; Elliott and Kieckhefer 1989; Guppy 1969). Where varying temperatures did affect developmental rate, the magnitude and direction of the effect were often dependent on the mean temperature chosen, relative to developmental thresholds and optima (e.g. Butler and Lopez 1980; Messenger and Flitters 1959; Mellors and Allegro 1984), and on the amplitude (e.g. Siddiqui and Barlow 1973; Lamb and Gerber 1985) or frequency of the oscillations (e.g. Behrens et al. 1983). These observations also pertain to Colorado potato beetles. Compared to rates at constant temperatures, variable temperatures accelerate larval development when the mean temperature is $\leq 22.5°C$, but slow development at higher mean temperatures (Chlodny 1975). Furthermore, Logan et al. (1985) demonstrated that egg development continued at a rate higher than expected for "more than 3h" on exposure to temperatures which are lethal on extended exposure. Because of these

diverse results, the only possible conclusion is that developmental rates under varying temperatures probably can not be determined with confidence directly from rate functions obtained under constant temperatures.

The second reason that attempts to transfer constant-temperature developmental rate information to variable conditions have met with limited success results from the difficulty in determining temperatures to which the insects are exposed in the field. Developmental rates of Colorado potato beetle populations in the field have been measured indirectly by several groups. They compared observed phenology to predictions based on constant-temperature developmental rate studies (Walgenbach and Wyman 1984; Tauber et al. 1988; Groden and Casagrande 1986). Each group observed that the free living populations developed consistently more rapidly than predicted. When Groden and Casagrande (1986) used an equation from May's (1981) thermoregulation study to adjust maximum daily temperature by a constant 6.54°C, the disagreement between observed and expected developmental rates in first instars was reduced to less than 6.5%. They did not say whether this approach was similarly successful in correcting the disagreement in other instars.

The approach used by these groups to estimate larval development is somewhat unsatisfying for two reasons. First, each group estimated daily mean temperature from daily maximum and minimum Stevenson screen temperatures, then estimated development and feeding from this value. In doing so they assume implicitly that the relationship between temperature and developmental rate is linear over the range of temperatures encountered during the interval. This is clearly an oversimplification. A further problem is that although mean daily temperatures in the north

eastern U.S.A., where these estimates were made, seldom exceeded levels which are lethal in constant-temperature studies (Logan et al. 1985), observed temperatures frequently exceeded this limit for brief periods. The use of the daily mean overlooks the impact of these transient temperature phenomena.

Daily feeding and developmental rates are best estimated by multiplying instantaneous temperatures by temperature-dependent development and feeding functions, then integrating over time (Curry and Feldman 1987); more practically, an approximation can be made by summation over short intervals, such as hours. This amounts to compiling a weighted average of hourly temperatures, where weights are temperature-dependent rates. When using daily mean temperatures, the sum is unweighted. The two types of sums agree only when the temperature dependence is linear over the range of temperatures encountered, an unusual circumstance.

A second objection to the use of Stevenson screen temperature data is that temperatures are measured in the shade, and correspond only weakly to temperatures experienced by Colorado potato beetles, which are exposed to sunlight and can choose among shaded and sunny microhabitats. Groden and Casagrande's (1986) use of May's (1981) regression model to adjust for body temperature elevation is a *post hoc* approximation, the effectiveness of which is limited by the poor temporal resolution of the temperature data, and by the inability to include the effects of varying insolation and of thermoregulatory behavior in the correction.

A superior approach would be to estimate larval body temperature directly during short time increments, using macroclimatic temperature and insolation data and information regarding behavioral thermoregulation.

This estimate could then be used as the independent variable in equations describing development and feeding.

2.2.6 **Conclusion** A review of the literature has demonstrated that there is a good deal of information on the basic biology of the Colorado potato beetle. In particular, thermal responses have been well studied under constant temperatures, but knowledge of Colorado potato beetle thermal biology under field conditions appears to be in a rudimentary state. Such information is fundamental to development of a model of Colorado potato beetle phenology under natural conditions.

2.3 THE POTATO

2.3.1 **Growth traits.** Plants assimilate 85-90% of their dry matter by photosynthetic conversion of light energy into chemical bonds (Milthorpe and Moorby 1974). Crop growth has been assumed to be proportional to photosynthesis, which is dependent on the amount of radiant energy intercepted by the foliage (Montieth 1979). This can be expressed as a function of the product of the amount of energy intercepted by the leaf surface, and the efficiency of its use (Montieth 1977). Under a specified set of conditions, the efficiency of energy use seems nearly constant (Allen and Scott 1980). Thus, where water and nutrients are not limiting, variation in yields of a given crop in a given area is due primarily to variation in the amount of energy intercepted. This concept has been corroborated for potatoes (Sale 1973).

The growth of the potato plant involves numerous simultaneous processes, all of which are affected by growing conditions. Initially, leaves, stems and fibrous roots develop most rapidly; later, tubers do.

Given that tubers are the valuable tissue, an understanding of the mechanism by which photosynthate partitioning changes to favor tuber growth is perhaps the most important requirement for detailed understanding of potato plant growth. This question has been the subject of considerable study.

The balance between vegetative growth and tuber growth is strongly influenced by temperature. High temperatures favor vegetative growth and flowering, accelerate leaf senescence, and reduce the number and total weight of tubers (Cho and Iritani 1983). These responses are universal among potatoes, but the exact relationships differ among cultivars (Marinus and Bodlaender 1975).

Increase in leaf area of the plants is a combination of leaf initiation and leaf expansion (Stone 1933). Most leaves are initiated in a short period early in the growing season; in some cultivars leaf initiation later ceases, but in others (including 'Russet Burbank'), it continues at a declining rate (Bald 1943).

The physiology of tuber formation and bulking (tuberization) is not well understood. Tuberization occurs after a change in the relative concentrations of inhibitory and promoting substance(s) in the plant; the inhibitor appears to be gibberellic acid, and abscisic acid is considered the main promoter, although other substances may also be involved. This change is induced mainly by short daylength and low temperature, but is inhibited by high nitrogen concentrations. After initiation, the tubers seem to be the main source of abscisic acid (Krauss 1985).

The number of tubers initiated by 'Russet Burbank' potato plants increases with temperature in the spring, and the rate of increase of

tuber mass per plant (bulking rate) is accelerated by cool summer temperatures (Cho and Iritani 1983). The bulking rate in the cv. 'Ostara' is limited by the amount of photosynthate produced, rather than by the capacity of the tubers to assimilate it, or by the capacity of the phloem to transport it (Engels and Marschner 1987); this is likely to be the case for all cultivars. The mean final size of tubers is inversely related to the number of tubers per hill (Bleasdale 1965; Iritani et al. 1983); this was interpreted to means that a fixed amount of photosynthate is partitioned among all tubers.

Fig. 1 (after Fishman et al. 1985, Johnson et al. 1988, and Ng and Loomis 1984) conceptualizes the basic processes of potato growth. Light energy intercepted, a function of leaf area index (LAI), is combined with nutrients and water during photosynthesis, which is heat driven; photosynthate ("dry matter") results. Most dry matter is actively partitioned among leaves, stems, tubers and roots; Johnson et al. (1988) observed that their model worked better if some photosynthate was held in a reserve pool, but they did not specify where this pool might be. Temperature also effects photosynthate partitioning.

The various tissues grow at different rates; this is because photosynthates are partitioned among the organs. Photosynthate going to leaf and root production feeds back positively to photosynthetic rate by increasing the ability of the plant to intercept light, and to take up nutrients and water, respectively. Therefore, early preferential partitioning of photosynthates to leaves and roots is desirable, but for a potato cultivar to be agronomically desirable, photosynthate partitioning must ultimately change to favor tuber growth.

To conclude, tuber growth is related to leaf area, but this relationship is affected by factors such as temperature and competition among tissues within plants. These interacting factors should be considered when examining the effects of defoliation on yield.

2.3.2 Effect of defoliation on tuber yield. Because leaf area is the source of almost all photosynthate which goes into the tubers, and because the strength of this source limits tuber growth, quantification of the effect of defoliation on yield is of interest. The earliest attempts involved 'artificial defoliation'; later, natural defoliation was used. Two types of defoliation are recognized: short-term (acute) and extended (chronic).

Studies of the effects of acute defoliation involved removing a given proportion of a plant's leaf area at a single time, by various methods, either artificial (e.g. Takatori et al. 1952; Snyder and Michelson 1958; Murphy and Goven 1962; Beresford 1967; Wellik et al. 1981) or natural (Hare 1980). The effect of acute defoliation varies according to the time at which injury occurs. Most of these studies indicate that potato plants are most sensitive to defoliation at the time of tuber initiation and rapid bulking, but not all studies demonstrated this effect (c.f. Cranshaw and Radcliffe 1980). The impact of natural acute defoliation by Colorado potato beetle on potato tuber yield is similar but reduces yield by only 65-70% as much as does the same amount of mechanical defoliation; this occurs because mechanical defoliation is indiscriminate, injuring stems and buds in addition to leaves (Hare 1980).

The effect of chronic defoliation has not been as thoroughly studied. Cultivars appear to respond differently. Wellik et al. (1981)

artificially maintained the leaf area of defoliated plants (cv. 'Red LaSoda') at a fixed proportion of the leaf area of control plants. The plants tolerated almost 30% leaf area reduction over the season without statistically significant yield loss; the yield fell linearly if proportional defoliation exceeded 30%. Senanayake and Holliday (1990) examined the impact of chronic natural defoliation by Colorado potato beetle on yield of caged plants (cv. 'Norland'). They adjusted Colorado potato beetle populations on caged plants weekly so that, over the season, each plant was exposed to a constant multiple of the population in a naturally-infested field. There was no evidence that plants of this cultivar tolerate low levels of chronic defoliation.

2.3.3 Conclusion. Defoliation studies in potatoes make two points directly relevant to the economics of pest control in this crop. First, acute yield loss studies show that the impact of a specified amount of defoliation varies over the season; therefore, control recommendations should consider the timing of the attack, relative to plant growth. Secondly, the impact of chronic defoliation varies among cultivars, and probably among years; these differences may reflect differences in plant growth traits. If yield is correlated with the integral of leaf area index over time (Bremner and Radley 1966), then yield differences in plants of similar canopy size are due at least in part to differences in the length of the bulking stage (Collins 1977) and the differences in the yield/defoliation response curves may be due to differences in the duration of the tuber bulking period. Together, these points emphasize that attempts to quantify the relationship between infestation and yield loss should consider not only the amount of leaf area removed, but also

the timing of leaf area reduction relative to the period of rapid bulking, and the duration of leaf loss relative to the lifetime of the plant. Because yield reduction due to defoliation by Colorado potato beetle results in less yield loss than does artificial defoliation (Hare 1980) these studies should be conducted using defoliating insects, rather than artificial defoliation.

Further, since yield loss is closely correlated to leaf area removed (Senanayake and Holliday 1990), some attempt must be made to express Colorado potato beetle populations in terms of the leaf area they eat per unit time. This conclusion is compatible with the suggestion that yield reduction should be expressed as a function of the duration of leaf area reduction relative to the duration of an undisturbed canopy.

Figure 1. Conceptual model of potato growth (Simplified after Ng and

Loomis 1984, Fishman et al. 1985, and Johnson et al. 1988).

Symbols: Circles are "forcing data" (Ng and Loomis 1984);

parallelograms are state variables; the oblate rectangle is

the key factor (LAI = leaf area index) which determines gross

photosynthetic rate; valves denote physiological processes.

Arrows denote influence.
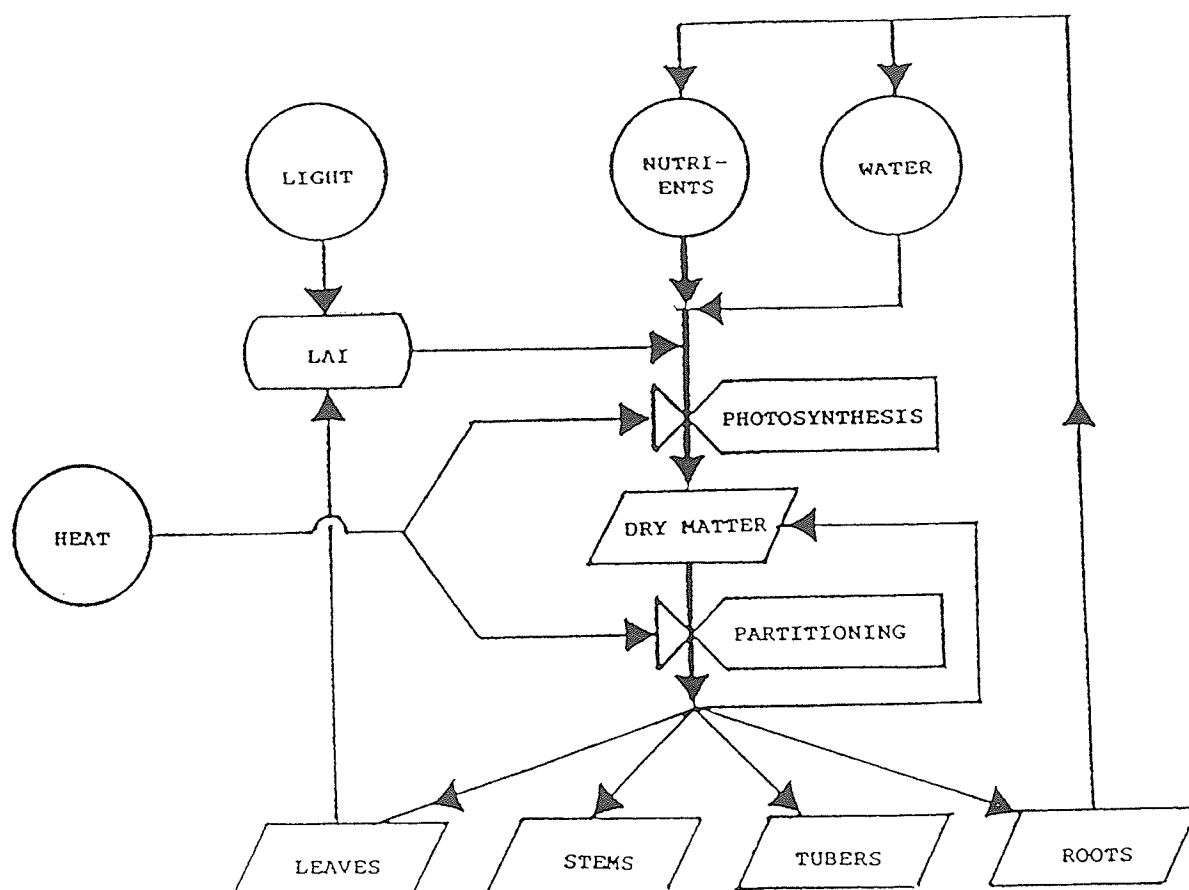
SECTION II.   CONSTANT-TEMPERATURE THERMAL BIOLOGY OF COLORADO POTATO
          BEETLES

Section II.   Chapter A)
        TEMPERATURE-DEPENDENCE   AND   CONSTANT-TEMPERATURE   DIEL
        APERIODICITY OF FEEDING BY COLORADO POTATO BEETLE LARVAE
        (LEPTINOTARSA DECEMLINEATA (SAY) (COLEOPTERA: CHRYSOMELIDAE))
        IN SHORT-DURATION LABORATORY TRIALS.

ABSTRACT

Feeding rates ($mm^2 \cdot h^{-1} \cdot larva^{-1}$) of larval Colorado potato beetles (<u>Leptinotarsa</u> <u>decemlineata</u> (Say) (Coleoptera: Chrysomelidae)) were measured in 2 - 2.5 h trials on excised 'Russet Burbank' potato (<u>Solanum</u> <u>tuberosum</u> L.) leaflets at constant temperatures from 14° to 42°C. In all instars, feeding rate was greatest at 29 - 32°C, and decreased symmetrically at higher and lower temperatures. Second, third and fourth instars fed at 42°C.

In 24h trials consisting of repeated 2 - 2.5 h measures at ≈ 6 h intervals, feeding rates at 23 and 29°C varied among and within groups of larvae, but no consistent diel pattern was detected.

INTRODUCTION

Pest management measures are justifiable only if their benefit exceeds their cost (Pierce 1934; Stern et al. 1959). Benefit is a function of reduced yield loss. Colorado potato beetles decrease potato tuber yield indirectly by reducing leaf area and hence photosynthate production; therefore benefit is related to the difference in leaf area removed in the presence and absence of control measures. In theory, potential future leaf loss due to Colorado potato beetle can be estimated by coupling a model which describes leaf consumption by each instar, with a second model which forecasts change in numbers and instar constitution of the population. Pest management benefit under various scenarios can be estimated by simulation using these coupled models. This approach requires adequate characterization of temperature-dependent feeding rates of each instar under the fluctuating conditions encountered in the field.

The simplest approach to estimating feeding by poikilotherms subject to varying temperatures is to use a rate : temperature function derived under constant temperatures. By applying this function to the temperature record from the field, feeding can be estimated for an interval by integration. This approach assumes that feeding rates respond instantaneously to temperature change, and that temperature responses in the field are equivalent to those under constant laboratory conditions. Neither assumption has been tested for Colorado potato beetles.

Logan et al. (1985) and Ferro et al. (1985), reared Colorado potato beetle larvae at constant temperatures and measured developmental time and

total leaf area consumed for each instar; leaf consumption per unit time
can be determined from these data. However, this method is feasible only
for temperatures at which larvae survive through the instar; in the field,
larvae commonly survive short exposures to high temperatures to which
prolonged exposure is lethal. Feeding at these high temperatures
contributes to the damage potential of the pest population, yet currently
available data provide no estimates of leaf consumption under such
conditions. To estimate population damage potential under fluctuating
temperature regimes, direct measurement of feeding rates under short
exposures to supraoptimal temperatures is necessary; this is the main
purpose of the present study.

A second purpose was to determine whether short-term feeding
measurements adequately characterize long-term feeding behavior. Colorado
potato beetle larvae appear to feed continuously (Gibson et al. 1925) but
the possibility remains that consumption rates may vary in a temperature-
independent diel pattern. Short-term feeding measurements sample only
part of the 24 h cycle, and so chance correlation between measurement
schedule and any such feeding cycle could lead to erroneous conclusions.
Therefore a trial was designed to test whether a diel pattern in feeding
rate exists.

MATERIALS AND METHODS

General

Feeding arenas were constructed of two 2.5 cm diameter petri dish
bottoms, placed with open ends aligned. An excised, fully-expanded potato
leaflet, cv. 'Russet Burbank' of minimum linear dimension > 2.5 cm was
placed between the two dishes with the adaxial surface uppermost and the

leaflet margin excluded from the enclosed area. The basic experimental unit consisted of three to six such arenas, sealed in a 14 cm diameter x 2 cm tall plastic petri dish, on six to eight layers of wet paper towel. The paper towel raised the arenas to contact the lid of the large dish, which was held in place with tape, thus firmly closing the arenas. Each experimental unit included several infested arenas and one or two control arenas.

In infested arenas, a known number of a given instar were placed directly on the adaxial surface of the leaflet. Numbers of larvae per arena were: first instar: four or five; second instar: three or four; third instar: two; fourth instar: one. Because larvae were denied access to leaflet margins, feeding damage was delimited unambiguously, and this allowed direct measurement of lesion area.

Control arenas were included to enable correction for changes in lesion area caused by leaflet shrinkage after injury. Each contained a leaflet in which a lesion of known area had been made using a scalpel or cork borer. The area of each control lesion was determined before and after the trial. Assuming that feeding rate and the change in lesion area were both constant during the trial, measured lesion areas in the infested arenas were adjusted by a percentage equal to one half the percentage change in control lesion area. This adjustment was always less than 2% and usually much less than 1%. Initial trials included two control arenas, but the shrinkage effect was so small that this number was reduced to one. Absolute shrinkage was independent of the initial size of the control lesions.

37

Lesion measurement

Immediately after each trial, feeding lesions were measured using an image analysis program developed by Dr. L.L. Lamari, Dept. of Plant Science, The University of Manitoba. The signal from a JVC TK-1070U® solid state color RGB video camera equipped with a Nikon® 50 mm planar focus macro lens was digitized using an 8-bit real-time framegrabber (PC vision plus®, Imaging Technology Inc., 600 West Cummings Park, Woburn MA 08101). Over all measurements, the object-to-lens distance was held constant. An empirically derived calibration constant was used to convert pixel count to lesion area. Measurement error (SD/mean) was relatively constant at $\approx$ 1% of the lesion area; in performance trials conducted under the conditions of this experiment, the greatest measured absolute error was less than 2 mm^2 (data not presented).

Short-term feeding rate trial

Feeding rates of Colorado potato beetle larvae were measured at 14°, 17°, 20°, 23°, 29°, 37°, and 42°C and a photoperiod of 14:10 (L:D) h. Larvae were reared from eggs laid by adults collected in summer 1991 from the University of Manitoba campus at Winnipeg, MB, Canada (49° 54′ N 97° 9′ W) (MB 'isolate') or from a home garden in Winfield, BC, Canada (50° 02′ N, 119° 24′ W) (BC 'isolate'). Experimental subjects of each isolate were reared in a nursery colony at 23° or 29°C, and a photoperiod of 14:10 (L:D) h. Approximately 2 h before each trial, larvae of the desired instar were moved into the test temperature and held in petri dishes supplied with fresh excised leaflets and moist paper towel. At 37° and 42°C, owing to rapid onset of mortality, larvae were moved to the test temperature 30 - 45 min before the trial.

Groups of larvae were assembled arbitrarily from those available, and placed in the arenas. Trials lasted for 2 to 2.5 h, measured to within 5 min. Trials were carried out at various times of the diel cycle.

In each instar, the temperature-dependent feeding response was fit to a quadratic model of the form:

$$Y = q + r \cdot T + s \cdot T^2 \qquad (1)$$

where Y is mean feeding rate ($mm^2 \cdot h^{-1} \cdot larva^{-1}$), weighted by sample size; q, r, and s are fitted parameters; and T is temperature in °C.

Diel feeding pattern trial

Repeated measures of feeding rate were made on groups of each instar (MB isolate only) at 23°C and 29°C and a photoperiod of 14:10 (L:D) h. Groups of larvae were assembled as needed from nursery colonies maintained at the test temperature. At both temperatures, five groups were tested for each of first and second instar, and seven for the third and fourth instars.

In each instar, several groups of larvae were repeatedly confined to arenas for 2 to 2.5 h at intervals of ≈ 6 h. Groups remained together for the duration of each 24 h trial. Feeding by each group was measured twice during each of the dark and light phases, comprising a complete diel cycle. Trials started at various times during the diel cycle; none of the measurements included a change in light phase, and none started within 0.5 h after such a change. Larvae were returned to the nursery colonies after use, and may have been reused as later instars.

To determine whether average feeding rates differed between light and dark phases, feeding rates for each combination of instar, measurement, group and temperature regime, were converted to $mm^2 \cdot larva^{-1} \cdot h^{-1}$

and weighted by the number of larvae per arena. The weighted means were analyzed using analysis of variance (PROC GLM, SAS Institute 1988), with independent variables being group and insolation phase nested within group.

Periodic regression (Batchelet 1981) was used to determine whether feeding rate varied cyclically over the 24 h period. The feeding rate of each group at a given measurement was standardized to a proportion of the 24 h mean for that group, and these rates were analyzed using a model of the form:

$$S_i = M + A \cdot \cos(t_i - \phi) \tag{2}$$

Parameters are as follows: S is mean scaled feeding rate $(mm^2 \cdot h^{-1} \cdot larva^{-1})$; t_i is hour of day at which the feeding measurement started; ϕ is the time at which maximal feeding rate occurred; M is the value of the feeding rate when $\cos(t_i - \phi) = 0$; and A is the amplitude of the daily feeding rate fluctuation. Both t and ϕ are expressed in radians, with 24 h = 2π radians. For each temperature and instar, the value of ϕ was first estimated by iterative nonlinear regression (PROC NLIN, DUD algorithm, SAS Institute 1988). This estimate was used to calculate $\cos(t_i - \phi)$, which was substituted into equation (2), after which estimates of M and A were obtained by weighted linear regression (PROC REG, SAS Institute 1988), where weight is sample size.

RESULTS

Temperature-dependent feeding rates

Feeding rates were not significantly affected by larval isolate or isolate-by-temperature interaction ($P > 0.05$), so pooled data are presented (Fig. 2, A - D). Sample sizes are summarized in Table 1.

Parameter estimates from the quadratic regressions of feeding rate on temperature are listed in Table 2.

Feeding was measurable at all temperatures in all but the first instar, in which no feeding occurred at 42°C (Fig 2, a-d). In all instars the quadratic model described the observations well, except that it overestimated feeding by first instars at 42°C. First instars feed relatively little and such temperatures occur briefly and infrequently, so this error is of little practical consequence. Feeding rate was maximal near at 29° - 32° C in all instars.

Diel feeding pattern

Figure 3 illustrates the results of the diel feeding pattern trial for each instar. Feeding rate by each group at a given measurement is standardized to a proportion of the 24 h mean for that group and plotted against time after lights-on. Table 3 summarizes results of the analysis of variance testing whether feeding rates varied between light and dark phases. There was no evidence that feeding rate differed between light and dark phases, except in first instars at 23°C, in which feeding by two of the five groups was significantly greater during the light phase. In these two groups (c and d), the measurements started during the late light phase and continued through to early in the following light phase. Measured feeding by groups c and d increased constantly during the trial to a maximum at the final measurement. Larvae in groups c and d were newly emerged at the start of the measurements ($\approx$ 2 - 6 h old, versus $\approx$ 12 h for other groups) and the apparent diel pattern may result from an age-dependent increase in feeding rate. If groups c and d are eliminated from the analysis, this significant difference disappears.

Results of the periodic regression of standardized feeding rates on time of diel cycle are presented in table 4. There was no evidence of a periodic trend in feeding rate, except in the first instar at 23°C, and in the first instar, pooled over 23° and 29°C. This result is also due to groups c and d. Deletion of groups c and d from the analysis renders the periodic regressions non-significant. In the remaining groups and instars, feeding rate was not constant, but variations were not related to diel cycle.

DISCUSSION

Short-term feeding rate trial

Comparison of the present hourly feeding rate data with those calculated from data presented in Logan et al. (1985) and Ferro et al. (1985) reveals both similarities and differences (Fig. 4). In our short-duration trials, larvae fed at a substantial rate during brief exposures to temperatures above 33°C, which is approximately the upper lethal limit defined by Ferro et al. (1985) in constant-temperature studies lasting for entire stadia. (Logan et al. [1985] identified no upper lethal limit but were unable to rear larvae at temperatures exceeding 33°C). Over larval development, the cumulative consumption at temperatures above 33°C could be significant, and should be considered explicitly when estimating population feeding rates under field conditions. Temperatures on potato leaflets frequently exceed 33°C (May 1982), and because Colorado potato beetle larvae elevate body temperature by behavioral thermoregulation (May 1982) this potential error is magnified.

Comparison of results at temperatures less than 33°C (Fig. 4) is also informative. Feeding rates measured in this study agree relatively

well with those of Ferro et al. (1985) except for the fourth instar and at 30° and 33°C in the second instar. Agreement is less good with data presented by Logan et al. (1985). At temperatures less than 33°C, the greatest disagreement between our results and those of the Ferro et al. (1985) and Logan et al. (1985) involves fourth instars. Feeding rates in our study are consistently much higher than the published data for all temperatures exceeding 17°C. Because the fourth instar has the longest stadium and the greatest feeding rate, it is the most injurious; therefore, an explanation of the difference in feeding rate estimates is important. Five possible explanations follow.

The first possible source of this discrepancy is a consequence of leaflet growth characteristics. The area:mass ratio of undamaged 'Russet Burbank' leaflets changes from $\approx 2,000$ mm$^2 \cdot$ g^{-1} at plant emergence to $\approx 5,000$ mm$^2 \cdot$ g^{-1} at mid-season (This thesis, Section IV, Chapter B). Larval foliage consumption is probably better measured by leaf mass than by area; if so, to obtain a given amount of food, a larva requires a greater area of a more mature leaflet than of a young one. Hence, the difference in feeding rate estimates may result from differences in the age of the leaflets used. Ferro et al. (1985) used "young terminal leaflets"; the leaflet area:mass ratio was probably near the smaller value. Logan et al. (1985) collected leaflets from 25 - 30 cm plants; only young plants are so small, and leaflets likely had an area:mass ratio near the lower value quoted above. In the present study, only fully expanded leaflets were used; while the area:mass ratios were not measured, they were probably near the high end of the range quoted. The difference in fourth instar feeding rate between our study and those of Logan et al. (1985) and Ferro

<u>et</u> <u>al</u>. (1985) is of the same magnitude as the difference in area/mass ratios of fully expanded and newly initiated leaflets. However, this possibility fails to explain the relatively better agreement between our data and published results, in instars other than the fourth.

A second possibility is that resource limitation occurred in the long-term trials due to surface fouling, depletion of the supply of preferred food items, or both. These limitations would be most serious in the fourth instar; thus this explanation is most broadly applicable.

A third possibility is that fourth instars may cease to feed for some period before abandoning the leaflet as prepupae. This would reduce average feeding rate over the full instar, but would not affect short-term measurements. This explanation is implausible because to yield the observed difference between our feeding rate estimates and those of Logan <u>et</u> <u>al</u>. (1985) and Ferro <u>et</u> <u>al</u>. (1985), any non-feeding period would occupy 40 to 50% of the stadium, i.e. more than a day. Inertia of this duration would be obvious; I have never observed it, nor have I encountered published reference to it.

A fourth possibility is that sample estimates in the present trial are erroneous because of non-representative sampling of a cyclic feeding pattern. The temporal aperiodicity of feeding observed in the diel feeding trial eliminates this possibility.

Finally, the differences may indicate that geographic populations feed at different rates; this possibility seems implausible in view of the lack of difference in developmental rates among geographic populations (Tauber <u>et</u> <u>al</u>. 1988).

Thus, the two most plausible explanations of the discrepancies in estimated feeding rate between our data and those of Ferro et al. (1985) and Logan et al. (1985) are that differences in area:mass ratios of leaves used in the estimation process may have differed among the trials, and that resource limitation may have occurred in the long-term feeding trials. If these explanations are correct, then the rate estimates in our trial probably best measure injury under natural conditions, for three reasons. First, leaves expand relatively quickly after initiation, and are 'fully expanded' for the greater proportion of their lifetime; unless feeding is synchronized with leaf phenology, injury is more likely to occur on leaflets which are at or near full size. Second, lesions inflicted on young leaves may expand as the leaf grows thereafter (Lowman 1987), so injury measured on young leaflets may underestimate ultimate lesion area. Third, under field conditions, larvae may move among leaflets; thus the impact of resource limitation is minimal unless the plant becomes heavily defoliated.

Diel feeding trial.

The inconstant but temporally aperiodic diel feeding pattern suggests that the larvae alternate periods of ingestion and digestion, independent of photic entrainment cues. The aperiodic larval feeding pattern indicates that estimates of feeding under varying temperatures are not complicated by temperature-independent cyclic responses.

Both the observed tolerance of Colorado potato beetle larvae to brief exposures to high temperature, and the apparent lack of an inherent temperature-independent diel feeding pattern are advantageous traits whose occurrence is consistent with the probable subtropical origin of L.

<u>decemlineata</u> in northern Mexico (Tower 1906), or the southern U.S. great plains (Neck 1983), where high day-time temperatures and warm night-time temperatures are common (National Oceanic and Atmospheric Administration 1980). Where daytime temperatures become hot enough to depress feeding rates for significant intervals, individuals which are more tolerant of high temperatures can feed more in a given interval, and presumably develop faster than less temperature-tolerant individuals. The advantage of diel aperiodicity in feeding is similar: larvae which are not constrained to cease feeding at night have an advantage over individuals which feed only diurnally.

Table 1. Numbers of larvae used to estimate constant-temperature feeding
rates of Colorado potato beetle larvae.

INSTAR	TEMPERATURE [°C]							
	14	17	20	23	29	32	37	42
1	36	26	23	22	16	20	26	7
2	7	17	17	13	33	22	14	13
3	17	17	17	11	15	12	18	10
4	11	11	11	10	8	10	12	24

Table 2. Parameter estimates of quadratic regression models describing feeding rates ($mm^2 \cdot h^{-1} \cdot larva^{-1}$) of Colorado potato beetle larvae under brief exposure to constant temperatures (T, °C). Regressions on means weighted by sample size.
Models are of form: $Y = q + r \cdot T + s \cdot T^2$
All models and parameter estimates are significant ($p \leq 0.05$).

INSTAR	PARAMETER						$F_{2,9}$	r^2
	q		r		s			
	EST.	S.E.	EST.	S.E.	EST.	S.E.		
1	-3.97	0.88	0.374	0.073	-0.00633	0.0014	20.0	0.89
2	-15.4	2.20	1.46	0.17	-0.0256	0.0029	39.2	0.94
3	-41.3	7.51	4.10	0.603	-0.0710	0.011	25.3	0.91
4	-224.1	30.9	20.72	2.38	-0.357	0.041	38.0	0.94

Table 3. Comparison of feeding rates of Colorado potato beetle larvae
(mm$^2\cdot$h$^{-1}\cdot$larva^{-1}) under light and dark conditions, at 23 and 29°C.

Instar	N[a]	Feeding (mm$^2\cdot$h$^{-1}\cdot$larva^{-1})				Model[b]		P(no effect)[c]	
		Dark		Light				Group[d]	Phase[e]
		Mean	SE	Mean	SE	F	df		
				23°C					
1	22	0.47	0.25	0.59	0.14	4.62	9,10	*	*
2	13	2.30	0.82	1.82	0.71	2.79	9,10	*	
3	11	13.37	2.94	15.16	5.15	2.05	11,10	*	
4	10	35.71	5.70	32.71	8.97	0.59	13,12		
				29°C					
1	21	1.01	0.38	1.05	0.23	2.82	9,10		
2	12	3.05	0.71	2.21	0.50	4.38	9,10	**	
3	10	20.99	6.12	29.20	4.89	1.40	10,10		
4	9	68.37	9.67	70.50	9.84	3.63	13,13	**	

[a] number of larvae surviving trial; initial numbers were occasionally slightly greater.

[b] dependent variable was (mm$^2\cdot$h$^{-1}\cdot$larva^{-1}); explanatory variables were group and light phase nested within group

[c] *, $P \leq 0.05$; **, $P \leq 0.01$

[d] Comparison of feeding rates among replicates.

[e] Comparison of feeding rates during light and dark phase, nested within group.

49

Table 4. Periodic regressions of mean value of standardized feeding rate ($mm^2 \cdot h^{-1} \cdot larva^{-1}$) on time of measurement during diel cycle, at two temperatures. Parameters are explained in the text.

INSTAR	°C	M EST	M SE	A EST	A SE	φ	F	df[a]	P[b]	r²
1	23	1.38	0.22	1.02	0.32	3.51	10.5	5	*	0.68
	29	1.16	0.19	0.40	0.27	3.43	2.2	5	ns	0.30
	both[c]	1.24	0.16	0.70	0.21	3.46	10.7	11	**	0.49
2	23	1.18	0.1	0.381	0.15	2.61	6.8	4	ns	0.63
	29	0.96	0.059	-0.047	0.087	2.68	0.29	4	ns	0.07
	both	1.07	0.065	0.17	0.10	2.14	2.8	9	ns	0.24
3	23	1.18	0.18	0.43	0.24	4.61	3.2	5	ns	0.39
	29	1.18	0.15	0.43	0.24	3.37	3.3	5	ns	0.40
	both	1.22	0.16	0.52	0.28	3.75	3.5	8	ns	0.31
4	23	1.00	0.11	0.025	0.15	4.15	0.02	5	ns	0.01
	29	1.03	0.044	0.11	0.060	2.74	3.0	5	ns	0.34
	both	1.01	0.056	-0.017	0.084	3.54	0.04	11	ns	0.00

[a] degrees of freedom in denominator

[b] ns, P > 0.05; *, P ≤ 0.05; ** P ≤ 0.01

[c] pooled data from 23° and 29°C

Figure 2. Mean feeding rate ($\pm$ 1 SE) of Colorado potato beetle larvae ($mm^2 \cdot h^{-1} \cdot larva^{-1}$) at different constant temperatures (T °C), and quadratic model of the response.
A) First instar
B) Second instar
C) Third instar
D) Fourth instar

A)

B)

C)
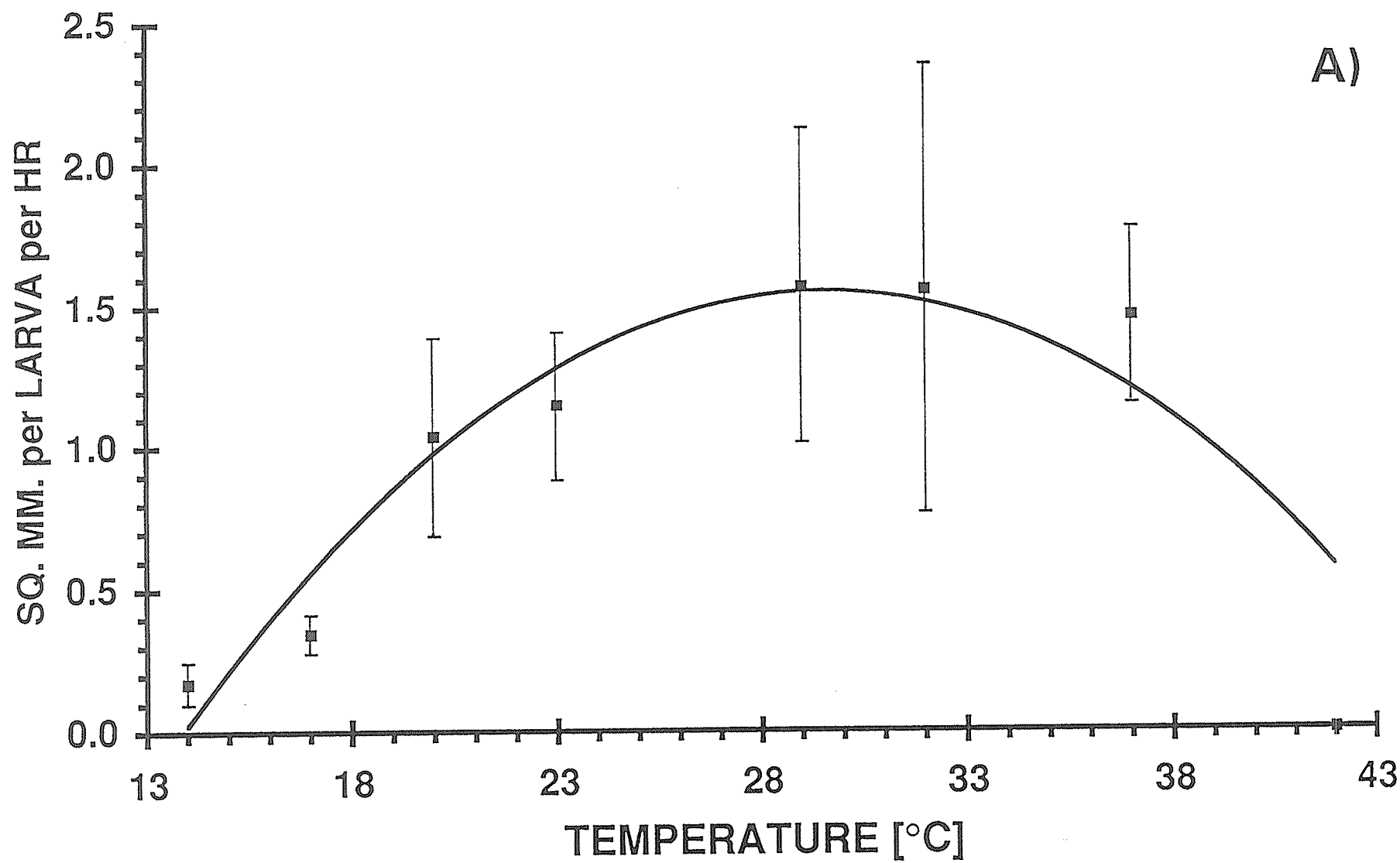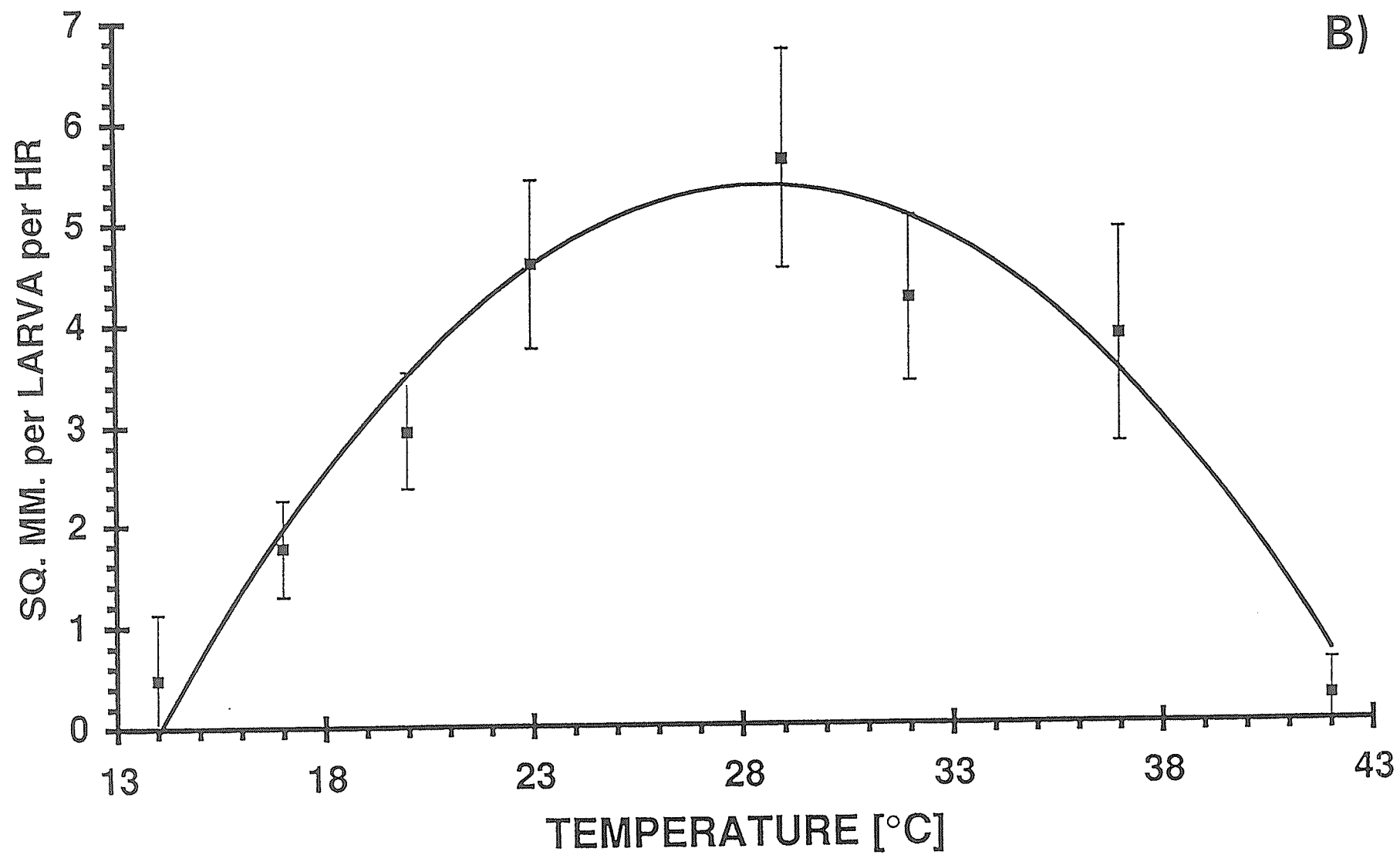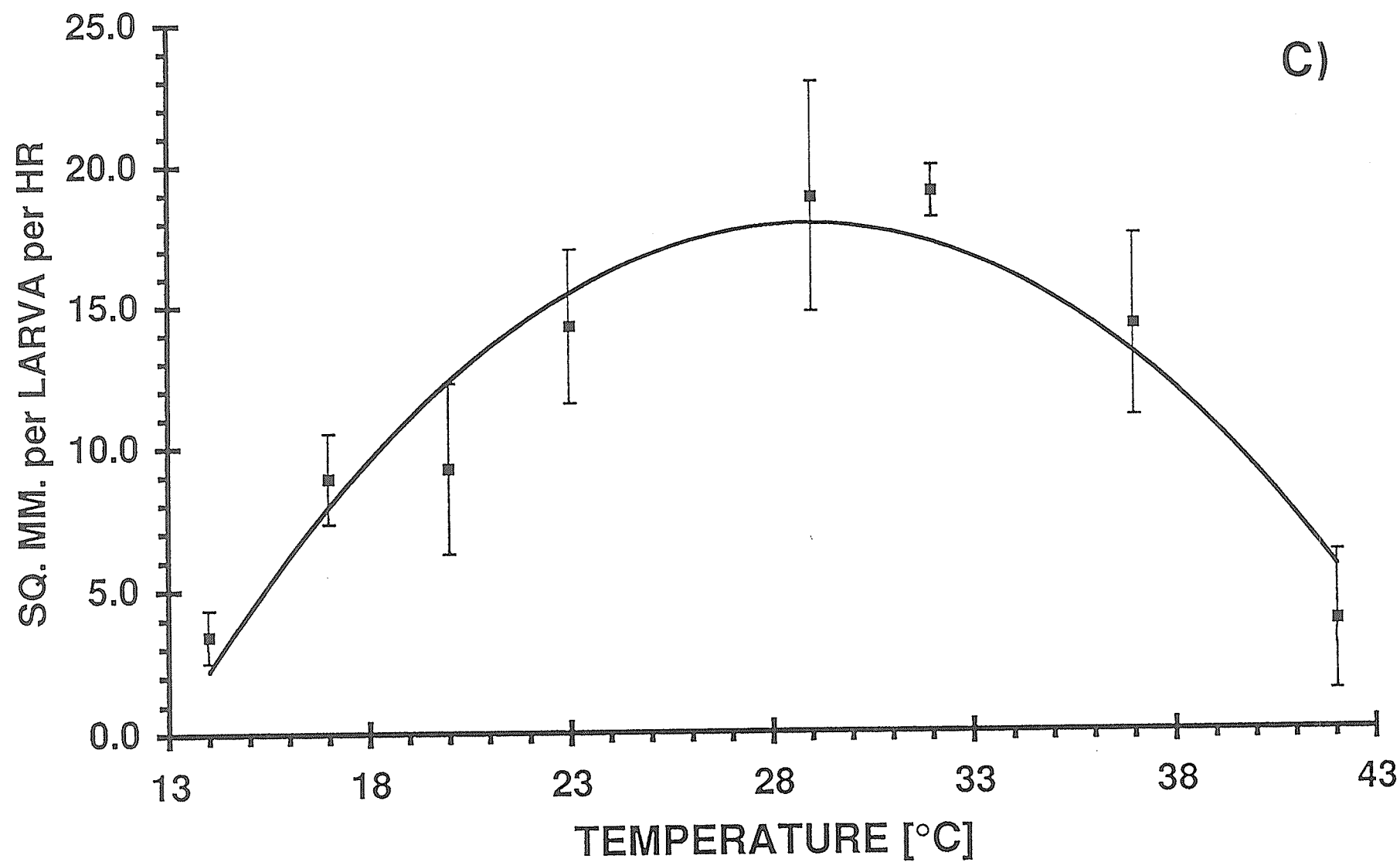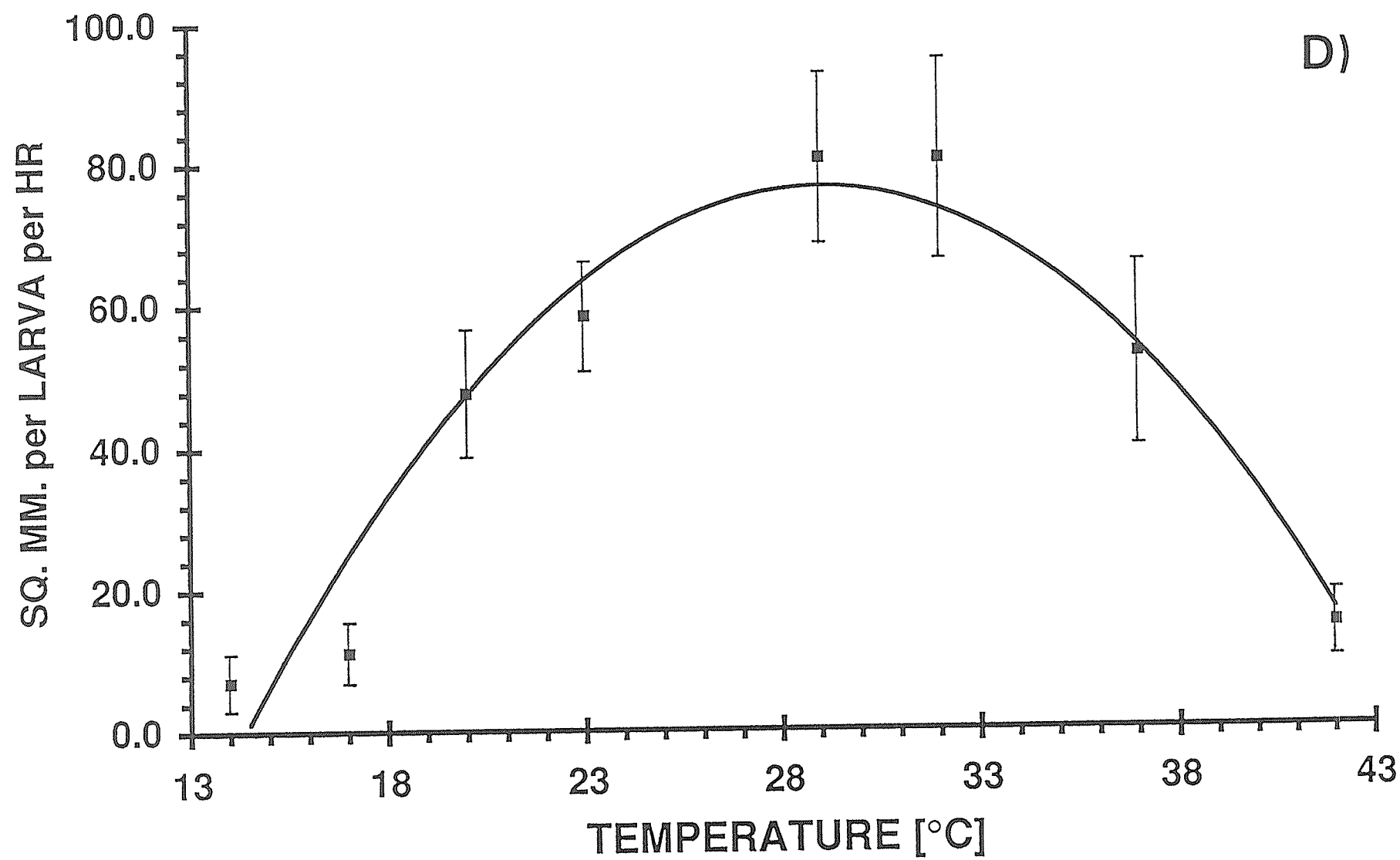
Figure 3. Scaled feeding rates of Colorado potato beetle larvae vs. time, at 23° (closed squares) and 29°C (open squares). Scaled rate = group mean at a given time, divided by the group mean over four sets of measurements spaced over a complete diel cycle. Vertical line marks change from light to dark (2200 h).
(A) first instar; (B) second instar; (C) third instar; (D) fourth instar.

HOURS AFTER LIGHTS ON
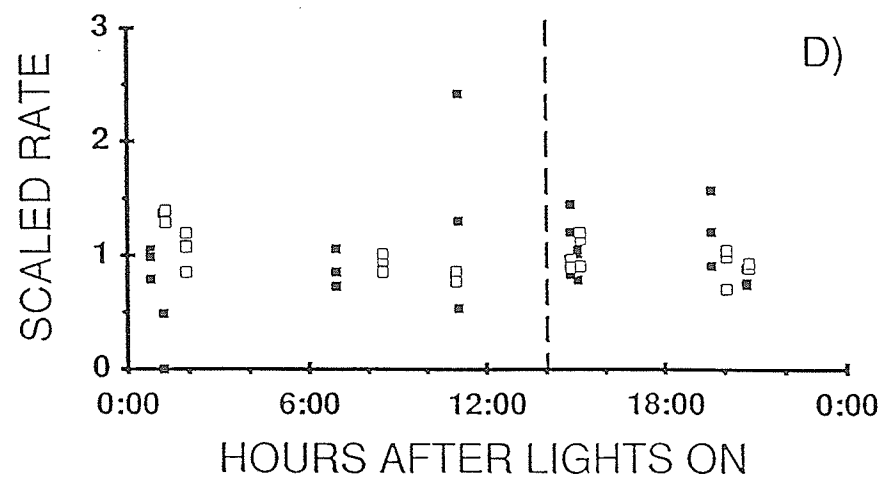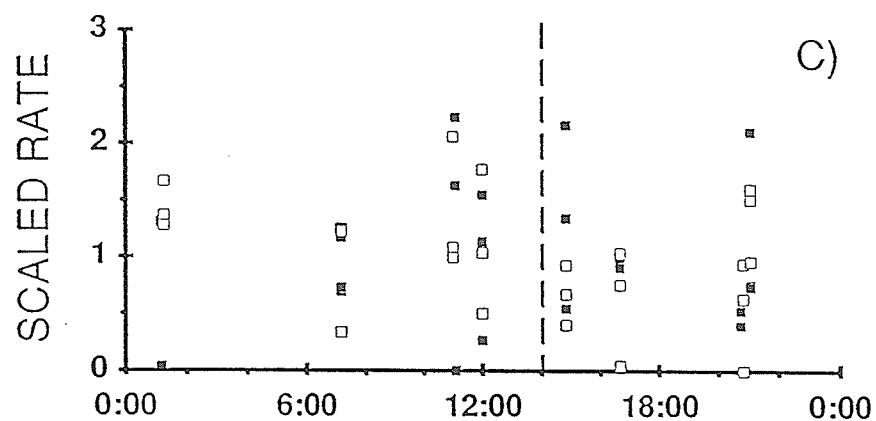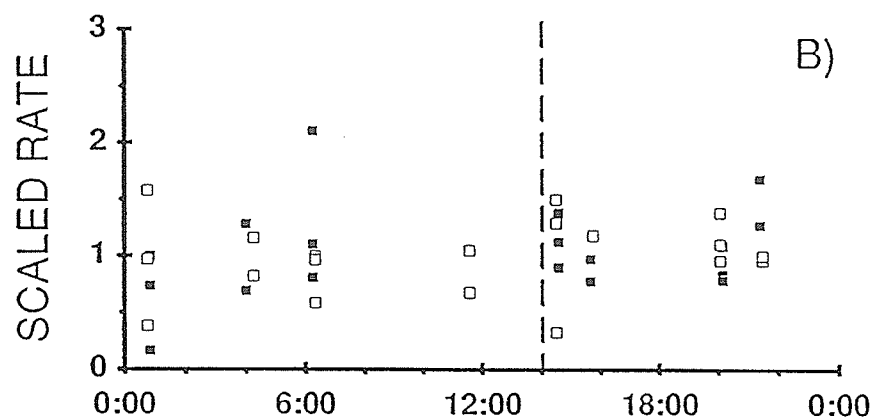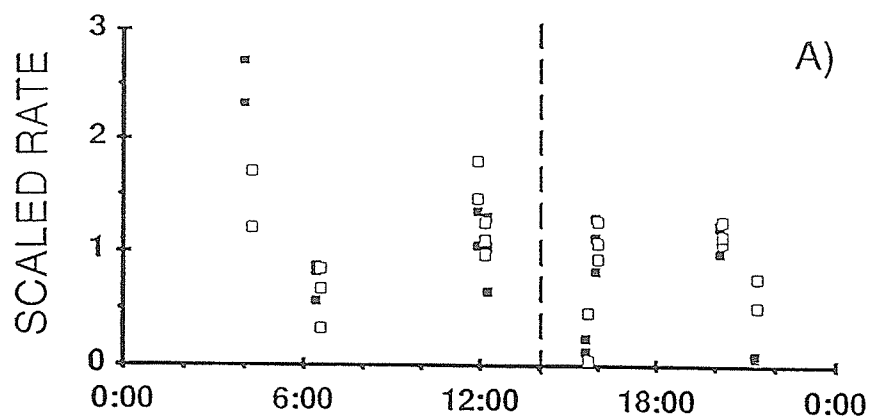
Figure 4. Comparison of feeding rates by Colorado potato beetle larvae
         ($mm^2 \cdot h^{-1} \cdot larva^{-1}$) at constant temperature, as measured by Logan <u>et</u>
         <u>al</u>. (1985) (filled squares) and Ferro <u>et</u> <u>al</u>. (1985) (open squares),
         with quadratic model obtained in the present study (solid curve).
         Cited rates are converted from $cm^2 \cdot day^{-1}$.
         (A), first instar; (B), second instar; (C), third instar; (D),
         fourth instar.
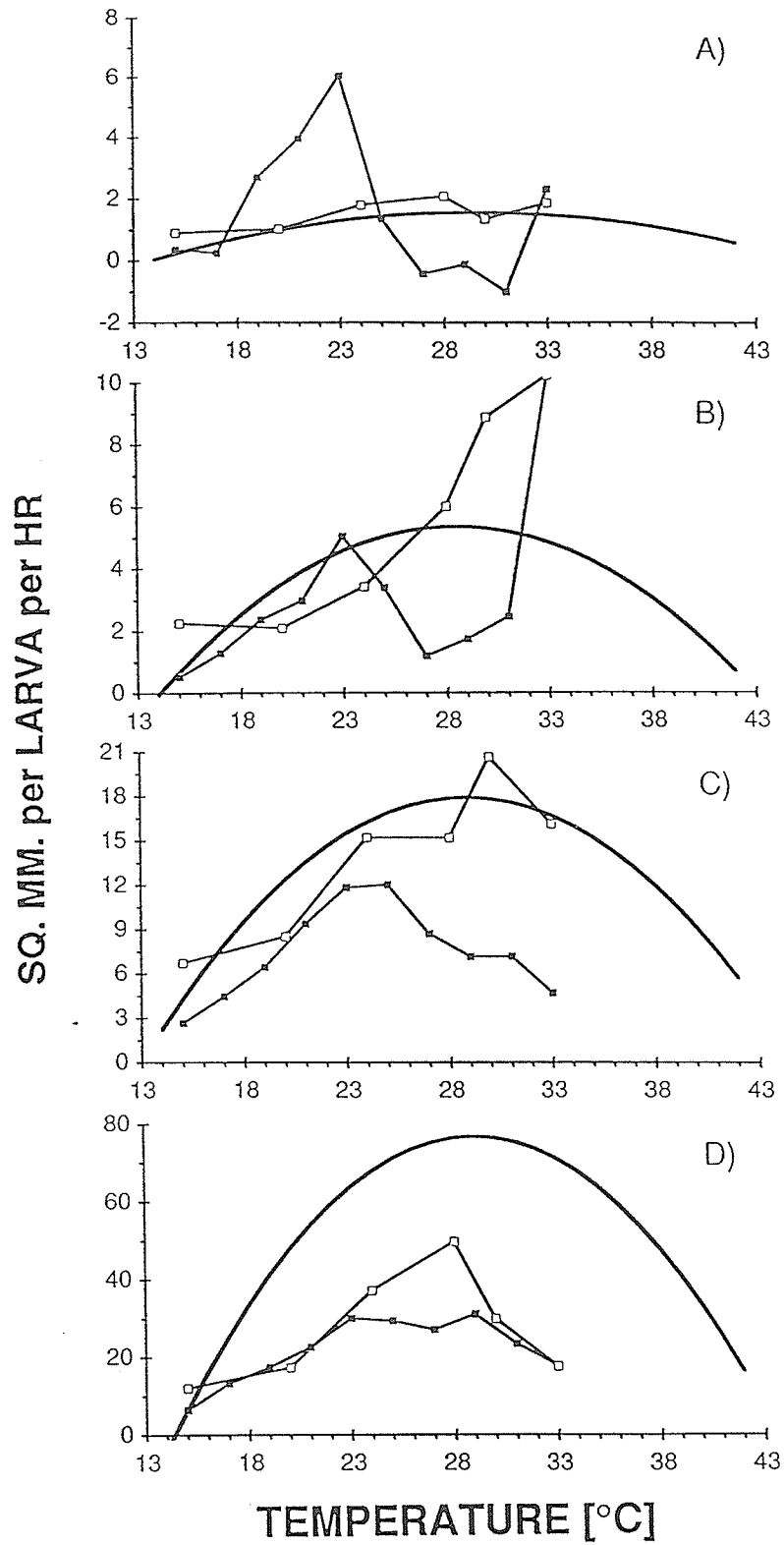
Section II, Chapter B)
        CONSTANT TEMPERATURE DEVELOPMENTAL RATES OF PRE-IMAGINAL COLORADO
        POTATO   BEETLES   (<u>LEPTINOTARSA   DECEMLINEATA</u>   (SAY)   (COLEOPTERA:
        CHRYSOMELIDAE)) FROM TWO CANADIAN LOCATIONS

ABSTRACT

Colorado potato beetle eggs and larvae from Winfield, British Columbia (50° 02' N, 119° 24' W), and Winnipeg, Manitoba (49° 54' N, 97° 9' W) (two collections) were reared at a range of constant temperatures. Developmental response to temperature was similar in the three collections. Developmental rates of larvae in the present study are similar to those in the literature, but among eggs in the present study, development was faster at low temperatures and increased more slowly with temperature than did the published values. Optimum temperature for development was ca. 29 - 31°C in all stages.

INTRODUCTION

To construct a predictive model of Colorado potato beetle population trends under field conditions, data on temperature:developmental rate relationships are necessary. Although several groups of researchers have measured Colorado potato beetle developmental rates under constant conditions, the study was repeated here because developmental rates may differ among populations from different geographic regions (Tauber et al. 1988) and because specimens used in the present trials were collected ca. 7° latitude (ca. 800 km) north of those tested in the other trials (Walgenbach and Wyman 1984, Wisconsin; Ferro et al. 1985, Massachusetts; Logan et al. 1985 and Groden and Casagrande 1986, Rhode Island; Tauber et al. 1988, coastal and inland New York state).

MATERIALS AND METHODS

All trials were conducted in environmental chambers during fall and winter 1990 and 1991 at the University of Manitoba (Winnipeg), under a 14L:10D diel cycle. The following rearing procedures were the same in all trials. Adult Colorado potato beetles were reared in transparent plastic boxes (10 x 10 X 30 cm), with moistened paper towels and excised 'Russet Burbank' potato foliage *ad libitum*. Eggs and larvae of the first, second and third instars were reared in 10 cm x 1.5 cm plastic petri dishes with fresh excised potato leaflets and moist paper towel. Fourth instar larvae were reared in 20 cm diam x 3 cm petri dishes with fresh excised potato leaflets and a 2 cm layer of moistened perlite as a pupation medium.

Leaflets in petri dishes were replaced at least daily and the paper towels or perlite were kept moist with distilled water.

To obtain egg masses, boxes with adults were established at the desired rearing temperature and inspected twice daily. Egg masses produced in known intervals were collected and placed in petri dishes. Eggs were considered individuals; this is distinct from Logan et al. (1985), who assigned this status to egg masses.

Petri dishes with eggs or larvae were inspected at least once each day. Dates and times of inspection ($\pm$ 15 min) were recorded for each dish. The number of eggs or larvae hatched, moulted, dead, or unchanged, was noted at each inspection. The fourth instar was considered to end when larvae entered the soil; the subterranean non-feeding 'prepupal' stage (sensu Groden and Casagrande 1986) was disregarded. At each temperature and instar, rearing groups were assembled from larvae which hatched or moulted in the same interval.

Adult beetles were collected near Winnipeg, Manitoba, Canada, (49° 54' N, 97° 9' W) in the spring of 1990 and 1991, and Winfield, British Columbia, Canada (50° 02' N, 119° 24' W) in the spring of 1992. For convenience, the three lineages descending from these two founder populations will be called isolates.

In all isolates, adults of the first filial generation (F1) produced the larvae used in the trials. F1 adults from both Winnipeg isolates were maintained in diapause at 5°C until required. Diapausing F1 adults were transported in soil from Winfield to Winnipeg in a cooler with ice, in October 1991. In each isolate, 20 to 30 adults provided the eggs used;

63

sex ratios of these samples, and the relative contributions by the individuals, are not known.

Developmental rates were measured for eggs and all larval instars of each isolate. Some methods varied among years.

1990

In 1990, only the Manitoba isolate was tested. Rearing temperatures were 17°, 21°, 25°, and 29°C.

Time limitation precluded following individuals from egg to pupation. Consequently, a stock colony was reared at 29°C in plastic boxes of the type used to rear adults, and this was used to supply larvae of the desired instar as follows.

First instar larvae all originated in the 29°C chamber. Egg masses at 29°C were inspected twice daily; larvae that hatched in a given interval were assigned randomly into groups of 10 - 15, and each group was assigned randomly to a nominal rearing temperature. Data obtained for the first instar appeared anomalous, even after adjusting for time spent in 29°C, and were discarded.

The supply of other instars at each rearing temperature was obtained by transferring larvae of the previous instar from the stock colony into the rearing temperature, and rearing these to the desired instar before initiating rate measurement. The interval from transfer to moult into the desired instar always exceeded 24 h.

1991

In 1991 both the Manitoba and British Columbia isolates were tested. Rearing temperatures were 17°, 21°, 24°, 27°, 29°, 31° and 33°C. Colorado potato beetles reared at temperatures ≥ 24°C were inspected twice daily.

In 1991, larvae remained at the same temperature throughout their lives wherever possible. Exceptions occurred at 31° and 33°C, due to high mortality rates; replacement larvae of a particular instar were obtained by moving larvae of the preceding instar from 29°C into the nominal rearing temperature and awaiting moult to the desired instar.

ANALYSIS

Only surviving larvae were included in the analysis. Egg or instar developmental time (in days) was estimated to be from the midpoint of the two inspections bracketing oviposition or moult into the instar, to the midpoint of the two inspections bracketing moult into the next instar (Logan et al. 1985). Developmental rate of each larva was calculated as the reciprocal of the time to complete the instar.

Temperature-dependence of developmental rates was modeled using equation (3) (Logan et al. 1976).

$$r_j(T) = \Psi\left[e^{\rho T} - e^{\left(\rho T_{max} - \frac{(T_{max}-T)}{\Delta}\right)}\right] \qquad (3)$$

Where T is °C above some arbitrary base temperature, usually the lowest used in the trial (in this trial, 17°C); $r_j(T)$ is developmental rate for life stage j, constrained to be non-negative; T_{max} is the upper temperature at which development ceases; Ψ may be a basal developmental rate, usually calculated at the lowest rearing temperature; ρ "can be interpreted as a composite Q_{10} for critical enzyme-catalyzed, biochemical reactions" (Logan et al. 1976); and Δ measures the upper temperature range in which developmental rate diminishes. Parameters were estimated using

iterative nonlinear regression (PROC NLIN, DUD algorithm; SAS Institute 1988).

Development functions for each instar obtained in the present study were compared to a literature data set consisting of pooled results from five studies of Colorado potato beetle development (Walgenbach and Wyman 1984; Logan et al. 1985; Ferro et al. 1985; Groden and Casagrande 1986 [only beetles reared on Solanum tuberosum]; Tauber et al. 1988). Alone among these groups of authors, Tauber et al. (1988) included the subterranean prepupal stage in the fourth instar; because of this difference in method, their fourth-instar data were not included in the following comparisons.

Analysis of covariance was used in statistical comparison of data sets. Because the developmental rate function (above) is nonlinear and apparently cannot be converted to a linear form, these comparisons considered data only from the approximately linear portion of the curve ($\leq 29°C$).

RESULTS AND DISCUSSION

Developmental rates and standard errors from the present study are plotted in Fig. 5; the data are given in appendix 1. Analysis of covariance on the linear portions of the developmental rate curves ($T \leq 29°C$) revealed no difference in slope ($F_{2,9} < 0.7$, $p > 0.05$) or intercept ($F_{2,9} < 1$, $p > 0.05$) among isolates in any instar, so data were pooled for analysis. Optimum temperature for development was $\approx 29 - 31°C$ in all stages.

Parameter estimates of the fitted models for the pooled data from the present study, and from the literature, are listed in Table 5. The estimate of the parameter Ψ depends on the basal temperature chosen; to simplify comparison among data sets, this temperature has been standardized at 17°C in the table.

At 31°C, eggs and first instar larvae survived better than did later instars; this trend accounts for the diminution of sample sizes with age at this temperature (appendix 1). At 33°C, all larvae (n ≈ 15 per temperature) died within 1 - 2 days and none moulted. This is a noticeable departure from the results of Logan et al. (1985), Ferro et al. (1985) and Groden and Casagrande (1986) who were able to measure larval development at 33°C, although survival was poor in all cases.

COMPARISON AMONG DATA SETS.

The developmental rate models as fitted to the present data are compared to data from the literature in Fig. 6. Response functions from the present trial, and the pooled literature data were compared by analysis of covariance on the linear portions of the data. Among larvae there was no significant difference in slope ($F < 0.9$, $df_e = 16 - 21$, $p > 0.05$) or intercept ($F < 1.19$, $df_e = 16 - 21$, $p > 0.05$) between the responses. Among the eggs, the intercept and slope calculated from the present data were significantly lower ($F_{1,13} = 5.34$, $p = 0.038$), and higher ($F_{1,13} = 5.25$, $p = 0.039$) respectively, than those describing the data from the literature review. Hence, development of eggs used in the present trial appear to be slower at low temperatures, and to increase more rapidly with temperature, than did the pooled literature values.

These analyses of covariance require a linear response. There is no way to linearize equation (3), and so it is not possible to quantify the apparent differences between the present data and those from the literature, in response at temperatures greater than 29°C.

Results at T ≤ 29°C corroborate those of Tauber et al. (1988), who detected no statistically significant difference in developmental rate curves between two populations of Colorado potato beetles from New York state. Observed (non-significant) variation among populations may simply derive from differences in experimental apparatus or procedure; difficulty in specifying the moment of ecdysis is a particularly important source of error.

One possible explanation of the similarity in thermal response among these geographically separated Colorado potato beetle populations is that the thermal physiology in this species may be relatively 'static', as suggested for some other species (Hertz et al. 1983) owing to lack of requisite genetic variance, or to resistance to directional selection. "Development" is a process involving the coordinated action of numerous enzymes; conceivably, a change in organismal thermal response might require substantial rearrangement to this coordinated system, with interim reduction in fitness (Ushakov 1964). If so, such changes would meet selective resistance. Other methods of ameliorating suboptimal conditions would be more likely to spread through the gene pool; behavioral adjustments, such as changes in timing of activity, or in intensity of basking, are some of the possibilities (van Damme et al. 1990).

Extant data do not allow assessment of the possibility that thermal physiology of this species is indeed static, because populations tested

originated in regions with similar daytime highs during larval development. This possibility should be tested by comparing developmental rate functions in populations drawn from areas having a range of climates.

Even if selection is acting on thermal physiology, the advantageous traits may be initially so uncommon in the populations that their spread is impeded by the rarity of chance meetings between bearers of the trait (Wright 1932), or by dilution by immigrant genetic material. Adaptation is expected to occur most rapidly in small, isolated populations under strong selective forces (Wright 1968). Because Colorado potato beetles occur in great numbers, and are relatively mobile as adults (Johnson 1969), there is extensive gene flow among populations (Hsiao 1985). Hence, lack of local adaptation in thermal physiology is not unexpected.

Table 5. Parameter estimates from nonlinear regression of developmental rates of Colorado potato beetle eggs and larvae on constant temperature. Model used (equation 3 in text) is equation 6 in Logan et al. (1976). For comparison purposes, base was temperature standardized at 17 C for estimation of Ψ in both data sets.

a) Present study.

INSTAR	Ψ EST	Ψ S.E.	ρ EST	ρ S.E.	T_{max} EST	T_{max} S.E.	Δ EST	Δ S.E.	r^2
EGGS	0.146	0.0	0.169	0.	35.18	1.88	4.68	11.52	
1	0.189	0.	0.153	0.0079	34.47	0.892	3.84	0.553	0.99
2	0.501	0.	0.191	0.0415	37.14	3.70	4.87	0.914	0.99
3	0.150	0.0715	0.162	0.0261	33.68	1.60	3.29	0.722	0.98
4	0.150	1.079	0.134	0.221	36.54	4.42	4.78	11.50	0.99

b) Pooled literature review data.

INSTAR	Ψ EST	Ψ S.E.	ρ EST	ρ S.E.	T_{max} EST	T_{max} S.E.	Δ EST	Δ S.E.	r^2
EGGS	0.328	0.	0.127	0.	38.65	0.378	6.89	0.487	0.99
1	0.349	0.	0.146	0.469	37.46	2.37	5.53	20.4	0.96
2	3.645	0.	0.145	0.	37.15	1.21	6.77	1.20	0.98
3	0.213	0.0432	0.104	0.0560	35.75	1.486	3.63	3.39	0.97
4	0.132	0.248	0.151	0.166	34.49	0.832	4.06	5.56	0.97

Figure 5. Mean constant-temperature developmental rates (stadia·day^{-1}) and standard errors of pre-imaginal Colorado potato beetles from Manitoba and British Columbia.

A) eggs
B) first instar
C) second instar
D) third instar
E) fourth instar

Symbols: Diamond = 1990 data, Manitoba isolate; open squares = Manitoba isolate 1991; filled squares = British Columbia isolate, 1991. Error bars for the British Columbia isolate 1991 and the Manitoba isolate 1991 are offset to the left and right, respectively.

C)

D)
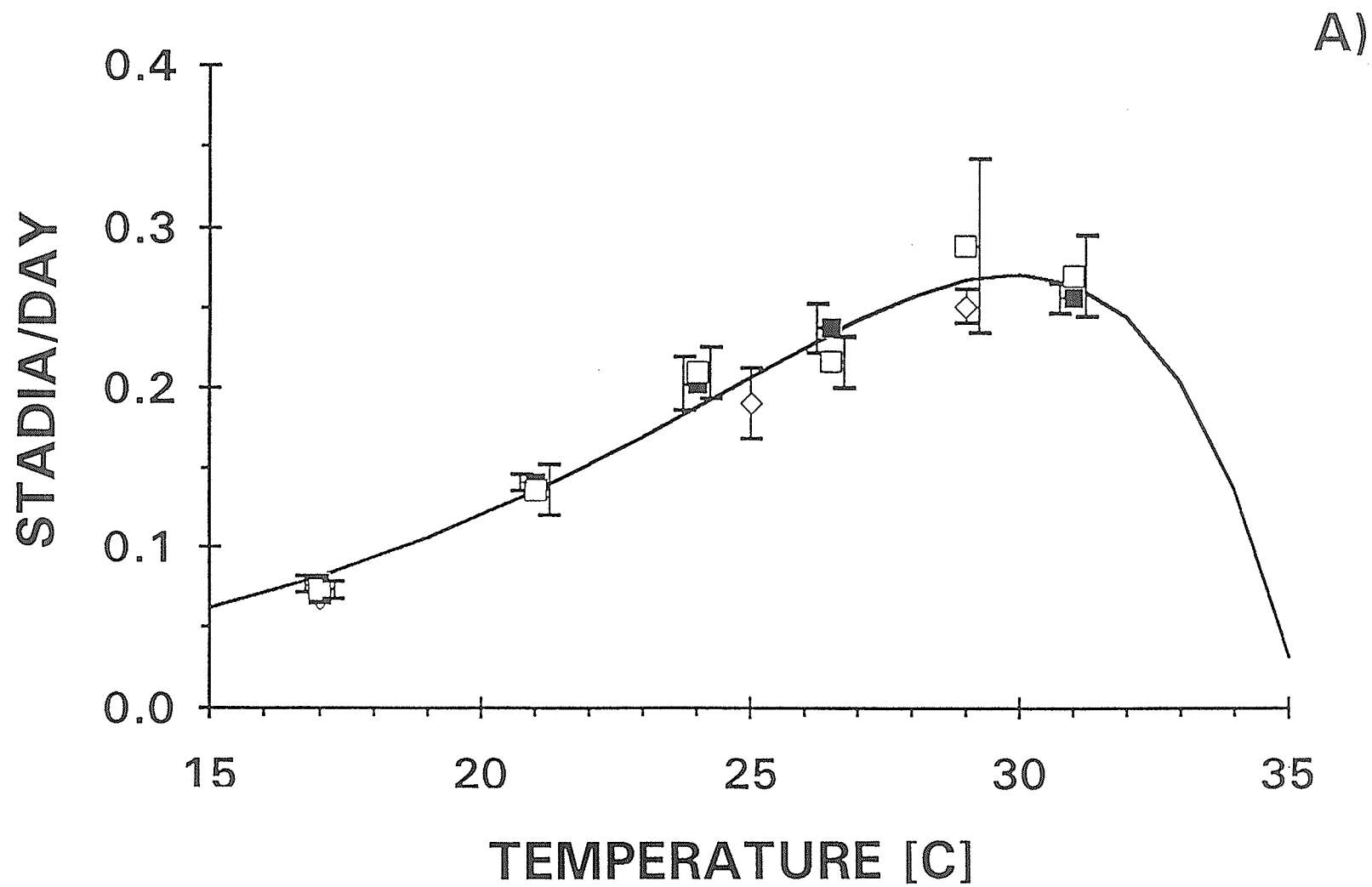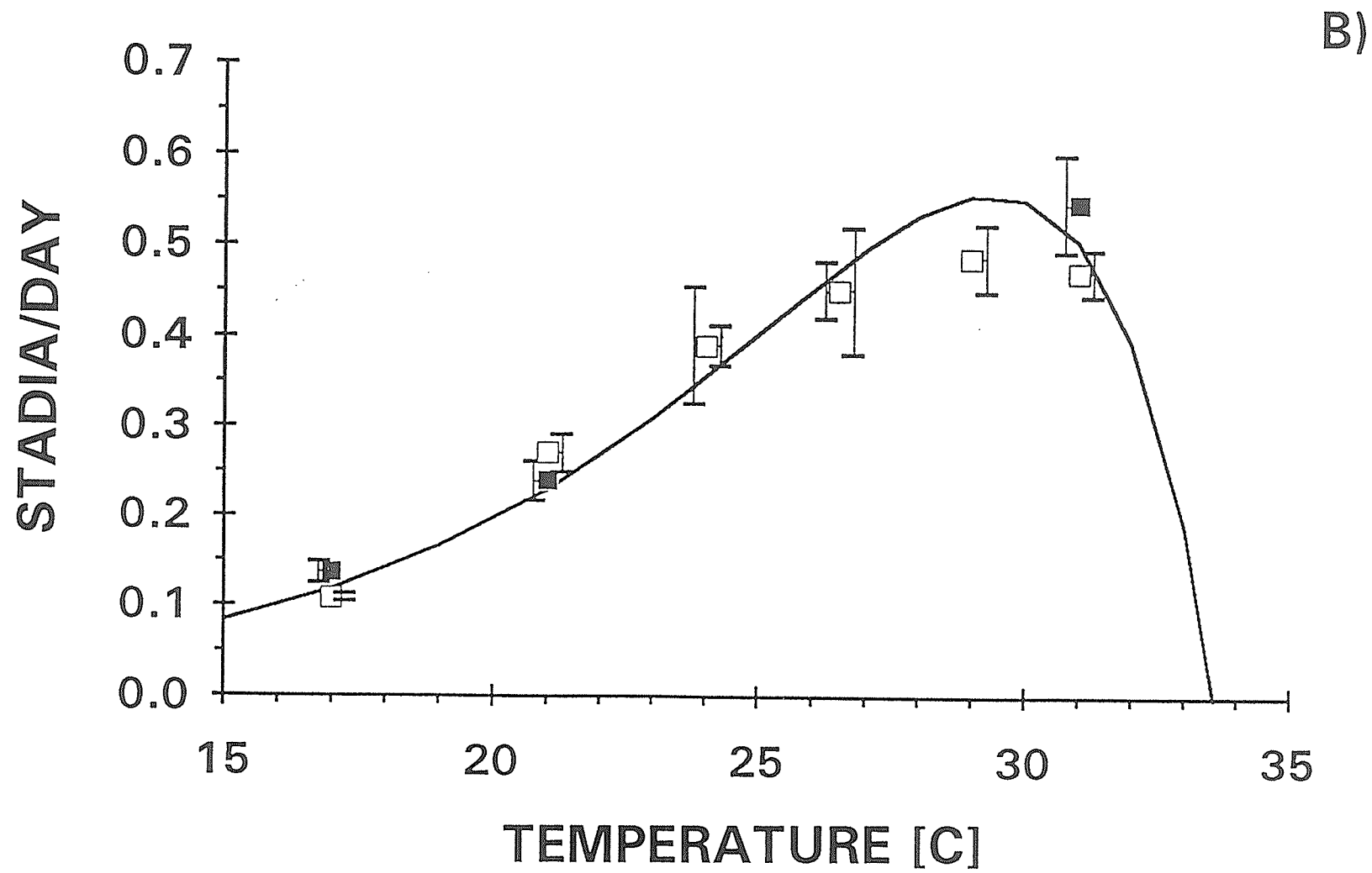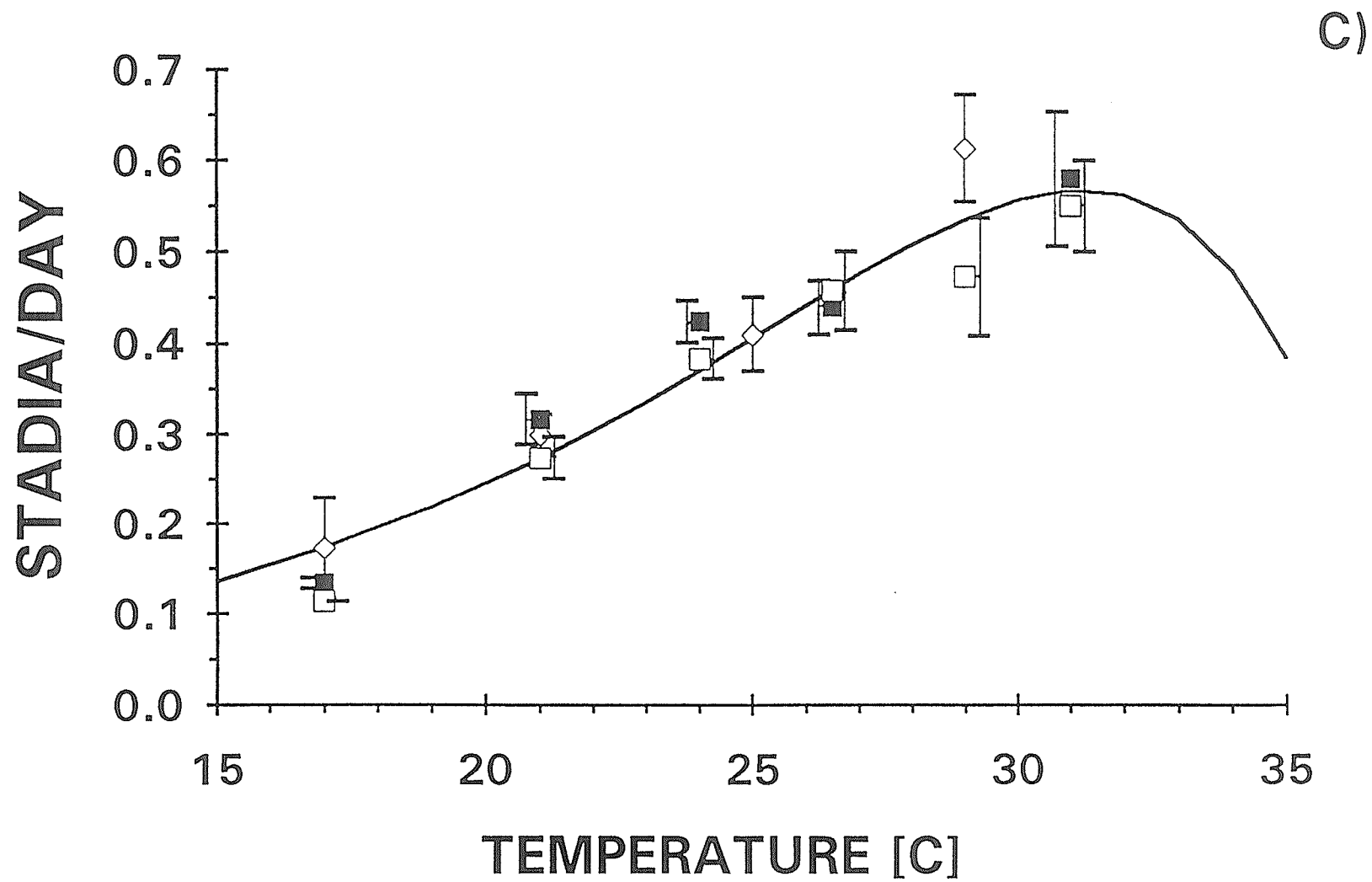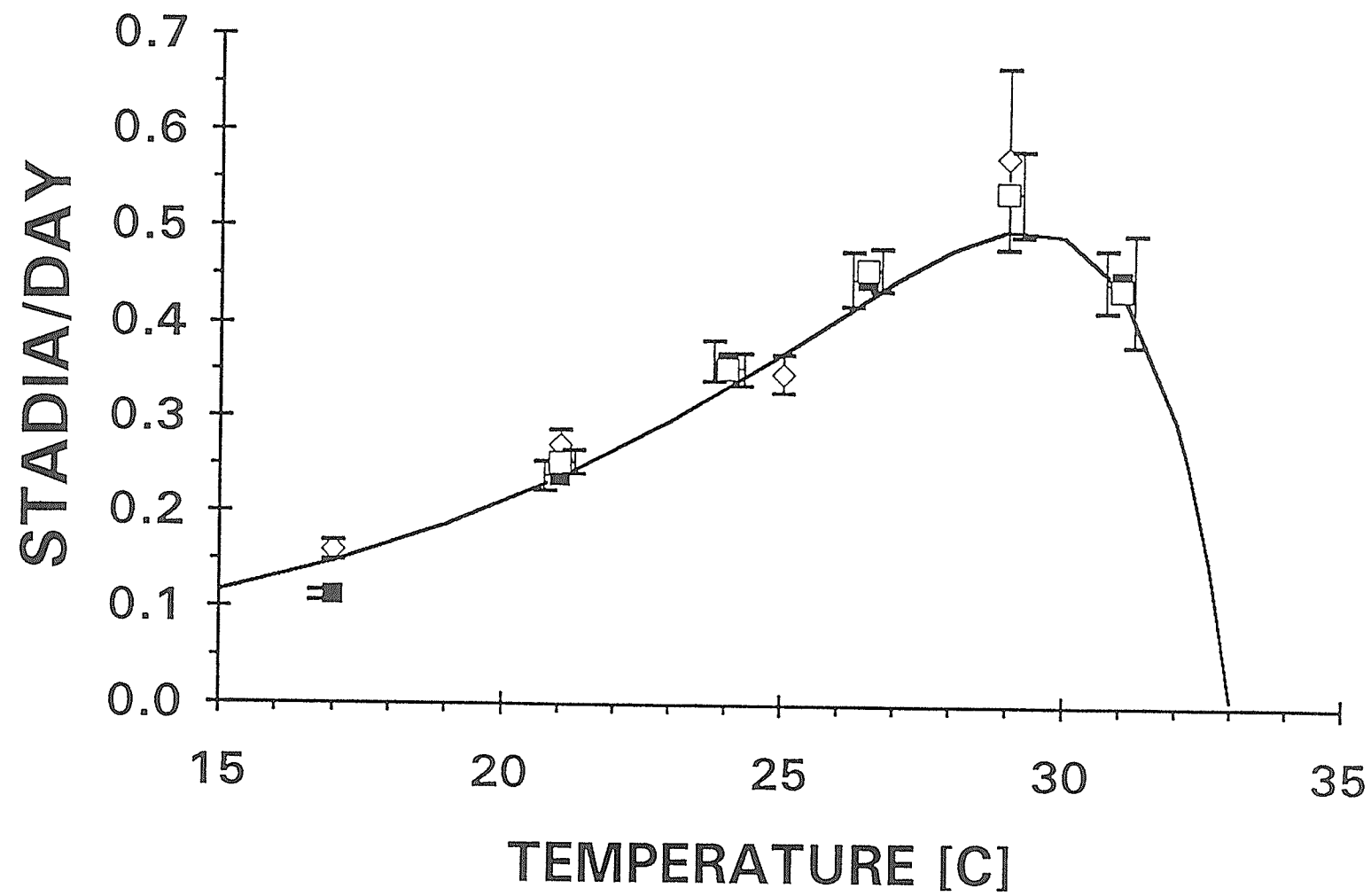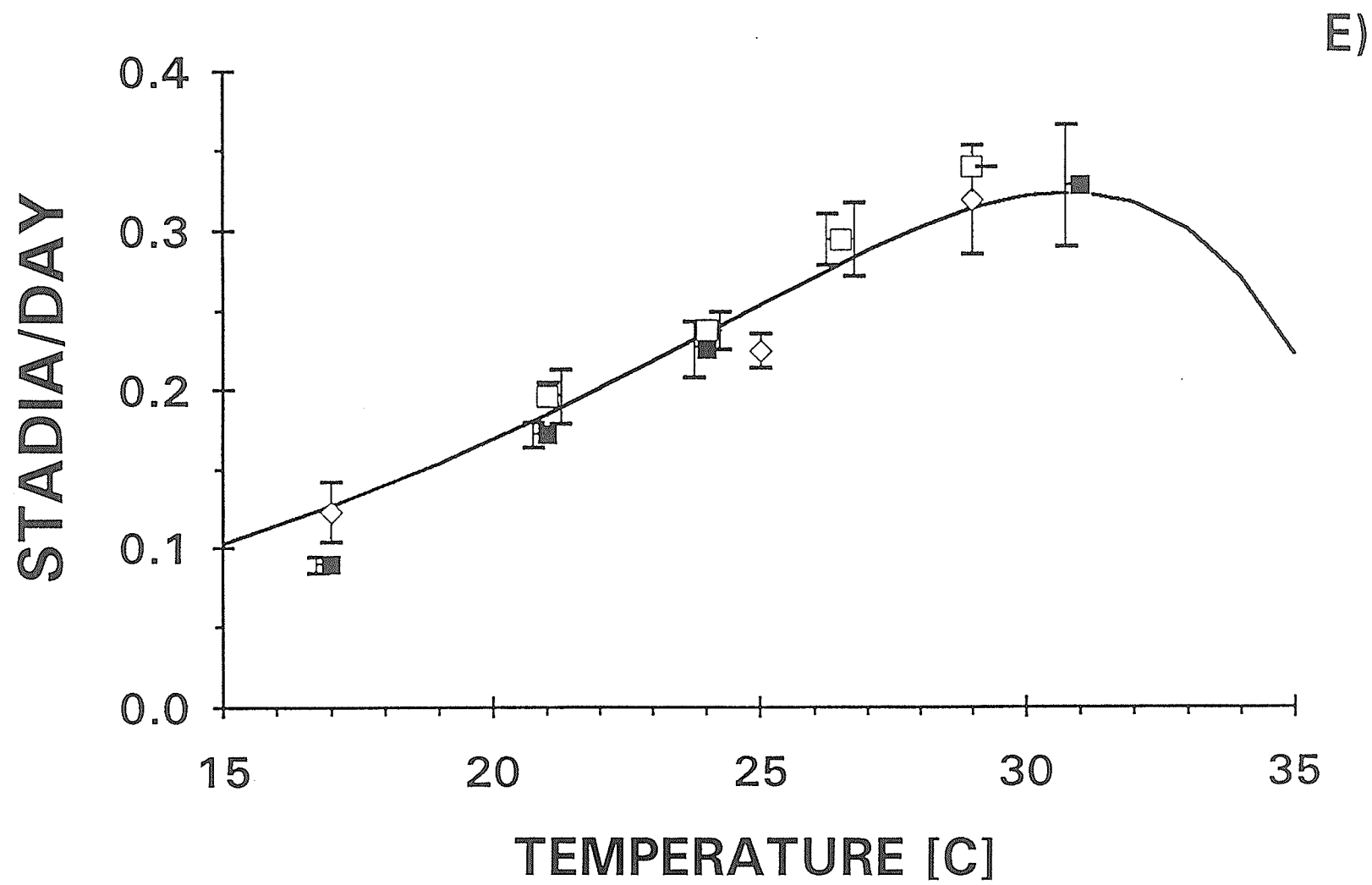
Figure 6. Temperature dependent developmental rates (stadia·day^{-1}) of pre-
    imaginal Colorado potato beetle eggs. Comparison of nonlinear
    regression description of data derived from the present study (solid
    line), to five sets of published data.

    A) eggs
    B) first instar
    C) second instar
    D) third instar
    E) fourth instar

    Symbols: Closed square   = Ferro et al. 1985;
                Open square   = Groden and Casagrande 1986;
                Closed diamond   = Logan et al. 1985;
                Open diamond   = Tauber et al. 1985, mean of two
                                     populations, weighted by sample
                                     size (absent in E)
                Solid triangle   = Walgenbach and Wyman 1984.

A)

B)

C)

D)

80

E)
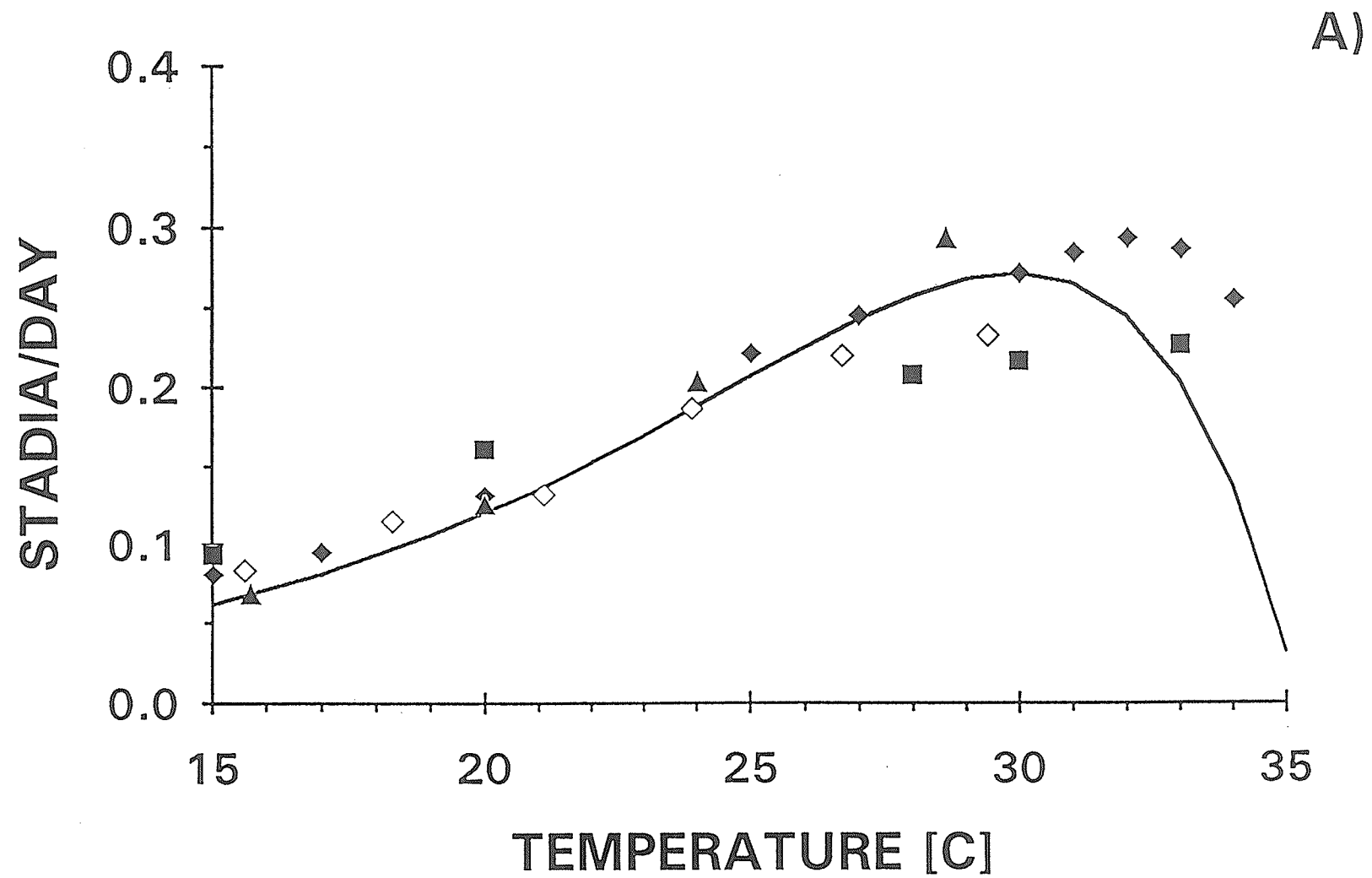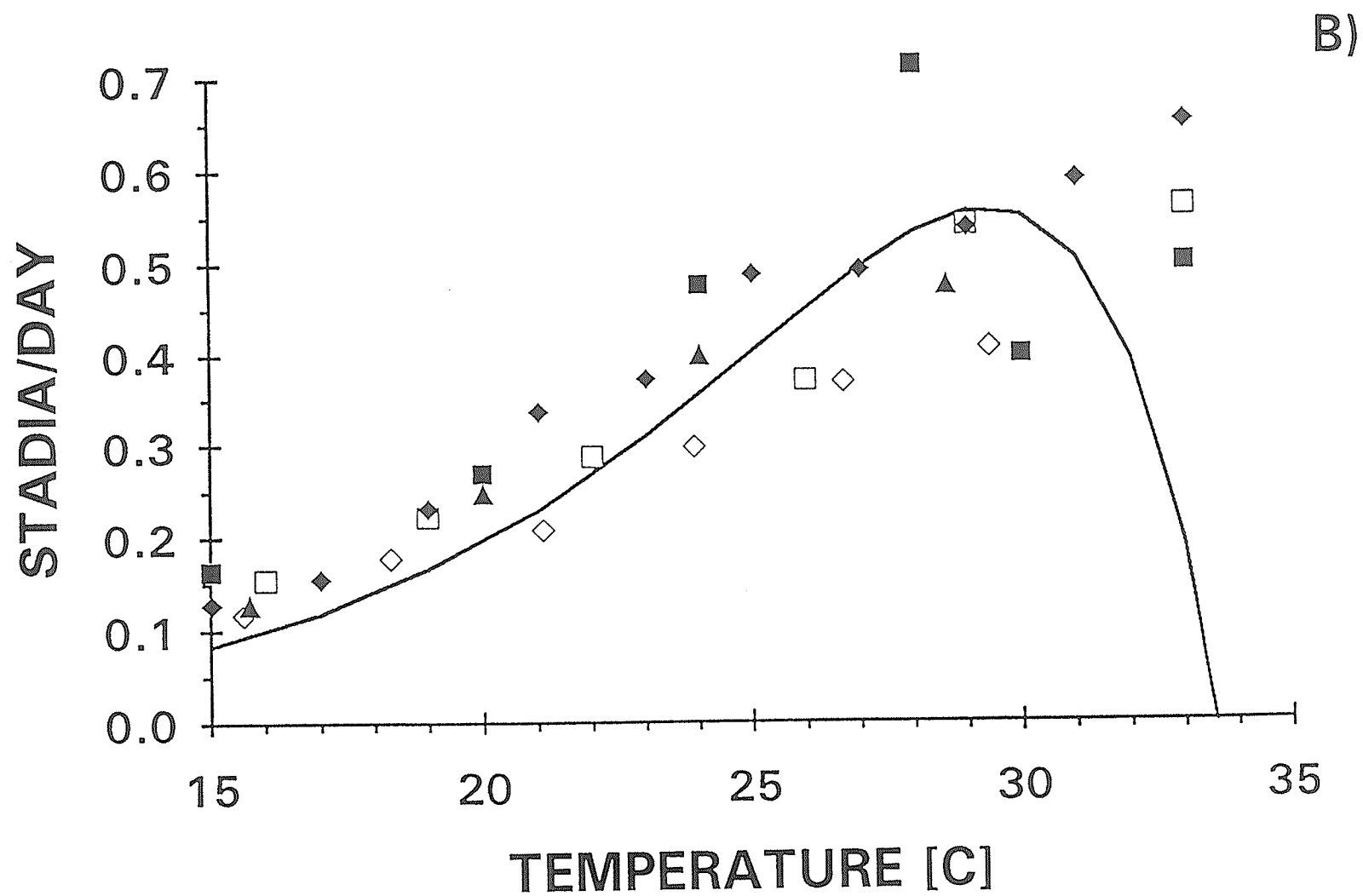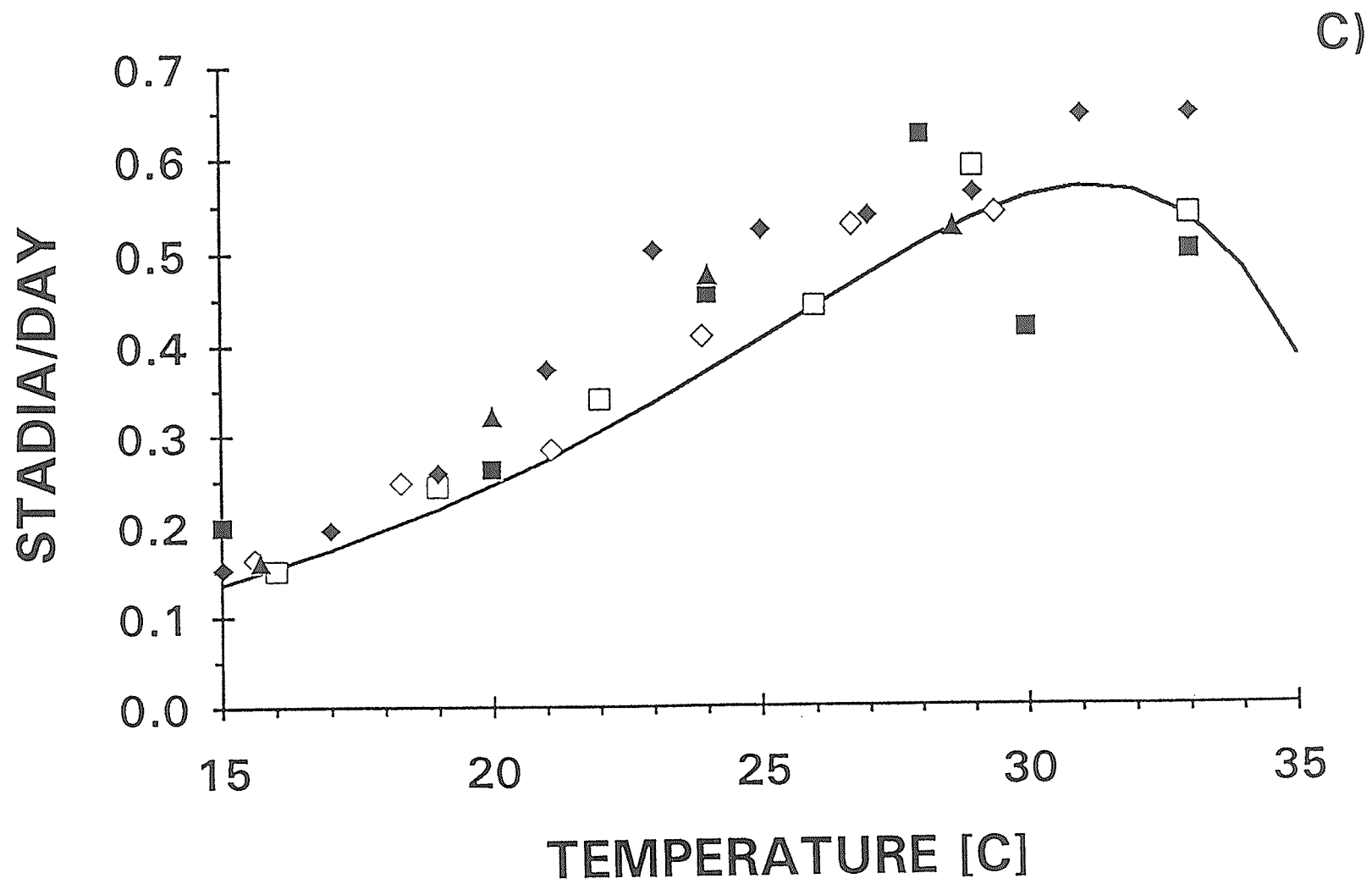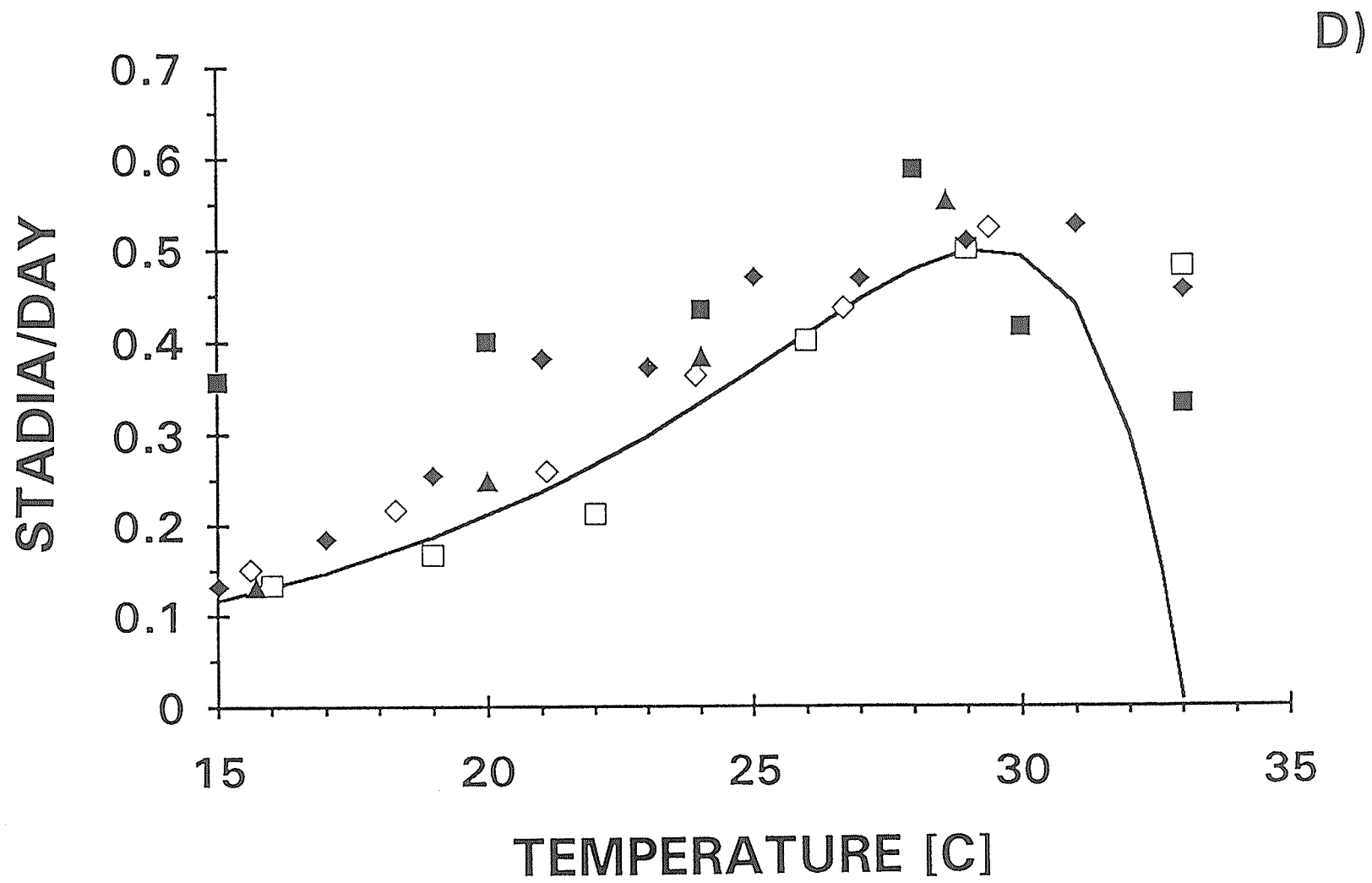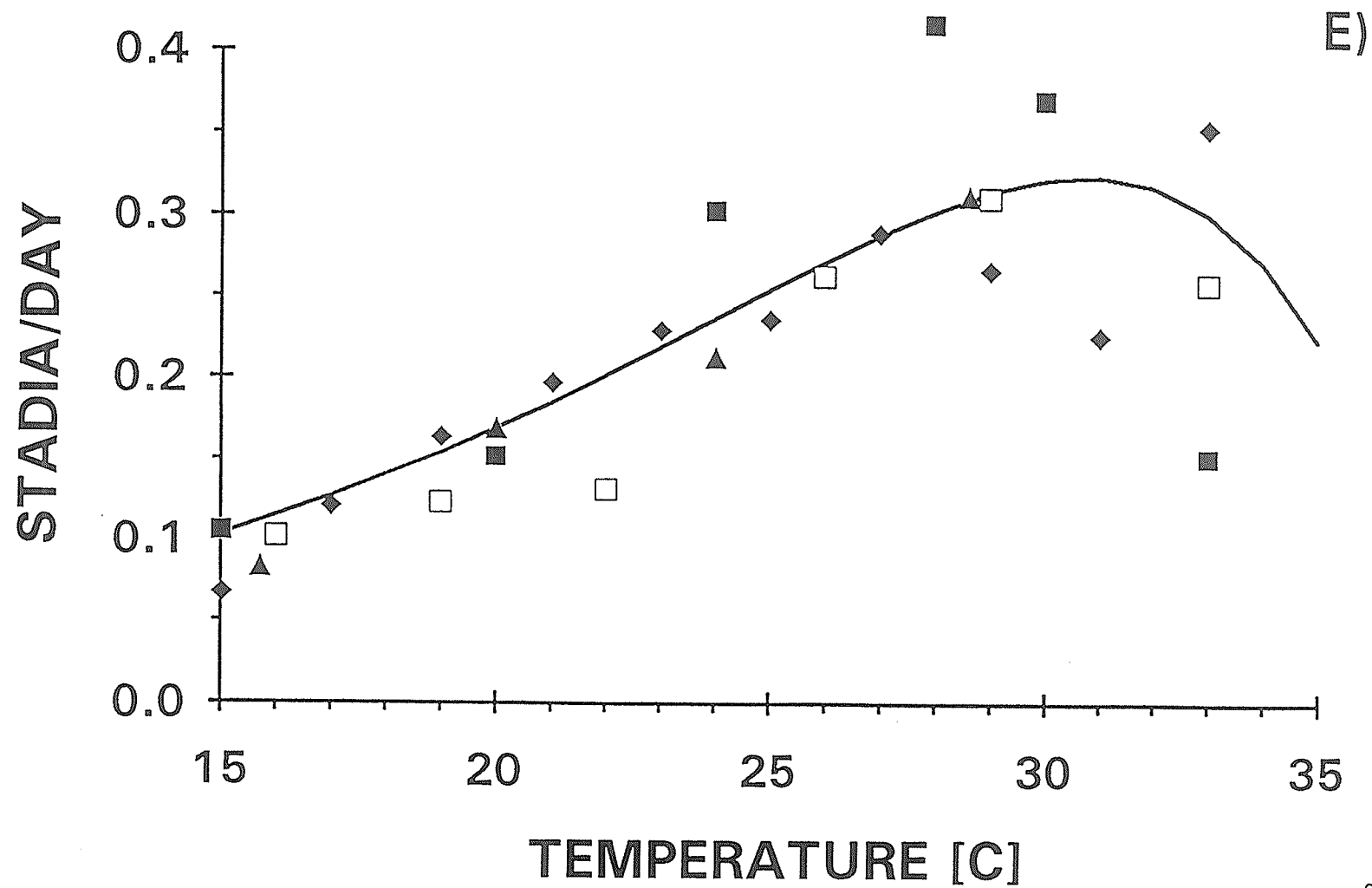
SECTION III.   THERMAL BIOLOGY OF COLORADO POTATO BEETLE
UNDER FIELD CONDITIONS

Section III. Chapter A)
    DERIVATION OF EMPIRICAL RELATIONSHIPS ALLOWING ESTIMATION OF
    MICROCLIMATE TEMPERATURE AND INSOLATION FROM MACROCLIMATIC DATA.

ABSTRACT

Empirical functions are derived which use macroclimatic data to estimate temperature and insolation in the microclimates above and below uncaged leaflets, and above and below leaflets within two types of cage. Microclimate temperatures exceeded macroclimate (Stevenson screen) temperatures by an amount related logistically to insolation. Microclimate insolation was a linear function of macroclimate insolation.

INTRODUCTION

Subsequent studies of behavior, feeding, and development by Colorado potato beetles were conducted under fluctuating conditions of temperature and insolation in potato fields; some were conducted in cages (Fig. 7) bearing one of two types of shade. Feeding, development, and behavior by Colorado potato beetles are temperature dependent (Logan et al. 1985; Ferro et al. 1985), and insolation affects body temperature (May 1979, 1981, 1982), and thus these quantities should be determined in the microclimates in which the insects exist. Most available climatic data are macroclimate measurements, but the relationships between macroclimate temperature and insolation, and the corresponding microclimate quantities are unclear. Therefore, characterizations of microclimate temperature and insolation are important to completion of several subsequent studies. The objectives of this section are (1) to characterize the temperature and insolation in the microhabitats above and below uncaged and caged leaflets, and (2) to establish relationships by which microclimatic temperature and insolation can be estimated from macroclimate data.

MATERIALS AND METHODS

Sources of data

All macroclimate observations were made at the Kelowna municipal airport, ca. 5 km from the experimental site, by Environment Canada meteorologists. Data are available from the National Climatological Archive (Canadian Climate Centre. 4905 Dufferin St., Downsview ON, M3H 5T4).

Insolation

Theoretical maximum hourly insolation was calculated using the "astrometeorological estimator" (Robertson and Russelo 1968), a model which calculates insolation on a horizontal surface (I_0, in $W \cdot m^{-2}$) in the absence of atmospheric attenuation, from site latitude, date, and time of day, and the solar constant.

Observed macroclimatic insolation data consisted of hourly estimates of total opacity (i.e. tenths of the sky covered by clouds). For analysis, opacity was converted to clarity (proportion of sky clear of clouds). Microclimate insolation was measured in full sun and below caged and non-caged leaflets at the same times on the same eight days as the microclimate temperature measurements, using a LICOR LI-210S® photometric sensor, connected to an LI-185B® Quantum radiometer/photometer. The sensor was horizontally leveled with the aperture upward.

Temperature

Macroclimatic temperature data consisted of hourly temperatures, measured in a Stevenson screen. Microclimate temperature data were sampled periodically using a Cole Palmer L-08523-00 'Digi-Sense'® thermometer, equipped with L-08430-00 general purpose thermistor probes. Measurements above and below the leaflet were taken for non-caged plants, and in each of two cages of each shade type, within 0.5 cm of the lamina. These measurements were collected periodically on the hour, over all or part of the light hours on eight days, spaced over the period 09 Jul 1991 to 21 Aug 1991. Cages and sites of measurement were relocated each day, but remained in place during the day.

Estimation of insolation

A linear multiple regression model was developed to calculate the photometer reading in full sun at hour h ($P_{h,d}$) from theoretical insolation intensity ($I_{0,h}$) as calculated using the astrometeorological estimator, and the total opacity data, as converted to clarity.

To enable prediction of microclimate insolation from macroclimate measurements, insolation was measured above and below the leaflet, in two separate cages of each type at two times during each of four days, and once on one additional day, during July and August 1991. Means by time, position and cage type were compared to contemporaneous measurements in full sun, using linear regression.

Estimation of microclimate temperatures

The relationship between microclimate and macroclimate temperatures was nonlinear. Preliminary analysis suggested that the appropriate measure was cage temperature minus external temperature, and that measured insolation was an important factor in the predictive model. The parameter measured was $DIFF_{c,p,h,d} = MICRO_{c,p,h,d} - MACRO_{c,p,h,d}$, i.e the difference microclimate and macroclimate temperature in cage of type c (no cage, opaque-shade or clear-shade) at location p (above or below leaflet) at hour h on day d. This value was compared to $P_{h,d}$. For analysis, $P_{h,d}$ was rounded to classes of 25 $W \cdot m^{-2}$, and the relationship between this value and the mean value of $DIFF_{c,p,h,d}$ per class, weighted by the number of observations per class, was fitted to a logistic model by iterative

nonlinear regression using the multivariate secant method (PROC NLIN, DUD algorithm, SAS Institute 1988). The model was of the form:

$$DIFF_{c,p,h,d} = \frac{K_{c,p}}{1 + \exp(-(\alpha_{c,p} + \beta_{c,p} \cdot P_{h,d}))} - \Gamma_{c,p} \tag{4}$$

Parameter K is the raw asymptote of the curve; α and β modify scaling and shape; use of Γ to shift the curve vertically circumvents the usual restriction that the logistic curve pass through the origin. The actual asymptote of the curve is given by K - Γ.

RESULTS AND DISCUSSION

Estimation of insolation

Figure 8 illustrates the general pattern of daily insolation readings over the eight days sampled. The readings follow a sinusoidal trend over time during daylight hours, but the actual values generally fall beneath the sine curve; this reduction is related to cloud cover (Fig. 9). Equation 5 (Smith 1959) relates the mean measured insolation by clarity class, weighted by the number of observations per class, at hour h on day d ($P_{h,d}$), to theoretical maximum insolation ($I_{0,h,d}$) and proportion of the sky clear of clouds.

$$P_{h,d} = I_{0,h,d} \cdot [0.1569 + 0.3576(b_{h,d}/B_{h,d})] \tag{5}$$

Standard errors are 0.0615 for the intercept and 0.0828 for the slope. The model has $F_{1,7} = 18.6$, $p < 0.01$, and $r^2 = 0.7270$.

Insolation above and below the leaflet outside cages, and in cages of the two types ($P_{c,p,h,d}$) were related to insolation in full sun ($P_{h,d}$), by simple proportions (equation 6).

$$P_{c,p,h,d} = \mu_{c,p} \cdot P_{h,d} \tag{6}$$

Parameter μ is a fitted proportionality constant, specific to cage type and position within cage. Estimates of $\mu_{c,p}$ are provided in Table 6; raw data are presented in appendix 3. In all cases, $\mu_{c,p}$ was significantly greater than 0; and it is also significantly different from 1 except above uncaged leaflets. Comparison of appropriate μ with the intercept of equation 5, reveals that insolation above the leaflet in opaque-shade cages in full sun was about 22% of that outside cages on a completely cloudy day.

Estimation of microclimate temperatures

The influence of insolation on the differences between various microclimate and macroclimate temperatures is consistent and predictable. Parameter estimates for models relating macroclimate temperatures to temperatures above or below the leaflet in the two types of cage or to uncaged leaflets, are summarized in Table 7. Scatter plots of the data are presented in Fig. 10. All of the curves reached 99% of the asymptotic maximum at measured insolation less than approximately 100 $W \cdot m^{-2}$. Measured insolation exceeded 100 $W \cdot m^{-2}$ except for short periods near dawn and dusk (Fig. 8) and did not fall below this limit during the rest of each day, even on overcast days (24, 26, and 27 Jul, and 01 Aug), or when cumulus clouds passed overhead (dark square marked with an arrow in Fig. 8).

The air temperature difference between corresponding microhabitats in the two cage types can be estimated by comparing the quantities $(K - \Gamma)$ (presented in Table 7). For most of each day, air temperature above the leaf in a clear-shade cage exceeded that in an opaque-shade cage by $(8.469 - 0.5251) - (3.483 - 0.3587) \approx 4.8°C$. Similarly, air temperature below

the leaf was ≈ 4.4°C greater in a clear-shade cage than in an opaque-shade cage. The difference in air temperatures above and below the leaflets was ≈ 0.5°C in a clear-shade cage and ≈ 0.1°C in an opaque-shade cage.

Temperatures above and below the leaflet in opaque-shade cages were very similar to corresponding temperatures near non-caged leaflets (Fig 11); results of linear regressions of corresponding microclimate temperature near caged leaflets in opaque-shade cages, and near uncaged leaflets, are given in Table 8. Although temperature differences do occur between corresponding microhabitats, those in opaque cages are similar to those encountered in nature, and hence results obtained in these cages apply to natural conditions.

Table 6. Parameter estimates $\mu_{c,p}$ from linear regression of measured insolation ($W \cdot m^{-2}$) at positions (p) above and below leaflet, in cages of each type (c) (Clear and opaque shade) and near uncaged leaflets, vs. measured insolation in full sun. In preliminary analyses, intercept terms were non-significant and were eliminated.

CAGE (c)	POSITION (p)	$\mu_{c,p}$ EST	S.E.	F	df	P(>F)	r^2
CLEAR	ABOVE	0.543	0.0216	632.2	1,8	≤0.0001	0.99
CLEAR	BELOW	0.164	0.0209	61.9	1,8	≤0.0001	0.89
OPAQUE	ABOVE	0.0345	0.0055	39.7	1,8	0.0002	0.83
OPAQUE	BELOW	0.0150	0.0019	64.8	1,8	≤0.0001	0.89
NONE	ABOVE	1.023	0.0228	2007.1	1,8	≤0.0001	0.99
NONE	BELOW	0.204	0.0095	464.3	1,8	≤0.0001	0.98

Table 8. Results of linear regressions of air temperature near the surface of uncaged leaflet on the corresponding temperature near a leaflet in an opaque-shade cage. Neither intercept is significant. Both slopes are significantly greater than 0 but not significantly different from 1.

	ABOVE LEAFLET	BELOW LEAFLET
F	903.3	626.4
df	1,67	1,77
r^2	0.9310	0.8905
intercept	-1.22 ± 1.01	0.269 ± 1.14
slope	1.06 ± 0.035	0.989 ± 0.040

Figure 7. Schematic side view of cage used in field studies of behavioral thermoregulation, feeding rate, and developmental rate.

CODES: Bottom (A) and top (B) of 10cm diameter plastic petri dishes; (C) 42 mesh·cm^{-2} nylon screen made to fit inside (A); straight pin support (D). (E) 2.5 mm wide notch melted in (A) to receive rachis of leaf; the screen at the corresponding position was frayed such that it sealed around rachis. (F) 15 x 20 cm rectangular shade of one of two types. Opaque shade: corrugated cardboard; clear shade: plastic cling film on a wire frame.

5-cm wooden cubes (G,H) attached to 50 cm wooden stakes (I). Cube G was attached using a wood-screw through a 5 cm vertical slot in the stake, and remained movable; the attachment to cube H was static.

The leaflet was secured with tape (J) from the rachis to (B). The tape held the leaflet in position and distributed forces to avoid damage to the leaflet.

The top superstructure (A, C, F, and G) was raised to introduce the leaflet, then lowered to enclose it. Attachments to G and H retained horizontal and rotational play, allowing for adjustment of fit.

I G F

A

C

D

B E J

H
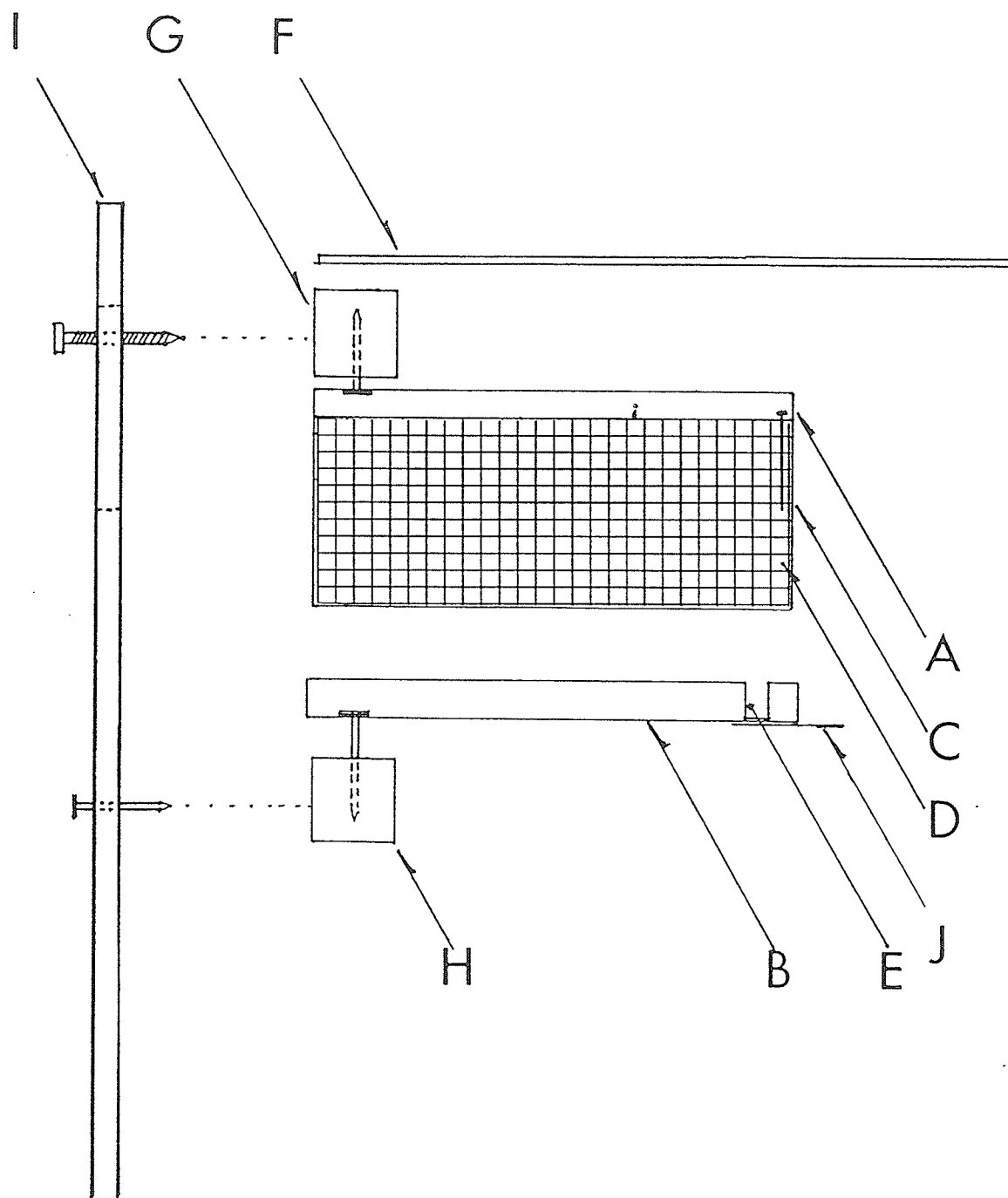
Figure 8.   Daily insolation patterns during eight days at Glenmore, British Columbia, July and August 1991.   At datum marked with an arrow, a large cumulus cloud obscured the sun.   Data are uncorrected photometer readings ($W \cdot m^{-2}$).
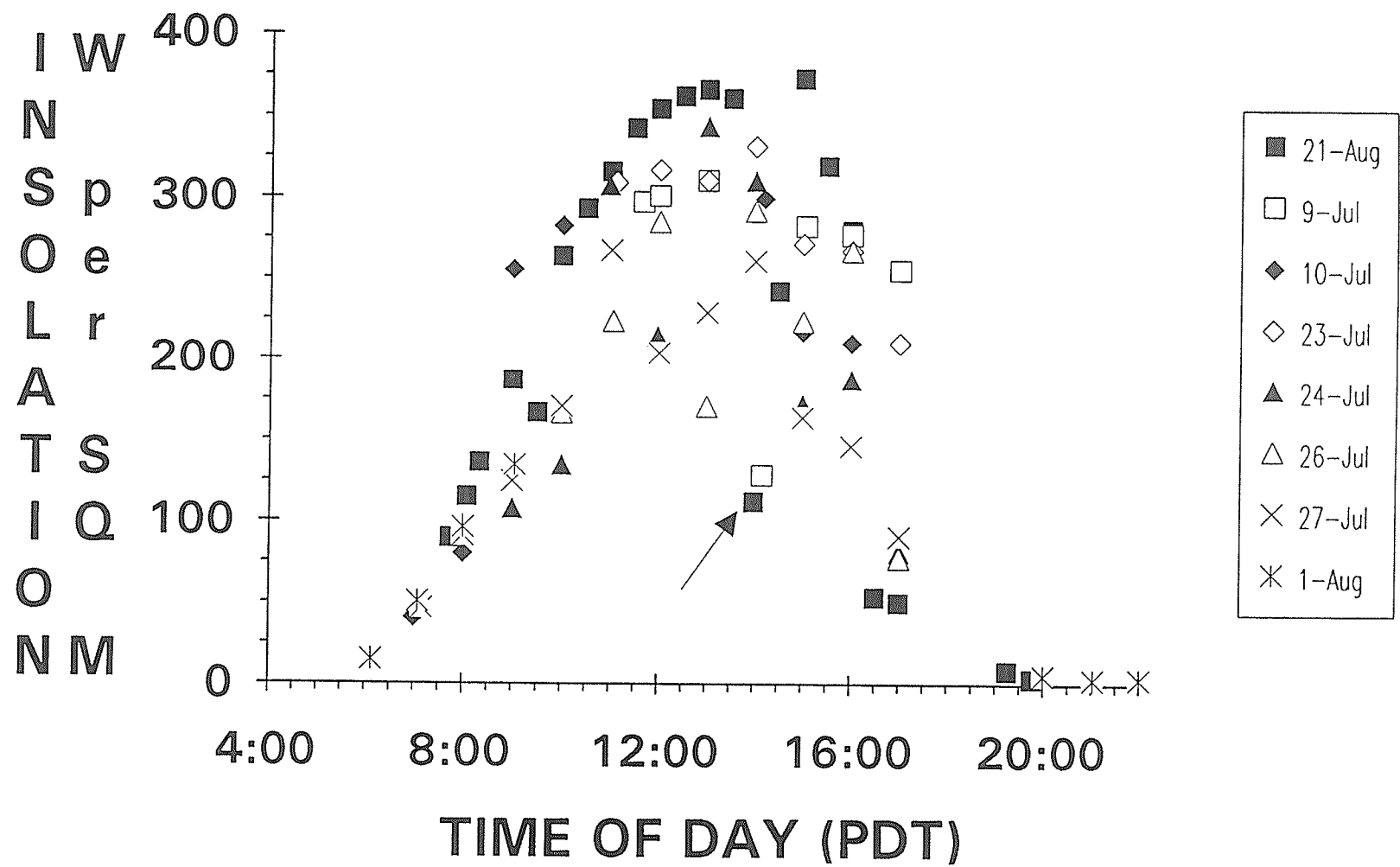
Figure 9. Ratio of (measured insolation)/(theoretical insolation) vs.
    proportion of sky clear of clouds during eight days. Glenmore,
    British Columbia, July and August 1991.
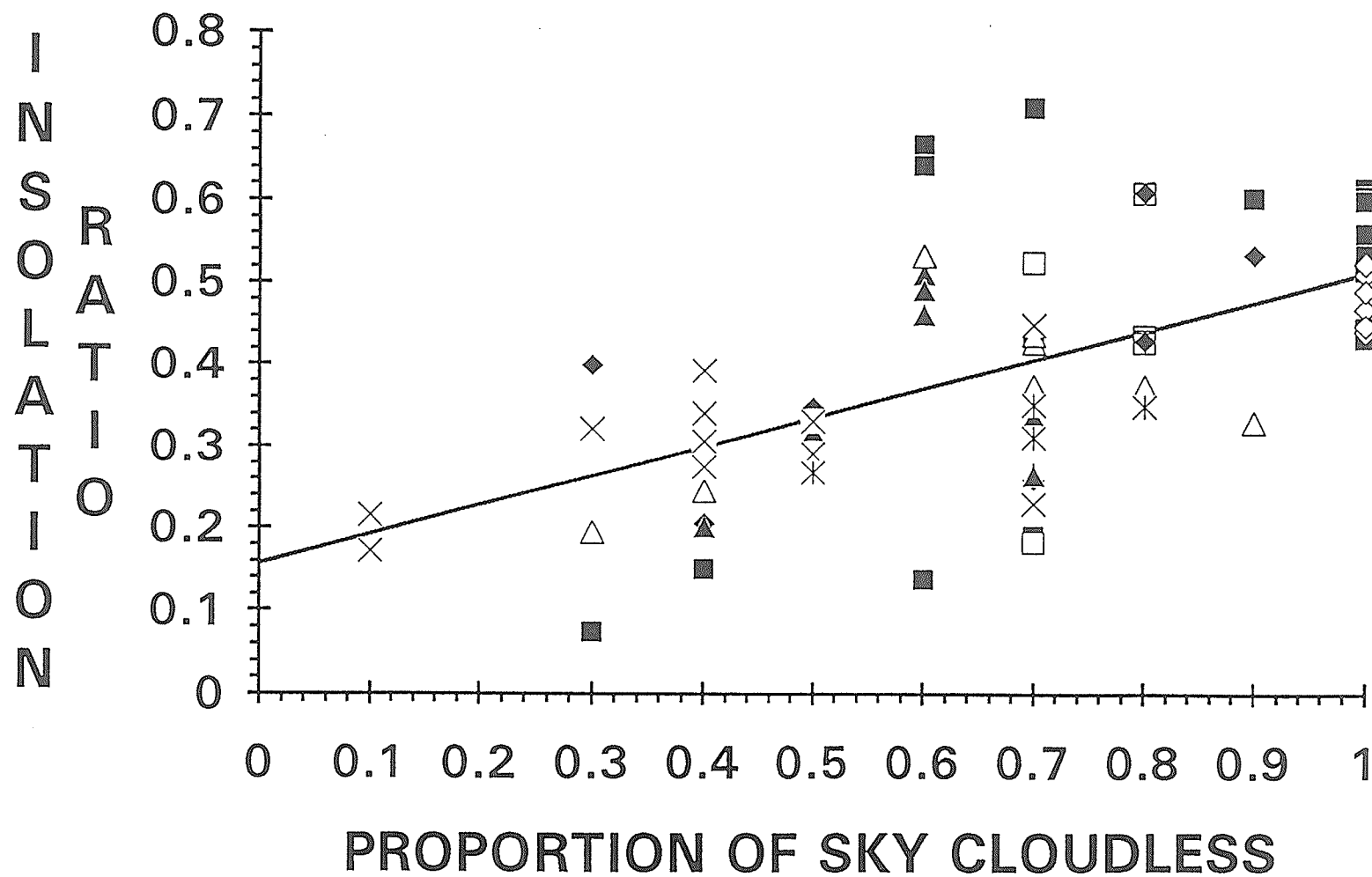
Figure 10.   Difference (°C) between macroclimatic temperature and temperature measured in cages above and below the leaflet, during eight days. Glenmore, British Columbia, July and August 1991.
A) Cages with clear shades
B) Cages with opaque shades

Symbols: Closed square and solid line: above leaflet.
            Open square and dashed line: below leaflet.

DIFFERENCE C

INSOLATION [W/(SQ M)]

B)

102
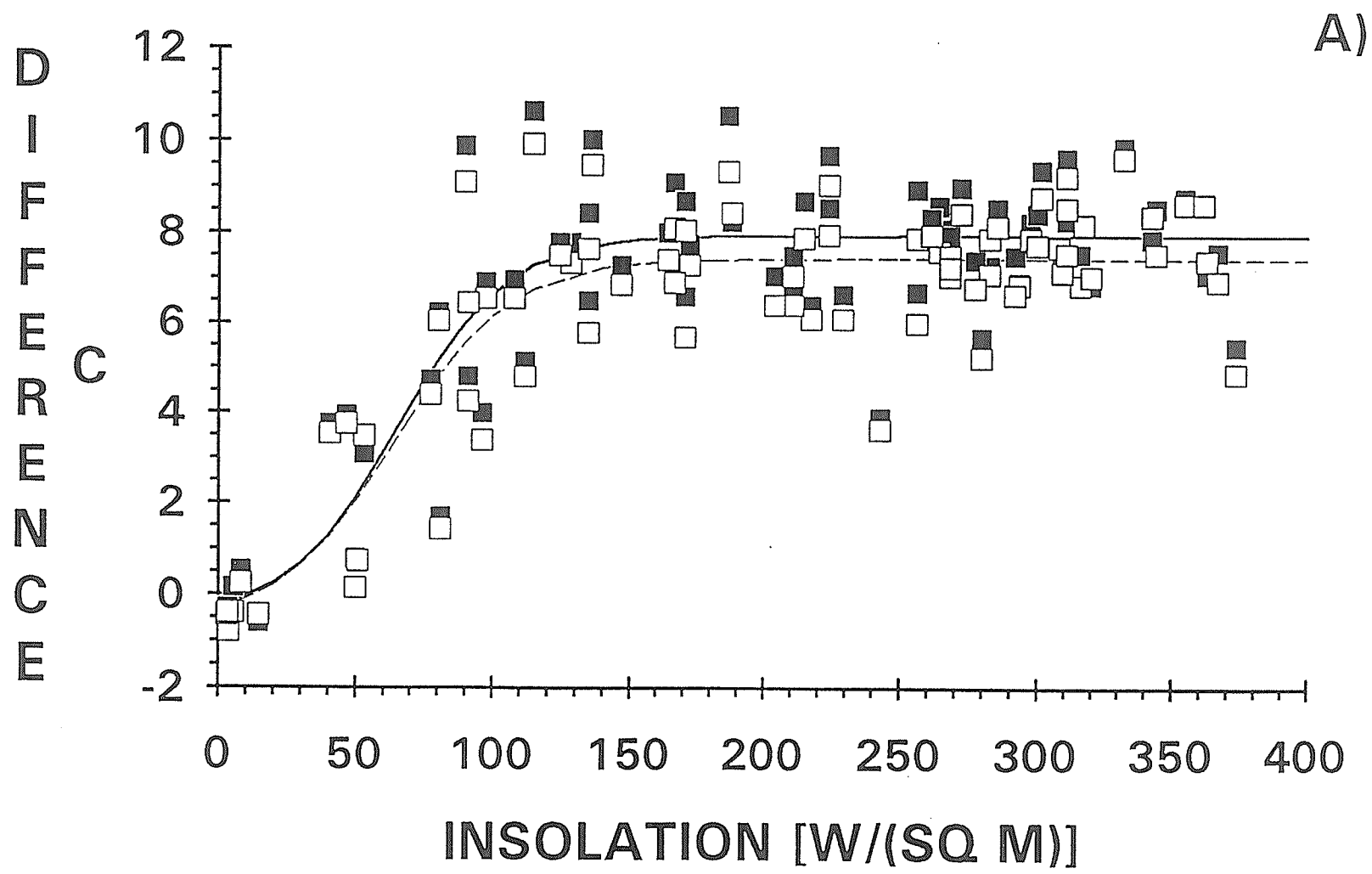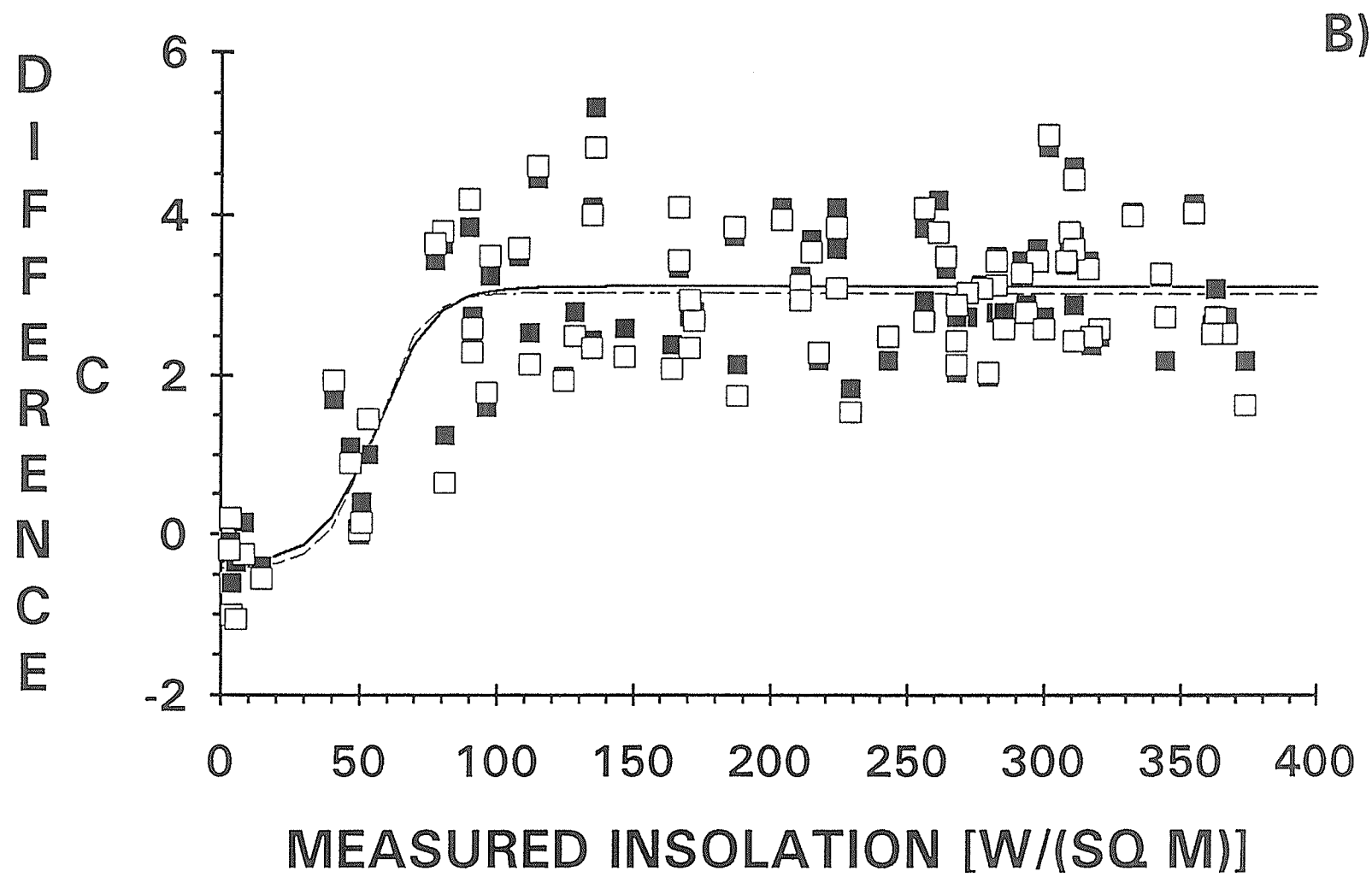
Figure 11. Comparison of temperatures (°C) above and below non-caged and
opaque-caged leaflets, during eight days. Glenmore, British
Columbia, July and August 1991.
Symbols: Closed square: above leaflet.
             Open square: below leaflet.
             Solid line: x = y

TEMPERATURE NEAR UNCAGED LEAFLET

TEMPERATURE (C) IN OPAQUE CAGE

- ■ ABOVE
- □ BELOW
- — x = y
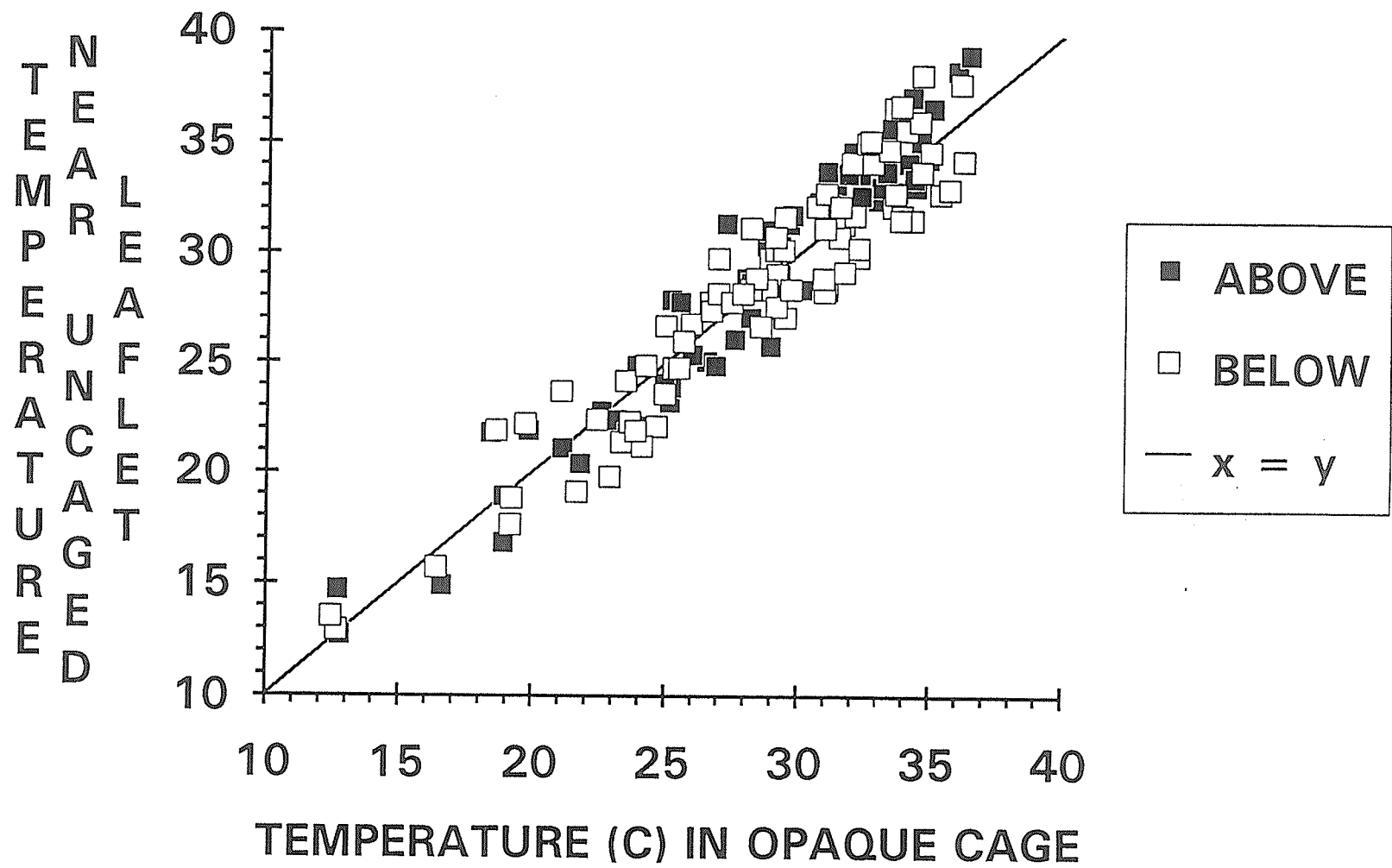
Section III. Chapter B)
     BEHAVIORAL   RESPONSE   OF   COLORADO   POTATO   BEETLE   LARVAE
     (LEPTINOTARSA DECEMLINEATA (SAY) (COLEOPTERA: CHRYSOMELIDAE))
     TO COMBINATIONS OF TEMPERATURE AND INSOLATION, UNDER FIELD
     CONDITIONS.

ABSTRACT

In short-term (< 5 min) trials, Colorado potato beetle larvae were released on top of potato leaflets under combinations of ambient temperature and insolation, and their response was observed and timed. Mean intervals required for larvae to start feeding or to move under the leaflet were independent of air temperature and measured insolation. Overall mean decision interval was 2.86 min (S.E. = 0.05, n = 350). Proportion of larvae moving under the leaflet increased logistically with both air temperature and insolation. A 1 $W \cdot m^{-2}$ change in insolation had the same behavioral effect as a 0.0838°C change in air temperature; hence the two variables were merged into a linear combination, $T^* =$ ambient temperature + 0.0838·P, which has units of °C. A logistic model described the proportion of larvae under the leaflet as a function of T^*.

In one-day trials in which temperature, insolation, and the proportion of larvae in sun and in shade were monitored repeatedly, larval distribution results agreed well with predictions from the short-term trial at $T^* > \approx 40$°C, but demonstrated increasing overrepresentation of larvae under the leaflet as T^* diminished. This systematic bias is consistent with thermoregulation by avoiding hostile conditions, as opposed to seeking optimum conditions. Results of the short-term and long-term trials are related by a simple linear model.

INTRODUCTION

Colorado potato beetles have been shown to respond to climatic variables by moving among available microclimates (May 1981, 1982). This affects their body temperature and hence the rates of temperature-dependent processes such as feeding and development.

The purposes of this study were to quantify the behavioral response of larval Colorado potato beetles to combinations of ambient temperature and insolation, and to derive a descriptive model of this response. This is a study of the short- and long-term behavior of individual larvae under known conditions, which complements an earlier study by May (1981, 1982), who studied mean distribution and body temperature elevation of populations.

Three field trials were undertaken. The first trial measured the short-term reaction of individual larvae to combinations of temperature and insolation. The other two trials monitored the long-term distributional responses of Colorado potato beetle populations to naturally varying combinations of temperature and insolation. Results from the first trial were used to generate a descriptive model of the behavioral response; the usefulness of this model to predict the long-term response, was evaluated in the other trials.

MATERIALS AND METHODS

Short-term response trials

The short-term behavioral response of Colorado potato beetle larvae to combinations of temperature and insolation, was examined by observing larvae placed on potato leaflets in a potato field. Preliminary trials revealed that under such circumstances, the larvae either start feeding, or move to the underside of the leaflet. These responses were interpreted to indicate that the larva had judged the conditions atop the leaflet to be acceptable or unacceptable, respectively. Because these responses are easily quantified and observed, they were chosen as the basis of the behavioral assay.

This trial was conducted in a plot of 'Russet Burbank' potato plants ca. 10km north of Kelowna, B.C. (49° 53' N, 119° 29' W) in late July and early August 1991. Larvae used in the trial were obtained from a colony maintained in an outdoor insectary in Winfield, B.C. (50° 02' N, 119° 24'W). This colony originated from adults collected in a private garden in Winfield. Instars used were of the first and second filial generations. Instars were kept separate in 10 x 1.5 cm plastic petri dishes, and were transported to the site in a cooler with ice (17 ± 4°C).

Ambient temperature was 'manipulated' by scheduling repetitions of the trial on different days and times of day. Ranges of insolation were created by making observations in full sun, or in the shade of one, two or four layers of black nylon window screen (by measurement, insolation ≈ 0.61, 0.40 and 0.25 times full sun), or an opaque card (by measurement, insolation ≈ 0.16 times full sun). The shading material was suspended on an 80 cm x 80 cm frame mounted ≈ 1 m from the larvae.

For each repetition of the trial, five healthy, horizontal leaflets were chosen arbitrarily from among those on the south side of the plant. All were approximately 40 cm from the ground, and before shading, entirely exposed to direct sunlight. The same leaflets were used repeatedly in each repetition of the trial.

Larvae were removed individually from the cooler, and each was placed near the centre of the upper surface of a separate potato leaflet. Each larva was observed until it either began feeding or moved to the underside of the leaflet (hereafter, this response will be termed 'under the leaf'). The times of placement of larvae on the leaflet, and of the behavioral decision were each measured to the nearest 5 s. In each trial, instars were tested in random order, with shade treatments assigned in random order within instars. After use, larvae were returned to the cooler, and ultimately to the insectary colony. Larvae may have been used as later instars in subsequent trials.

Air temperature and insolation were measured within 30 cm of the larvae. Temperature was measured within 0.5 cm of the upper surface of a leaflet, using a Cole-Palmer L-08532-00 'Digi-Sense'® thermometer, equipped with L-08439-00® general purpose thermistor probes. Insolation was measured using an LI-210S® photometric sensor, attached to a LI-1858® Quantum radiometer/photometer (Lambda Instrument Corp.). The sensor was levelled horizontally with the aperture upward. Both measuring devices were shaded in the same manner as the larvae. One temperature and insolation measurement was taken for each combination of instar and shade; over the interval ($\approx$ 10 min), changes in temperature and insolation were

negligible. Trials were conducted only under calm wind conditions, in order to minimize losses of experimental subjects.

Long-term response trials

Two trials were conducted in which the locations of larvae on potato leaflets were monitored repeatedly over time. Both trials were conducted in Winfield, B.C. in August 1991, on potted 'Russet Burbank' potato plants. The plants were $\approx$ 40 cm in diameter, i.e. small enough that self-shading was negligible; hence larvae could enter the shade only by moving to the underside of a leaflet. Larvae were obtained from the colony described in the previous section, which was less than 10 m from the experimental site.

i) Caged trial

This study was conducted in the cages shown in Fig 7. The study was replicated twice per cage type per instar on each of two separate days. Terminal leaflets were introduced into the cages. These leaflets remained attached to the plant. Six to ten larvae of a given instar were released in each cage on the upper surface the potato leaflets. Starting $\approx$ 1 h later, the number of larvae on the upper and lower leaflet surfaces was noted periodically in each cage. At each observation, the time, temperature and insolation were measured above and below the leaflets in separate cages of each type. The first and second repetitions in the caged trial consisted of 11 and 5 sets of measurements per instar (60 and 40 data points), respectively.

ii) Free-range trial

At $\approx$ 0600 h PDT (i.e. $\approx$ 0.5 h before sunrise) on 09 Aug 1991 and 15 Aug 1991, 15 Colorado potato beetle larvae of each instar were placed

individually on the upper surfaces of uncaged leaflets on potted potato plants. Throughout each day, the time, insolation and ambient temperature above and below the leaflets, and numbers of larvae of each instar on the upper and lower leaflet surfaces, were noted at intervals of 0.5 to 1 h until ≈ 1915 h PDT (i.e. ≈ 0.5 h after sunset), and then at longer intervals until ≈ 2300 h.

RESULTS

Short-term response trials

This trial consisted of five repetitions spaced over four days in 1991. Appendix 3 presents dates and times of each repetition, and summarizes ambient temperature, insolation and proportion of larvae moving under the leaf by instar in each repetition.

When placed on the leaflet, each larva remained motionless for ≈ 5 to 10 s, then became progressively more active, starting with head movements and progressing to apparently undirected motion on the leaflet surface. Larvae then either began feeding or moved under the leaf by crawling over the upper surface in a direction away from the sun until they reached the edge; there seemed to be no orientation to leaflet edges.

Analysis of variance revealed no significant instar effect on response or time to response, so data were pooled over instars. Over all instars, mean time to make (either) behavioral decision was 2.86 min (S.E. = 0.05; n = 350), and 95% of decisions were made within 4.6 min. In a behavioral model, the response can be reasonably considered instantaneous.

Proportions (U) of larvae of each instar which moved under the leaf at various combinations of air temperature and measured insolation are summarized in figure 12. Each point represents the mean response of one

instar in one trial; in most cases, n = 5 per point. For presentation, responses are divided into three categories: U = 0; 0 < U < 1, and U = 1.

The effect of environmental variables and larval instar on proportion of larvae which moved under the leaf was analyzed by analysis of variance on arcsin-transformed proportions. Descriptive variables were temperature, insolation and instar, plus all possible interactions. The model was highly significant ($F_{15,56}$ = 7.05, p ≤ 0.0001, r^2 = 0.6538). U was significantly affected by temperature ($F_{1,56}$ = 17.28, p ≤ 0.0001), insolation ($F_{1,56}$ = 11.32, p ≤ 0.01) and by the interaction of temperature and insolation ($F_{1,56}$ = 3.89, p = 0.05). U did not differ significantly over instars ($F_{3,56}$ = 0.54, p > 0.05); nor did instar interact significantly with temperature ($F_{3,56}$ = 0.52, p > 0.05) or insolation ($F_{3,56}$ = 0.41, p > 0.05), so instars are pooled for subsequent analysis.

A bivariate model (7) was derived, which describes U as a logistic function of both temperature (T, °C) and photometer reading (P, W·m^{-2}) (PROC LOGISTIC, SAS Institute 1991).

$$U = \frac{1}{1 + \exp\left(-\left(x + y{\cdot}T + z{\cdot}P\right)\right)} \tag{7}$$

The parameter estimates were: x = -10.9530 ± 1.3113; y = 0.2910 ± 0.0383, and z = 0.0244 ± 0.00282 (model χ^2 = 136.1; df = 1; p ≤ 0.0001); all parameter estimates are significant to p ≤ 0.0001. The solution to this equation is presented in Fig. 13. The interaction of temperature and insolation was not significant (p > 0.6), and was ignored. Equation (7) was used to solve for combinations of temperature and insolation at which a specific value of U was expected. The curves so defined are contours of

constant behavioral response, which are overlain on the data in figure 12.

Equation (7) can be linearized (8):

$$\ln[U/(1-U)] = \text{logit}(U) = x + yT + zP \tag{8}$$

This form reveals that parameters y and z measure the impact of single-unit changes in T and P, respectively, on logit(U). A 1 $W \cdot m^{-2}$ change in P has the same behavioral impact as a z/y = 0.0838 °C change in T (appendix 4). This relationship also allows simplification of equation (7) by merging the two explanatory variables into a linear combination,

$$T^* = T + 0.0838 \cdot P. \tag{9}$$

T^* has units of °C (appendix 4).

he quantity U is related to T^* by equation (10).

$$U = \frac{1}{1 + \exp(-(x_1 + y_1 \cdot T^*))} \tag{10}$$

The parameter estimates were: x_1 = -10.9570 ± 1.2184; y_1 = 0.2912 ± 0.0322, (model χ^2 = 136.2; df = 1; p ≤ 0.0001); both parameter estimates are significant to p ≤ 0.0001. Equation (10) can be solved to demonstrate that for fixed U, T^* is also fixed. For U = 0.5, T^* = 37.6°C.

Long-term response trials

The results of the caged and the free-range long-term response trials are similar, and will be presented together. Fig. 14 illustrates the time trend in proportion of larvae under the leaf. Data are pooled over instars. On uncaged leaflets, and in clear-shade cages, larvae show a pronounced tendency to move under the leaflet when direct sunlight falls in the leaflet. In opaque-shade cages, larvae showed a small but consistent tendency to be above the leaflet.

The results of the long-term and short-term trials agree only incompletely. Fig. 15 overlays the proportion of larvae under the leaf as observed in the long-term trial (Obs[U]), on the curve representing the proportion of larvae predicted to be under the leaf (Pred[U]), using equation (10), i.e. the behavior predicted from the short-term trials.

Agreement between long-term behavior and the model derived from the short-term trial is good at high values of T^*, but at lower T^* values, significantly more larvae occurred under the leaf in long-term trial than was predicted by the short-term trial. Over the range of T^*, Obs[U] and Pred[U] are related by the regression formula

$$\text{Obs}[U] = 0.211 + 0.804 \cdot \text{Pred}[U] \tag{11}$$

The model has $F_{1,70} = 467.2$, $p \leq 0.0001$, and $r^2 = 0.80$. The standard errors of the intercept and slope are 0.0306 and 0.0647, respectively; both parameters are significantly greater than 0 ($p \leq 0.0001$), and the slope is significantly less than 1 ($p < 0.01$). The following relationship, which can be used to calculate the proportion of larvae under the leaf in the long-term trial, is calculated by substituting U from equation (10) for Pred[U] in equation (11). This curve is included in fig. 15.

$$\textit{Obs}[U] = 0.211 + \frac{0.804}{1 + \exp(-(10.9570 + 0.2912 \cdot T^*))} \tag{12}$$

DISCUSSION

The results of these trials agree qualitatively with those of May (1982) in that both demonstrate that the tendency of Colorado potato beetles to avoid sunshine increases with ambient temperature.

Comparison of the results of the short- and long-term distribution trials provide insight into the mechanism of larval microhabitat choice. The short-term response trial was a simple behavioral bioassay that examined an easily quantifiable response to easily measured microclimatic conditions. A decision to move under the leaf indicates that the larva judged conditions unacceptable and adopted an avoidance behavior. The converse response, failure to move from the top of the leaflet, could mean either that the larvae actively chose to remain on top of the leaflet, or that they did not choose to leave, i.e. that the response was passive.

Results of the long-term study allow evaluation of these two interpretations. There was significant excess of larvae beneath the leaflet under conditions which in the short term trial resulted in no larvae actively choosing this niche. The most plausible explanation of this result is that these are larvae which moved under the leaf when conditions above the leaflet became intolerable, and which remained there even after conditions above the leaflet ameliorated. The failure of these larvae to move to the upper surface of the leaflet, when we know that larvae released on the upper surface would remain there, implies that larvae do not actively seek optimal conditions, but accept ambient conditions unless they become intolerable. By extension, larvae which remained on top of the leaflet in the short-term study did so because they simply did not choose to leave; i.e. the decision was passive.

The behavioral decision-making strategy of moving only when conditions leave some characteristic range, is common among ectotherms (Cowles and Bogert 1944; Heath et al. 1971). It is a strategy which is

compatible with the relative behavioral simplicity of the larvae and the spatiotemporal heterogeneity of its environment.

Most terrestrial ectotherms maintain their body temperature within a relatively restricted range, which is usually above ambient temperature (Heinrich 1977). Such discrimination is attained by microclimate selection, particularly by heliotaxis or heliokinesis (May 1979). Where appropriate microclimates are available, this thermoregulatory behavior results in body temperatures which approximate the optimum for one or more measures of ecological performance (Huey and Kingsolver 1989).

If the observed larval movement under the leaf is a thermoregulatory response, then z/y may be the amount by which larval body temperature is potentially elevated per unit measured insolation. If so, then T^* may be body temperature. Because larval body temperature was not measured directly, this hypothesis requires testing. It may be tested by determining whether it accounts well for temperature-dependent behavior.

Figure 12. Proportion (U) of Colorado potato beetle larvae moving to the underside of the leaflet, in relation to air temperature and measured insolation. Open diamonds: U = 0; crosses, 0 < U < 1; solid diamonds, U = 1. Lines join points of selected constant U, obtained by solving equation 10: from top to bottom these are U = 0.95, 0.75. 0.5, 0.25, and 0.05.

119
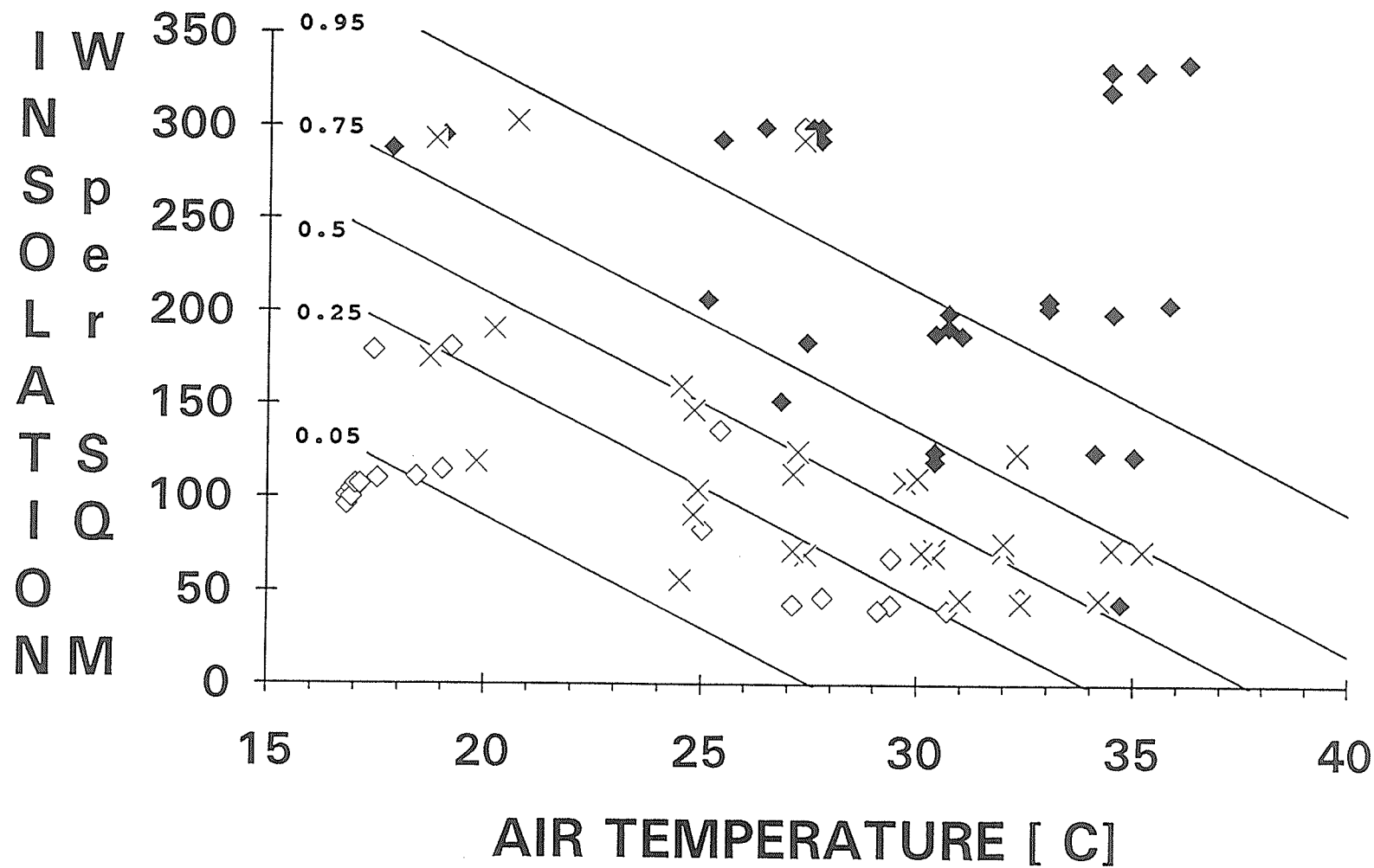
Figure 13.   Idealized response surface depicting proportion of Colorado

potato beetle larvae moving to the underside of the leaflet (Under),

in relation to air temperature and measured insolation, in short-

term response trials.

PPN UNDER LEAF

INSOLATION

[°C]

450 300 150 0

42 32 22 12 0

1.0 0.5 0.0
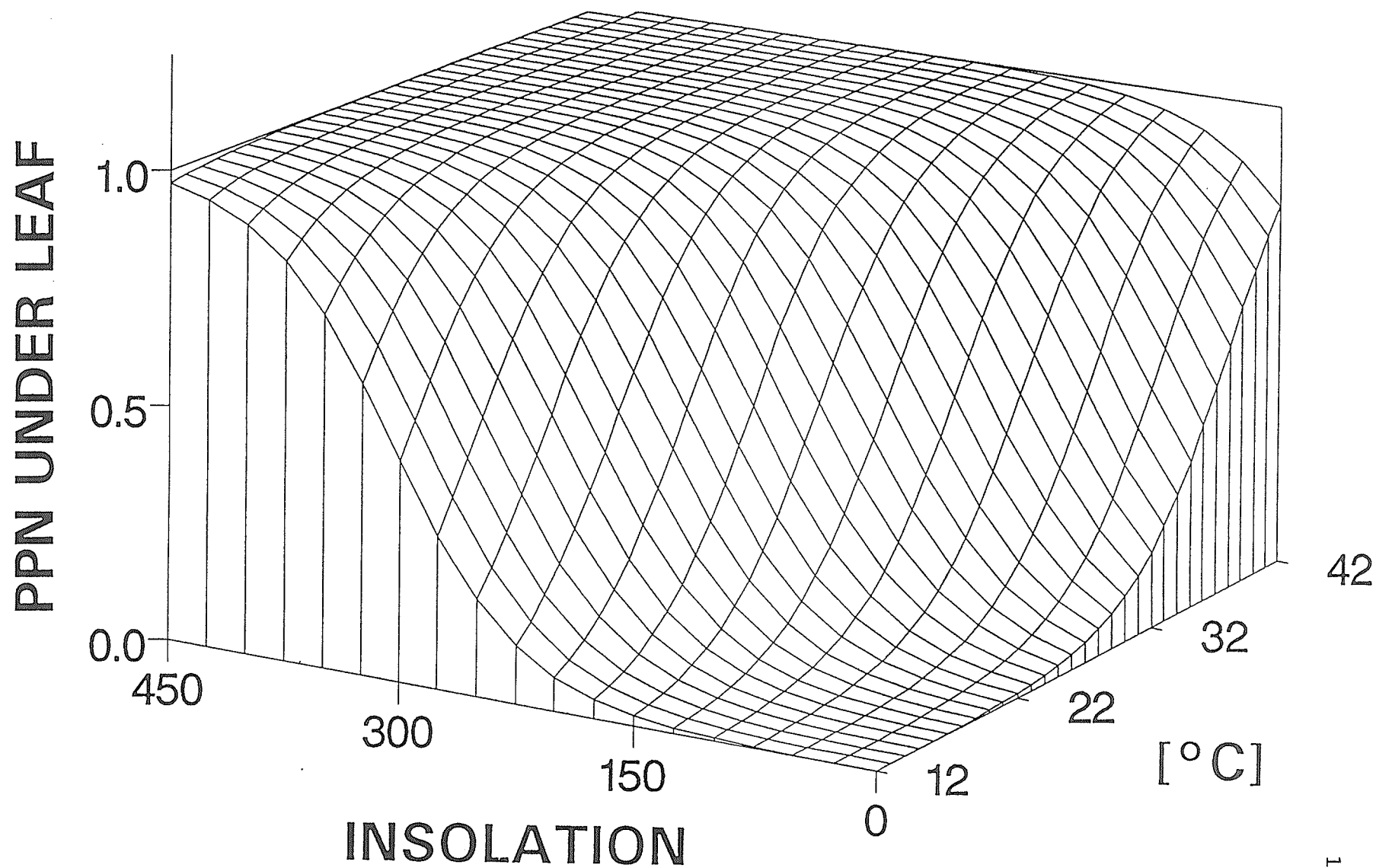
Figure 14. Proportion of larvae moving under leaflet vs. time of day in
long-term response trials.

Symbols: open square: clear-shade cage

closed square: opaque-shade cage

closed diamond: no cage

Sun fell directly on experimental area only during the interval
between the dashed vertical lines; this differs from sunup to
sundown due to obstruction by building.
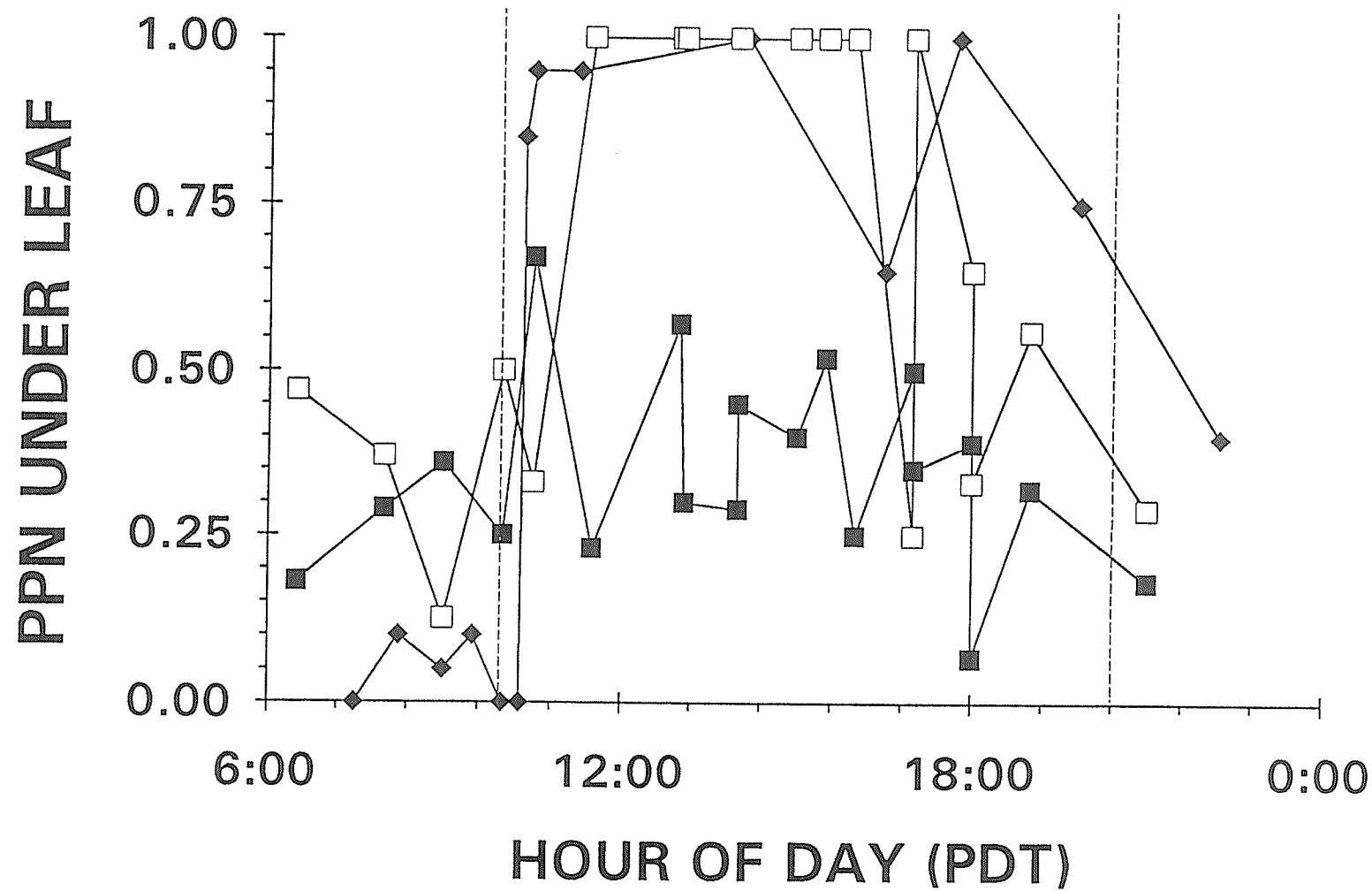
Figure 15. Comparison of proportion of Colorado potato beetle larvae on
underside of leaflet in long-term behavioral trials, to proportions
predicted from short-term trials using equation 10 (= PRED[U]).
FREE 1, FREE 2 = larvae allowed to move unconstrained on plants,
trials 1 and 2, respectively. OPAQUE and CLEAR = larvae constrained
in opaque-shade and clear-shade cages, respectively. OBS[U] =
nonlinear fit to observations (equation 12).

Independent   variable, T^*,   is   air   temperature   +
0.0838·insolation.
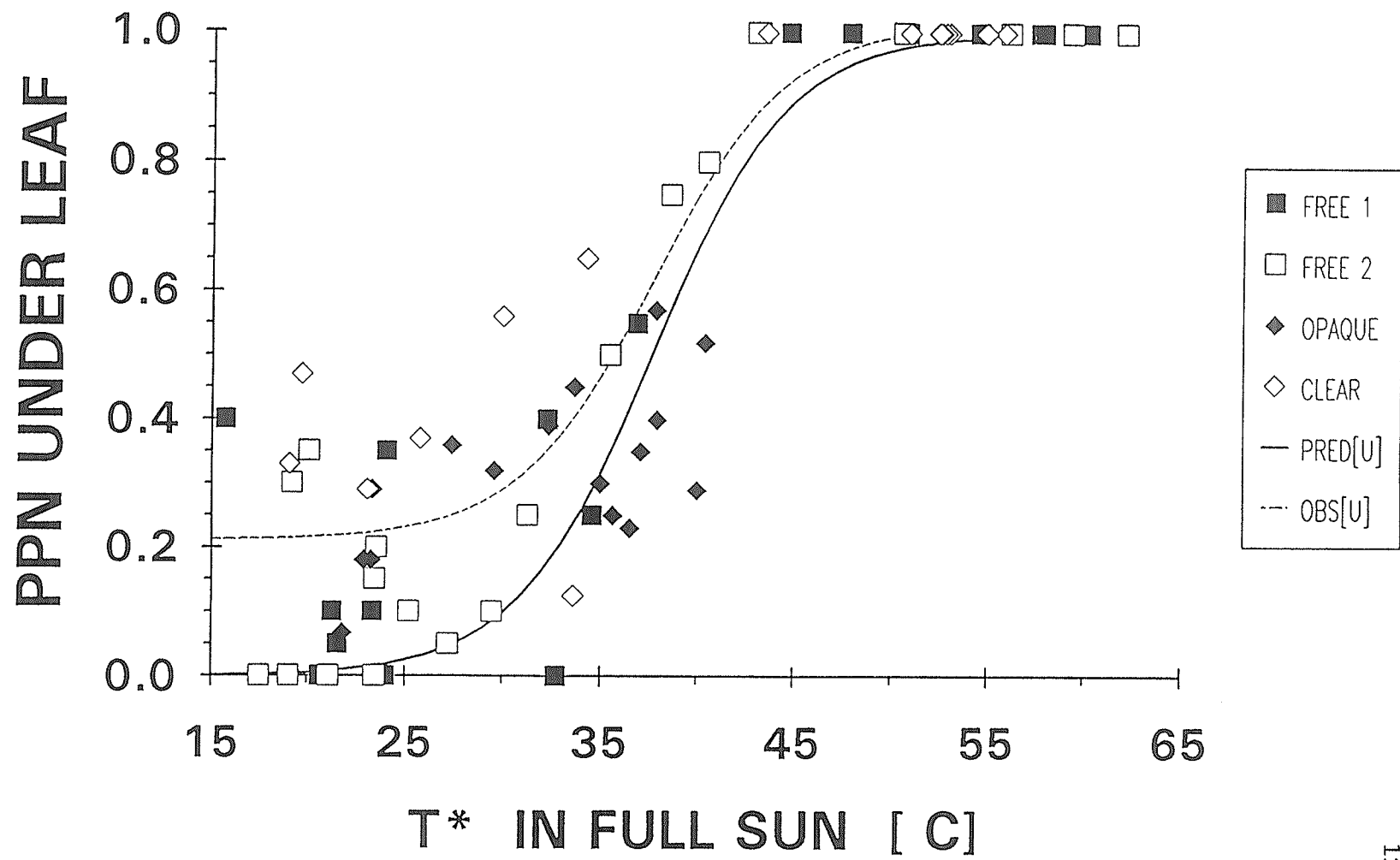
Section III.   Chapter C)
      FEEDING RATES OF LARVAL COLORADO POTATO BEETLES (LEPTINOTARSA
      DECEMLINEATA (SAY) (COLEOPTERA: CHRYSOMELIDAE)) UNDER FIELD
      CONDITIONS AND ASSEMBLY OF A MODEL SIMULATING THIS PROCESS

ABSTRACT

Feeding rates of Colorado potato beetle larvae were measured under field conditions. Measured feeding was independent of mean air temperature during the trial, and less than the amount predicted from laboratory temperature-dependent feeding rate parameters, using daily mean temperature as the predictive variable.

Four models of feeding were developed; these differed in their inclusion of the effects of behavioral response to insolation, and the effect of insolative heating on larval body temperature which was hypothesized in Section III, Chapter B. Model versions were evaluated by comparing predictions to measured values. The version which included both behavioral response and hypothetical insolative heating performed best; simulations using this version suggest that feeding rates are maintained near 80% of maximum during the sunny part of each day.

INTRODUCTION

Although the temperature-dependence of Colorado potato beetle feeding rates has been thoroughly characterised under constant conditions (Logan et al. 1985; Ferro et al. 1985; this thesis, Section II, Chapter A), no published accounts exist which explicitly test the applicability of these data to conditions in which temperature varies. Gibson et al. (1925) and Tamaki and Butt (1978) reared Colorado potato beetle larvae under variable temperatures, but did not report the amplitude or period of the temperature variations, so their results cannot be interpreted in this context. However, in an analogous comparison, Hagstrum and Milliken (1991) determined that developmental rates of numerous insect species, obtained under constant temperatures do not accurately predict developmental rates under varying temperatures. Because feeding and development are both temperature-dependent phenomena in poikilotherms, this observation suggests that a similar problem might occur when applying constant-temperature feeding rate data to variable conditions. Explicit comparison of feeding rates under constant temperatures and varying conditions in the field is desirable. In addition, a mechanistic model which predicts feeding rates under field conditions could provide insight and predictive capability. This study is intended to fulfil these requirements for larval Colorado potato beetles.

In addition to the direct effect of temperature fluctuations on feeding rate, other possible sources of disagreement between feeding rates under laboratory and field conditions include the effects of solar heating

on larval body temperature, and the ability of larvae to move among microclimates (Section III, Chapter B); the model developed in this chapter assesses the effects of each of these possible influences.

MATERIALS AND METHODS

FIELD EXPERIMENT

This study was conducted in a plot of 'Russet Burbank' potatoes in Glenmore, British Columbia, approximately 10 km north of Kelowna (49° 53' N, 119° 29' W). Colorado potato beetle larvae were maintained in a culture where they were reared in petri dishes in an outdoor insectary. Larvae used were first and second generation offspring of adults collected in Winfield, British Columbia (50° 02' N, 119° 24' W) during the summer of 1991. Details of rearing and transport are provided in Section III, Chapter B.

Feeding rates of Colorado potato beetle larvae under field conditions were measured by using cages to confine them for known intervals ($\approx$ 24 h) to potato leaflets. The leaflets remained attached to the plants for the duration of each trial. Cages (Fig. 7) were of two types; one had an opaque shade, and the other had a clear shade. The shade-type differences created a range of microclimates and feeding rates, which were exploited in the analysis.

The study was comprised of 10 trials over 4 weeks in July and early August, 1991. Feeding rates of each instar were measured in six or seven trials. The number of individuals per cage varied among instars: four or five first instar; four or five second instar; two or three third instar, or two fourth instars. Within each trial, measurements of each larval

instar were replicated in three to seven cages (mode = five) of each type. Specific trials in which instars appeared, the number of replicates per cage type, and numbers per cage were dictated by natural larval phenology, specimen availability, and the need to balance treatments, respectively.

To initiate each trial, healthy plants were chosen arbitrarily and on each, sufficient leaves were selected to accommodate all instars to be tested, plus one uninfested control. All leaves were the fourth to sixth fully expanded leaf on a stem (plants had 3 to 5 stems), and were of approximately uniform size within plant. Cage type was assigned randomly to plants, and treatments were assigned randomly to cages within plants.

Terminal leaflets on the chosen leaves were flattened individually against a sheet of graph paper backed with plywood, using a piece of hard transparent plastic, and photographed with a 200 mm flat-focus macro lens using a 35 mm camera mounted perpendicular to the graph paper. After being photographed, the terminal leaflets were caged; to facilitate this action, the subapical leaflet pair was removed.

Colorado potato beetle larvae were placed individually on the upper surface of the specific leaflet using a stem of grass (instars 1 and 2) or soft forceps (instars 3 and 4). Age of larvae within instar was unknown. All required larvae were placed on a leaflet before moving to another leaflet, and larval placement was completed on a given plant before moving to the next plant. The time at which larval placement was completed on each plant was noted to the nearest 5 min. Depending on the instars tested, and the number of replicates, placement required from about 1 to about 2.5 h per trial.

At the conclusion of each trial, the larvae were removed from each cage. Caged leaflets were removed individually from the plants and within 1 min were photographed as before. The time of removal was noted to the nearest 5 min. Removal of larvae occurred in the same order as placement, and the process was paced to ensure that the total confinement interval was 24 h $\pm$ 10 min.

Leaf areas were estimated from the photographic negatives using a computerized image analysis program, described in section II, Chapter A. Pixel count was calibrated to area using the graph paper background in the photographs. Relative precision of the method was $\pm$ ca. 1% of the measured leaflet area, equivalent to an absolute precision of $\pm$ ca. 30 mm^2.

Leaf area removed was calculated by comparing leaflet areas before and after infestation, compensating for leaf growth in the uninfested controls. Preliminary analyses revealed that control leaflet growth in the interval was proportional to leaflet size at the start of the trial, but at a rate which varied among trials and plants. Potential growth of infested leaflets on a given plant was assumed to be proportionately the same as that of the control leaflet on the same plant, and this growth was incorporated into the feeding estimate as follows. A proportional leaflet expansion factor was calculated for each plant; this is the ratio of control leaflet area at the end of the trial to area at the start of the trial. The expected final area of each infested leaflet on a given plant was calculated by multiplying its initial area by the plant-specific leaflet expansion factor. The estimate of feeding rate per individual was obtained by subtracting actual final leaflet area from expected final

area, and dividing by the number of larvae originally placed on the leaflet. Larval mortality was rare and its effects were disregarded.

FEEDING RATE MODEL

Assumptions The premises of this model are (i) that larval feeding rate is related to body temperature; (ii) that this rate is unaffected by previous thermal experience; and (iii) that body temperature and feeding rate both respond immediately to changes in ambient temperature.

Four model versions are derived in this section; these differ in their methods of estimating body temperature from climatic and behavioral data. The model evaluation process is a determination of which of these estimates is superior. Body temperature was never actually measured.

Fig. 16 outlines the logical flow of the model. The model is assembled from relationships derived in earlier sections; equation numbers from those sections are retained. For each iteration, all calculations were performed for each hour (h), day (d), cage type (c) and position (p) within cage (i.e. above or below the leaflet) using parameters specific to each variable. Where possible, subscripts are omitted for clarity in the following description.

Constituent information The model is based most fundamentally on hourly macroclimatic measurements of:

1) Airport temperature (MACRO) at the Kelowna municipal airport, ≈ 5km north of the experimental site.

2) Proportion of sky clear of clouds (CLARITY), as calculated from cloud cover (total opacity) estimates at the same airport.

3) Theoretical insolation on a horizontal surface before atmospheric attenuation (I_0) calculated using the astrometeorological estimator (Robertson and Russelo 1968).

Driving variables The model is driven by microclimatic variables derived from the macroclimatic measurements via empirically-derived relationships (Section III, Chapter A). These are:

4) External photometer reading P, estimated from I_0 and CLARITY by the relationship

$$P \quad = \quad I_0 \cdot [0.1569 + 0.3576(\text{CLARITY})] \qquad (5)$$

5) Photometer reading above and below leaflets in cages of each type, as derived from the estimated external reading via an empirically derived scalar multiplier (μ), which is specific to cage type and position (Table 4, Section III. Chapter A):

$$P_{c,p,h,d} = \mu_{c,p} \cdot P_{h,d} \qquad (6)$$

6) Microclimate air temperatures (MICRO), calculated from macroclimate temperatures and estimated external photometer readings by the logistic relationship

$$MICRO = MACRO + \frac{K_{c,p}}{1 + \exp(-(\alpha_{c,p} + \beta_{c,p} \cdot P_{h,d}))} - \Gamma_{c,p} \qquad (4')$$

The prime in the equation designation indicates that this model is slightly modified from equation 4, i.e. by substituting (MICRO - MACRO) for DIFF, and rearranging. The parameter estimates are specific to cage-type and position within cage; values are listed in Table 6 (Section III, Chapter A).

Behavioral variables In alternative versions of the model, the effects of behavioral microhabitat choice, and the possible effect of insolative heating on body temperature, which was hypothesised in Section III, Chapter B, were added to the model singly or together.

7) Apparent effect of insolation on body temperature was modelled by increasing microclimate air temperature by a quantity related to microclimate insolation. The operative quantity is

$$T^*_{c,p} = MICRO + 0.0838 \cdot P_{c,p} \tag{9}$$

This relationship was derived in Section III, Chapter B.

8) Behavioral response to T^* (proportion (U) under the leaflet) was modelled as:

$$U = 0.211 + \frac{0.804}{1 + \exp(-(10.9570 + 0.2912 \cdot T^*))} \tag{12}$$

Where T^* was measured on the upper surface of the leaflet.

9) Temperature-dependent leaf area consumption ($EATEN_i$, in mm^2) by each instar (i) in each hour was calculated in each microhabitat using the quadratic relationship derived in constant-temperature trials. Instar-specific parameter values (q, r, and s) are summarized in table 1 (Section II. Chapter A).

$$EATEN_i = q_i + r_i \cdot T_b + s_i \cdot T_b^2 \tag{1}$$

Where T_b = body temperature, as estimated by either MICRO or T^*.

Model versions Initial tests of the model compared four versions, which included or excluded insolative heating (equation 9) and behavioral thermoregulation (equation 12) in all four possible permutations. In version 1.1, body temperature was assumed to equal microhabitat air

temperature as calculated using equation (4'). Thermoregulatory behavior was ignored: i.e. larvae were assumed to spend half of their aggregate foraging time above and below the leaflet, regardless of climatic conditions; this distribution approximates that expected if dispersion is random.

In version 1.2, body temperature was calculated as in version 1.1, and larval dispersion with respect to leaf surface was assumed to follow the behavioral response to temperature and insolation described in equation 12.

In version 2.1, body temperature was assumed to equal T^*, which was calculated separately above and below the leaflet (equation 9). Behavioral thermoregulation was ignored; larval dispersion was as in version 1.1.

In version 2.2, body temperature was estimated as in version 2.1, and thermoregulatory behavior was modelled as in version 1.2.

Procedure The model iterated hourly. At each iteration, larval body temperature was calculated separately for microhabitats above and below the leaflet. Feeding rates in each microhabitat were estimated from this calculated body temperature. The estimate of larval feeding was calculated as the mean of the rates in each microhabitat, weighted by the proportion of larvae estimated or assumed to be in each microhabitat. Hourly feeding rate estimates were summed to estimate daily feeding.

To determine whether measured daily feeding rates were related to the average temperature which larvae experienced, mean daily larval body temperature was calculated in each cage. Hourly body temperature

estimates were obtained by weighted means, in the same manner as the feeding rate estimates, and the estimates were averaged over the day.

Model version assessment Predictive performance of the four model versions were compared using linear regression of model prediction (ordinate) on measured feeding value (abscissa). Model predictions were considered good if the regressions had intercept not significantly different from zero, a slope significantly greater than zero but not significantly different from one, a high coefficient of determination (r^2), and a low $\sqrt{MSE}$. The model version which fulfils these criteria most consistently was deemed best.

Modelled diel feeding pattern To obtain further insight into the mechanisms by which results were obtained, simulation output was examined over time within days. To eliminate impact of cages on modelled behavior, the model was modified to pertain to free-ranging larvae by replacing parameters in equations 5 and 6, with values pertaining to free-range conditions (Tables 4 and 5, Section III, Chapter B).

RESULTS AND DISCUSSION

FIELD EXPERIMENT

Table 9 lists dates and times of each experimental trial, larval instars tested, and summaries of macroclimatic data. Also included are estimates of mean larval body temperature during the trial, as output by the four model versions. For each instar, feeding rate varied among cage types and trials (Table 10). The two negative estimates of first instar

feeding rate probably occurred because daily consumption by these larvae is comparable to the resolution of the area estimation procedure. Similar levels of experimental error presumably occurred in all trials. In instar 2, trial J, in clear cages, the mean and standard error of feeding rate measurement are very high, as a result of a very high feeding rate estimate in one cage (182.8 mm^2), which differed from the mean value of the remaining cages in the trial (81.3 mm^2) by 4.6 times the standard deviation of the latter mean. This observation is clearly anomalous. One or more of the five larvae in this cage may have moulted to the third instar early in the trial, thus inflating the feeding measurement.

Relationship of measured feeding to ambient temperature

Figures 17 and 18 plot mean measured daily feeding rates per larva and linear regression models of this response, against daily mean ambient temperature as estimated by model version 1.1 This estimate was chosen because it invokes the fewest assumptions; it is equivalent to the mean of microhabitat temperature above and below the leaflet. Parameter estimates of linear regressions of mean daily feeding per larva on mean body temperature during experimental trial, as estimated by all model versions, are presented in Table 11. Regression on means, rather than on individual measurements, is appropriate because the population trend is the change of interest (Snedecor and Cochran 1980). All slopes are positive, but none is significant, although in instar 3 in opaque cages, $0.05 < P < 0.06$. In instars 3 and 4, where measurement error is proportionally smallest, the slope of the regression of feeding on body temperature is clearly lower in the clear-shade cages, than in opaque-shade cages. This comparison suggests that when larvae are provided with

a range of microclimates (clear-shade cages), they are able to maintain a feeding rate which is independent of air temperature.

Figures 17 and 18 also include total daily feeding predicted by the quadratic feeding-rate equations from Section II, Chapter A, using mean daily temperature as the independent variable. This model consistently overestimates measured feeding except for a few cases in the first and second instars. These results reveal that mean daily body temperature is not a good basis for estimation of feeding by larval Colorado potato beetles.

MODEL VERSION ASSESSMENT

Measured vs. modelled feeding Comparisons of model predictions and field observations are presented by instar in Figs. 19 to 22. To facilitate comparisons, the results from opaque- and clear-shade cages are presented as separate panels within the figures. In each panel, all four modelled values are plotted against the mean feeding rate from the field study; vertical ranks of four points correspond to the same measured value. A reference line representing 1:1 agreement of modelled and measured values is included.

In the opaque-shade cages (Figs. 19 - 22, A), feeding rates as estimated by the four model versions are so similar that the points overlay at the resolution of the graphics; this is due to the virtual elimination of solar heating effects by the opaque shade, and a consequent reduction in the efficacy of behavioral thermoregulation. In clear-shade cages (Figs. 19 - 22, B), model versions give different feeding estimates, as a consequence of the modelled impact of solar heating and behavioral thermoregulation on body temperature.

For each model version, the relationship between modelled feeding and observed feeding did not differ between cage types (Analysis of Covariance, P > 0.05) except in instar 2, in which a significant cage effect was attributable to the anomalously high measured feeding rate in trial J in the clear cages. Removal of this mean eliminated the cage effect. Hereafter, the second instar feeding rate measurement mean from clear cages in trial J will be disregarded as an outlier, and the data for each instar will be pooled by cage type. Ultimately, this elimination will be inconsequential to the conclusions of the following analysis.

Results of the regressions of modelled on observed feeding rates, pooled over cage type, for each model version, are summarized in Table 12.

In the first and second instars, none of the model versions predicted feeding well. All regressions have very low r^2, the intercepts are all significant, and the slopes are not significantly different from 0 for any model version. Therefore, in these instars, the predictions of these model versions are relatively independent of the observations.

In the third instar, conclusions drawn from regression analyses differ among model versions. In versions 1.1 and 1.2, the intercepts are significant, and the slopes are significantly greater than 0 and not significantly different from 1. These results indicate that these models overestimate third instar feeding rates at low temperatures. For model versions 2.1 and 2.2, the intercept terms were positive, but not significant, and the slopes were significantly greater than 0 and not significantly less than 1. These results indicate that these model versions estimate third instar feeding rates relatively well. The slightly positive intercepts represent distant extrapolations; within the

range of the data, there does not appear to be any serious disagreement between model predictions and observed feeding. The r^2 is higher and $\sqrt{MSE}$ lower for version 2.2 than for version 2.1; these statistics indicate that model version 2.2 predicts feeding of instar 3 Colorado potato beetles better than does version 2.1. This conclusion is confirmed by inspection of figure 20.

In the fourth instar, the intercept was significantly different from 0 and the slope was not significantly different from 0 for both model versions 1.1 and 1.2. Therefore, these versions do not predict feeding well. In regression analysis for model version 2.1, neither intercept nor slope is significantly different from 0; hence modelled and observed feeding rates are statistically independent. In model version 2.2, the intercept is not significantly different from 0, and the slope is significantly greater than 0 and not different from 1; hence, this version appears to model larval feeding well. The relationship between prediction and observation has higher r^2 and lower $\sqrt{MSE}$ for version 2.2 than for version 2.1; thus model version 2.2 performs better than version 2.1.
Model assessment conclusion Performance of all model versions was better in simulating feeding rates of instars 3 and 4, than of instars 1 and 2. This may occur because measurement imprecision is of magnitude similar to the feeding rate of instars 1 and 2, so that any relationship between modelled and observed feeding rates may be obscured. Thus the assessment of versions is based on their performance in estimating feeding by instars 3 and 4.

The inclusion of hypothesised effects of solar heating in the prediction algorithm (versions 2.1 and 2.2) results in a clear improvement

in the agreement between modelled and observed feeding in instars 3 and 4. Feeding rate in growth chambers (Section II, Chapter A) is temperature dependent, and these studies can be assumed to measure the relationship of feeding rate to body temperature, because the growth chambers lack high-intensity illumination. The superiority of model versions 2.1 and 2.2 which base their predictions on T^*, over versions 1.1 and 1.2, which use ambient temperature, supports the hypothesis from Section III, Chapter B, that T^* is body temperature.

The inclusion of microhabitat choice (2.2 vs 2.1) further improves the predictive performance of the model, although the case for this improvement is less distinct. Nonetheless, model version 2.2, which incorporates the effect of microhabitat choice, in addition to the hypothetical impact of insolation, is the most successful at predicting feeding rate in field cages.

The observation that in instars 1 and 2, the range of observed feeding values greatly exceeds that of modelled values may be attributable to measurement error, or to the effects of larvae moulting during the trials. Performance of the models in later instars suggests that the basic model is sound.

MODELLED DIEL FEEDING PATTERN Observed feeding by Colorado potato beetle larvae was independent of mean daily air temperature (Figs 17, 18; Table 11); particularly in the clear-shade cages, where larvae were given the opportunity to thermoregulate behaviorally. Examination of hourly output from simulations of feeding by free-living Colorado potato beetles provides insight into the mechanism by which this occurs. The simulations were performed using model versions 2.1 and 2.2 and two extreme

thermoregulatory strategies: "ALL TOP", in which all larvae remain on the upper leaflet surface at all times; and "ALL UNDER", in which larvae remain below the leaflet at all times.

Fourteen simulations were performed, using meteorological data from the days on which field feeding rate measurements were made. Results are similar for all instars; for brevity, only those for instar 4 are presented. Two representative examples are provided (Fig. 22 A and B). In all cases the thermoregulatory strategy "ALL TOP" resulted in no feeding for much of each day, as a result of T^* in the microclimate above the leaflet exceeding temperatures at which feeding by Colorado potato beetle larvae ceases (Section II, Chapter A). In many of the simulations, this circumstance persisted for 6 h or more. In constant-temperature laboratory feeding trials, larvae showed signs of severe stress in 2 h exposures to 42°C; hence these simulation results suggest that under field conditions, "ALL TOP" is a poor strategy. The diurnal feeding pattern occurring in the strategy modelled by version 2.1 also shows a distinct drop during the hottest part of the day; this is because larval distribution with respect to leaflet surface is random, resulting in their spending 50% of their aggregate feeding time on top of the leaflet, regardless of T^* there.

The diel feeding patterns resulting from "ALL UNDER" and the strategy modelled by version 2.2 are similar. On most days (e.g. Fig. 22), feeding rate is greatest near dawn and dusk, and falls slightly in the late afternoon. For most of each day, feeding rate in the "ALL UNDER" thermoregulatory strategy exceeds that in the strategy modelled by version 2.2, but the latter has a large advantage in that larvae feed at a much

higher rate for 2 to 3 h early each day, because they exploit the heating potential of early morning sunshine. This initial feeding rate boost was sufficient advantage that in 8 of the 14 days in the simulation, total daily leaf consumption in the strategy modelled by version 2.2 was greater than that modelled by "ALL UNDER".

If model version 2.2 is an adequate approximation of the process by which larval feeding is driven, then these simulation results suggest that the behavioral thermoregulation strategy modelled by this version may optimize a trade-off between early-morning advantage and mid-day disadvantage (compared to "ALL UNDER").

Hourly feeding rates of all 14 simulations for model version 2.2 are overlain in Fig. 24. One symbol is used to depict all simulated rates, regardless of the date, and the mean response is represented by a solid line. In all cases, modelled feeding rate increased from dawn ($\approx$ 0600 h PDT) until 0700 - 0900 h, then remained approximately stable until $\approx$ 1100 h. On most days, modelled feeding rate dropped to some extent until $\approx$ 1800 h, then resurged briefly until dusk ($\approx$ 2000 h). The average modelled feeding pattern is somewhat crepuscular. Colorado potato beetle larvae do not show a temperature-independent diel feeding pattern (Section II, Chapter A), so the modelled pattern is due to variation in modelled body temperature.

Over the 14 days included in this simulation, the mean hourly feeding rate by fourth instar Colorado potato beetles during daylight hours ranged from $\approx$ 60 to $\approx$ 70 $mm^2 \cdot h^{-1}$. Maximal feeding by fourth instar Colorado potato beetles is $\approx$ 75 $mm^2 \cdot h^{-1}$ (Section II, Chapter A); thus during daylight hours, the thermoregulatory strategy modelled by version

2.2 appears to maintain feeding rate at greater than ≈ 80% of maximal, when possible. (Simulations for all instars give the same result.) This is a consequence of the thermal niche preference which was observed in the behavioral thermoregulation trial (Section III. Chapter B) and which is an important component of this model version.

BIOLOGICAL CONTEXT

Thermoregulatory behavior involves both benefits and costs. The chief benefit is that body temperatures are maintained within a relatively narrow range (Heinrich 1977), generally centred on the optimum for one or more ecologically significant physiological processes (Hamilton 1973; Huey and Kingsolver 1989). Costs include energy expended in moving, and possible increased risk of predation (Huey 1974). Microclimatic niches can be considered to be resources, and behavioral thermoregulation is analogous to foraging (Huey and Slatkin 1976). Assuming that thermoregulatory behavior has a genetic component with an associated variance, selective forces can be expected to modify the frequency of relevant alleles in a population until a fitness peak in the thermoregulation "adaptive landscape" (*sensu* Wright 1968) is reached, thereby attaining at least a local maximum in the balance of costs and benefits.

Where temperature and insolation vary within the ambit of an ectotherm, behavioral adjustments are by far the most effective way to change body temperature: by moving between shaded and sunlit micro-habitats, body temperature may change by as much as 28°C (Stevenson 1985). Under such conditions, the ability to choose among microhabitats is advantageous. Placed in this context, comparison of the predictive

performance of model versions is an "experiment" which evaluates the importance of insolative heating and behavioral thermoregulation to feeding rate, and reveals that both factors are required to produce a model which predicts observed feeding rates well. Thus, model version 2.2 functions in a manner which is credible in an ecological and evolutionary context.

This is the first model of feeding by Colorado potato beetle larvae under field conditions. (I have also failed to locate any such model for any poikilotherm.) Considering the long series of empiricisms and approximations entailed in derivation of the feeding estimates, I think that the agreement between measured feeding and that modelled by version 2.2 is remarkable. Model version 2.2 appears to adequately abstract the essence of the mechanism by which feeding is determined in the field.

The importance of both insolative heating and behavioral thermoregulation to the production of an unbiased feeding rate estimate strongly suggests that these factors should be considered in models of any temperature-dependent physiological process under field conditions.

Table 9. Background to study of feeding rates of Colorado potato beetle larvae in small cages under natural weather conditions. Trial codes, date, instars, macroclimate maximum and minimum temperatures, day length (observed sunrise to observed sunset), and instars tested. All trials occurred in 1991.

TRIAL	START		MACROCLIMATE MEANS			DAY LENGTH	INSTARS TESTED				ESTIMATED MEAN LARVAE BODY TEMPERATURE [°C]							
											OPAQUE SHADES				CLEAR SHADES			
	DAY	TIME (PDT)	TEMP °C	INSOLATION[a] W·m⁻²	CLARITY[b]	(hh:mm)	1	2	3	4	1.1[c]	1.2	2.1	2.2	1.1	1.2	2.1	2.2
A	4Jul	14:00	19.5	435.0	0.96	14:44	*	*	*	*	23.2	23.2	23.4	23.5	25.7	25.6	29.3	27.9
B	5Jul	17:00	15.1	434.0	0.35	14:42	*	*	*	*	17.9	17.9	18.0	18.1	19.9	19.9	22.1	22.2
C	9Jul	11:00	21.9	430.6	0.71	14:36			*	*	25.5	25.5	25.8	25.8	27.9	27.8	31.3	29.8
D	10Jul	14:00	19.3	429.2	0.51	14:34		*	*	*	22.7	22.7	22.9	22.9	24.9	24.9	27.7	26.8
E	11Jul	17:00	20.5	427.8	0.27	14:32	*			*	23.9	23.9	24.1	24.1	25.8	25.8	27.9	27.3
F	23Jul	11:00	21.6	409.8	0.92	14:02	*	*			25.3	25.3	25.6	25.6	27.7	27.6	31.5	30.0
G	24Jul	13:00	20.8	407.6	0.37	14:00	*				24.3	24.3	24.4	24.5	26.2	26.2	28.6	27.8
H	26Jul	10:00	18.5	404.0	0.41	13:54	*				21.5	21.5	21.7	21.7	23.4	23.6	26.1	25.3
I	29Jul	12:00	16.8	397.3	0.69	13:46	*	*	*	*	19.9	20.0	20.2	20.2	22.4	22.3	25.0	24.6
J	30Jul	13:00	17.9	394.9	0.90	13:44	*	*	*	*	21.4	21.3	21.6	21.6	23.7	23.6	27.2	25.8

[a] Mean insolation at top of atmosphere, from 06:00 to 20:00h inclusive, as calculated using the astrometeorological estimator (Robertson and Russelo 1968).

[b] Mean proportion of sky clear of clouds 06:00 -- 20:00h PDT inclusive

[c] Temperatures are estimated for the duration of the trial, using model versions 1.1 -- 2.2 as described in the text.

Table 10. Measured feeding rates ($mm^2 \cdot day^{-1} \cdot larva^{-1}$) of Colorado potato beetle (CPB) larvae under natural conditions in cages of two types. Background information for each trial is given in table 9.

		CLEAR				OPAQUE		
TRIAL	#CAGES	#CPB	MEAN	S.E.	#CAGES	#CPB	MEAN	S.E.
				INSTAR 1				
A	3	15	10.5	12.3	3	15	15.7	9.4
E	6	27	9.3	22.8	6	24	45.3	4.9
F	5	25	22.8	10.8	5	25	20.6	10.0
G	6	30	50.7	10.2	6	30	19.6	4.2
H	5	20	-9.2	13.1	5	20	7.4	5.2
J	5	18	-5.0	15.2	5	18	20.0	16.0
				INSTAR 2				
A	5	25	65.9	21.4	4	20	71.8	45.7
B	6	30	57.2	7.8	6	28	68.2	17.5
D	5	25	76.6	10.3	5	25	73.4	9.1
F	5	20	84.8	12.1	5	20	76.8	7.7
I	6	30	59.8	5.1	6	30	48.8	7.3
J	4	18	106.7	53.8	4	18	49.6	23.2
				INSTAR 3				
A	4	12	223.2	5.5	5	15	326.0	129.8
B	6	18	279.9	11.9	5	15	186.3	15.9
C	7	21	304.2	50.5	6	18	286.5	26.6
D	5	15	271.7	41.8	5	15	256.0	63.3
H	5	15	250.3	37.4	5	14	316.0	35.0
I	5	15	219.8	13.2	5	15	198.0	57.1
J	5	14	238.1	87.8	4	11	274.9	10.0
				INSTAR 4				
A	4	8	829.7	110.0	4	8	921.2	138.8
B	6	12	927.0	125.0	6	12	675.6	77.3
C	5	10	1059.1	225.5	6	12	1338.3	158.4
D	5	10	1074.1	123.6	5	10	1156.6	227.7
E	6	12	1223.1	159.2	6	12	845.7	189.4
I	7	14	1059.3	65.6	7	14	925.0	102.7
J	4	8	873.8	117.4	5	10	984.3	51.0

CAGE SHADE TYPE

Table 11. Regressions of measured feeding rates ($mm^2 \cdot day^{-1} \cdot larva^{-1}$) on estimated mean daily body temperature as output by four model versions (abscissa). Estimates and significance values of parameters. Temperature estimates by version 1.1 are equivalent to means of microhabitat temperature above and below leaflets.

(., $p > 0.05$; *, $p \leq 0.05$; **, $p \leq 0.01$; ***, $p \leq 0.001$). Refer to text for codes of simulation model versions.

a) CLEAR-SHADE CAGES

INSTAR	VERSION	INTERCEPT EST	S.E.	P	SLOPE EST.	S.E.	P	MODEL df	F	r^2
1	1.1	-233.0	119.0	.	9.68	4.68	.	1,4	4.29	0.52
	1.2	-238.0	121.6	.	9.89	4.79	.	1,4	4.28	0.52
	2.1	-167.2	138.5	.	6.34	4.86	.	1,4	1.70	0.30
	2.2	-221.6	142.9	.	8.60	5.23	.	1,4	2.71	0.40
2	1.1	2.36	74.1	.	3.03	3.06	.	1,4	0.98	0.20
	1.2	4.40	75.5	.	2.95	3.13	.	1,4	0.88	0.18
	2.1	0.53	67.7	.	2.75	2.48	.	1,4	1.23	0.24
	2.2	-2.74	84.9	.	3.00	3.23	.	1,4	0.85	0.18
3	1.1	184.9	128.6	.	2.94	5.34	.	1,5	0.30	0.06
	1.2	182.2	130.0	.	3.05	5.40	.	1,5	0.32	0.06
	2.1	205.8	125.4	.	1.84	4.63	.	1,5	0.16	0.03
	2.2	178.1	146.3	.	2.96	5.59	.	1,5	0.28	0.05
4	1.1	628.9	545.3	.	15.5	22.3	.	1,5	0.48	0.08
	1.2	613.2	547.3	.	16.2	22.5	.	1,5	0.52	0.09
	2.1	847.4	559.2	.	5.85	20.4	.	1,5	0.08	0.02
	2.2	670.8	642.8	.	12.7	24.3	.	1,5	0.28	0.05

b) OPAQUE-SHADE CAGES

INSTAR	VERSION	INTERCEPT EST	S.E.	P	SLOPE EST.	S.E.	P	MODEL df	F	r^2
1	1.1	-55.8	86.0	.	3.32	3.69	.	1,4	0.91	0.17
	1.2	-53.7	85.0	.	3.23	3.65	.	1,4	0.78	0.16
	2.1	-53.7	87.3	.	3.20	3.71	.	1,4	0.75	0.16
	2.2	-52.0	86.9	.	3.13	3.69	.	1,4	0.72	0.15
2	1.1	12.4	44.5	.	2.41	2.04	.	1,4	1.40	0.26
	1.2	11.8	44.7	.	2.44	2.04	.	1,4	1.42	0.26
	2.1	13.5	44.8	.	2.34	2.03	.	1,4	1.33	0.25
	2.2	12.7	44.7	.	2.37	2.02	.	1,4	1.37	0.26
3	1.1	-82.4	150.2	.	15.9	6.88	.	1,5	5.35	0.52
	1.2	-80.9	152.7	.	15.8	7.00	.	1,5	5.14	0.51
	2.1	-82.3	151.1	.	15.8	6.85	.	1,5	5.29	0.51
	2.2	-81.9	151.6	.	15.7	6.86	.	1,5	5.24	0.51
4	1.1	-363.9	563.9	.	60.8	25.4	.	1,5	5.73	0.53
	1.2	-374.2	565.7	.	61.2	25.5	.	1,5	5.78	0.54
	2.1	-385.3	561.7	.	61.2	25.1	.	1,5	5.96	0.54
	2.2	-387.4	562.1	.	61.2	25.0	.	1,5	5.97	0.54

Table 12. Model version assessment. Regressions of observed feeding rates (ordinate) on feeding rates as estimated by four model versions (abscissa). Estimates and significance values of parameters (., $p > 0.05$; *, $p \le 0.05$; **, $p \le 0.01$; ***, $p \le 0.001$). Units of feeding are $mm^2 \cdot day^{-1} \cdot larva^{-1}$.

Data are pooled over cage type (justified by analysis of covariance). The feeding rate estimate for instar 2, in clear-shade cages in Run J is anomalous (Table 10), and has been eliminated as an outlier. Therefore, in the regression models, denominator degrees of freedom are: 10 for first instar; 9 for second instar, and 12 for instars 3 and 4.

Versions of the simulation model are coded; for details refer to text.

INSTAR	VER-SION	INTERCEPT			SLOPE				r^2	$\sqrt{MSE}$
		EST	S.E.	P(=0)	EST	S.E.	P(SLOPE) =0	=1		
1	1.1	24.3	0.80	***	0.019	0.031	.	***	0.04	8.6
1	1.2	24.4	0.78	***	0.020	0.030	.	***	0.04	8.3
1	2.1	21.0	1.79	***	0.047	0.069	.	***	0.04	19.2
1	2.2	23.1	1.20	***	0.020	0.046	.	***	0.02	12.9
2	1.1	57.1	16.8	**	0.21	0.25	.	*	0.08	44.7
2	1.2	56.5	16.7	**	0.23	0.25	.	*	0.08	44.6
2	2.1	74.0	23.8	*	-0.15	0.36	.	*	0.02	63.5
2	2.2	71.3	18.9	*	-0.059	0.28	.	**	0.00	50.4
3	1.1	123.6	52.0	*	0.60	0.20	*	.	0.44	118.4
3	1.2	124.9	52.2	*	0.60	0.20	*	.	0.43	118.8
3	2.1	90.2	66.4	.	0.62	0.25	*	.	0.34	151.1
3	2.2	96.1	48.7	.	0.67	0.18	**	.	0.53	110.8
4	1.1	674.4	284.2	*	0.46	0.28	.	.	0.18	592.8
4	1.2	676.5	285.5	*	0.48	0.28	.	.	0.18	595.5
4	2.1	398.2	305.7	.	0.60	0.30	.	.	0.25	637.7
4	2.2	424.5	233.8	.	0.64	0.23	*	.	0.39	487.6

149

Figure 16. Flowchart outlining structure of feeding rate models. Refer to text for details. (The same structure applies to development models in Section III, Chapter D.)
BODY TEMP. is body temperature;
CONSTANT-T FUNCTIONS refers to equations relating feeding (or development - Section III, Chapter D) rate to temperature, as derived in laboratory studies.
Binomial codes (1.1 - 2.2) in the box on the right, refer to model versions as described in the text.

151
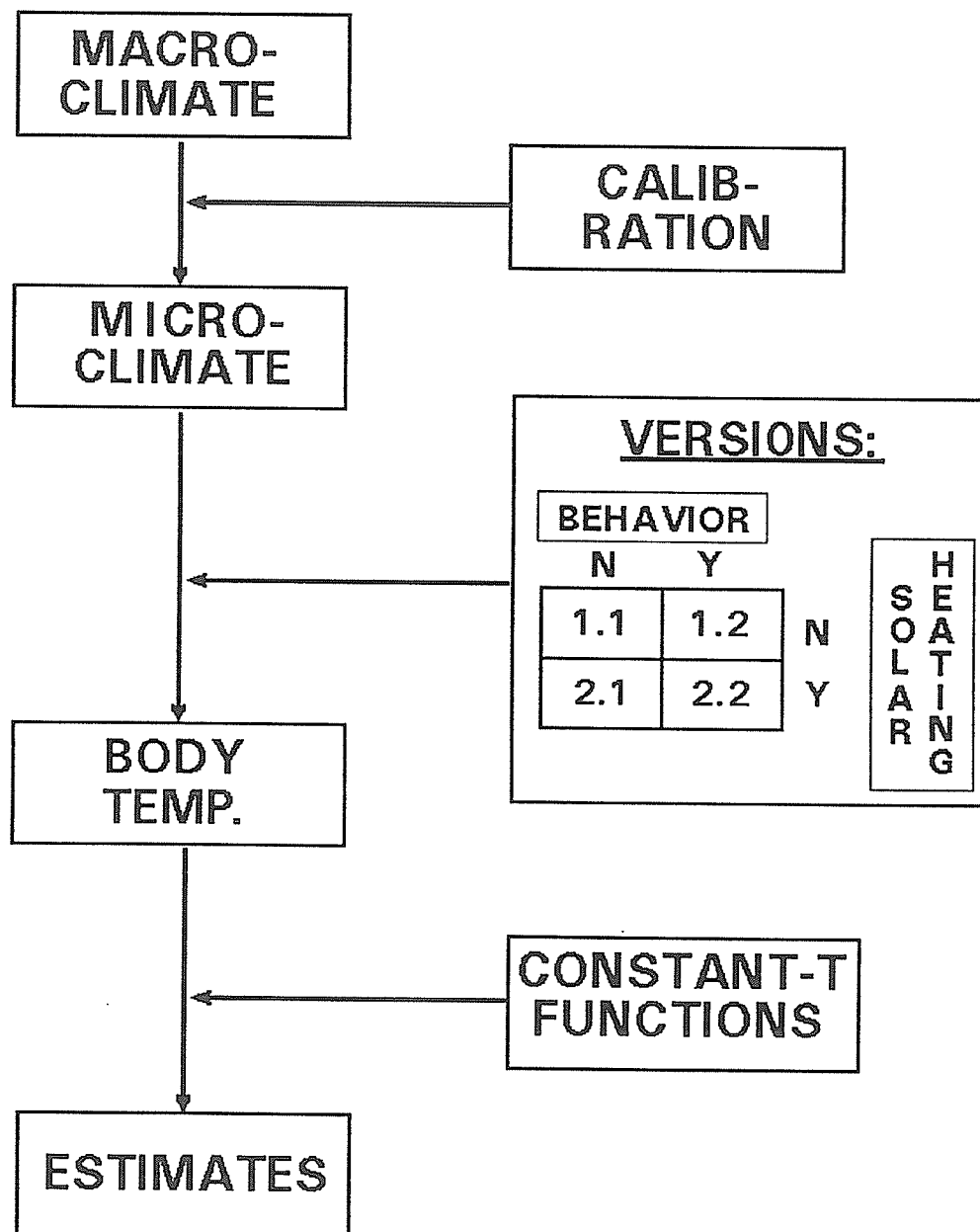
Figure 17.   Larval Colorado potato beetle feeding rates (mm$^2\cdot$day^{-1})
      measured in field trials in cages of two shade types (see text),
      plus lines representing regression of feeding on estimated mean
      daily body temperature, estimated using model version 1.1.
      Regression results are similar for all model versions.
            Instars 1 (Panel A) and 2 (Panel B)
      <u>Legend codes</u>:
      CLR   =   Cages with clear shades
      OPQ   =   Cages with opaque shades
      P(CLR)   =   Prediction from regression of feeding in clear
                          cage on mean body temperature.
      P(OPQ)   =   Prediction from regression of feeding in opaque
                          cage on mean body temperature.
      QUAD   =   Prediction from quadratic description of feeding
                          (Section II, Chapter A), assuming larvae respond
                          to mean daily temperature as they do to constant
                          temperature.

A) INSTAR 1

MEAN DAILY BODY TEMP. [°C]

B) INSTAR 2

MEAN DAILY BODY TEMP. [°C]

Figure 18.   Larval Colorado potato beetle feeding rates $(mm^2 \cdot day^{-1})$ measured in field trials in cages of two shade types (see text), plus lines representing regression of feeding on estimated mean daily body temperature, estimated using model version 1.1. Regression results are similar for all model versions.

Instars 3 (panel A) and 4 (Panel B)

<u>Legend codes</u>:

CLR	=	Cages with clear shades
OPQ	=	Cages with opaque shades
P(CLR)	=	Prediction from regression of feeding in clear cage on mean body temperature.
P(OPQ)	=	Prediction from regression of feeding in opaque cage on mean body temperature.
QUAD	=	Prediction from quadratic description of feeding (Section II, Chapter A), assuming larvae respond to mean daily temperature as they do to constant temperature.

A) INSTAR 3

B) INSTAR 4

Figure 19. First instar Colorado potato beetle feeding rates ($mm^2 \cdot day^{-1}$).
Predictions by model version (ordinate) plotted against mean value
measured in field trial. A) Clear-shade cages; B) Opaque-shade
cages
Legend codes:
Diagonal line represents 1:1 agreement.
Binomial codes refer to model versions (see text for details).

A) OPAQUE

B) CLEAR

157
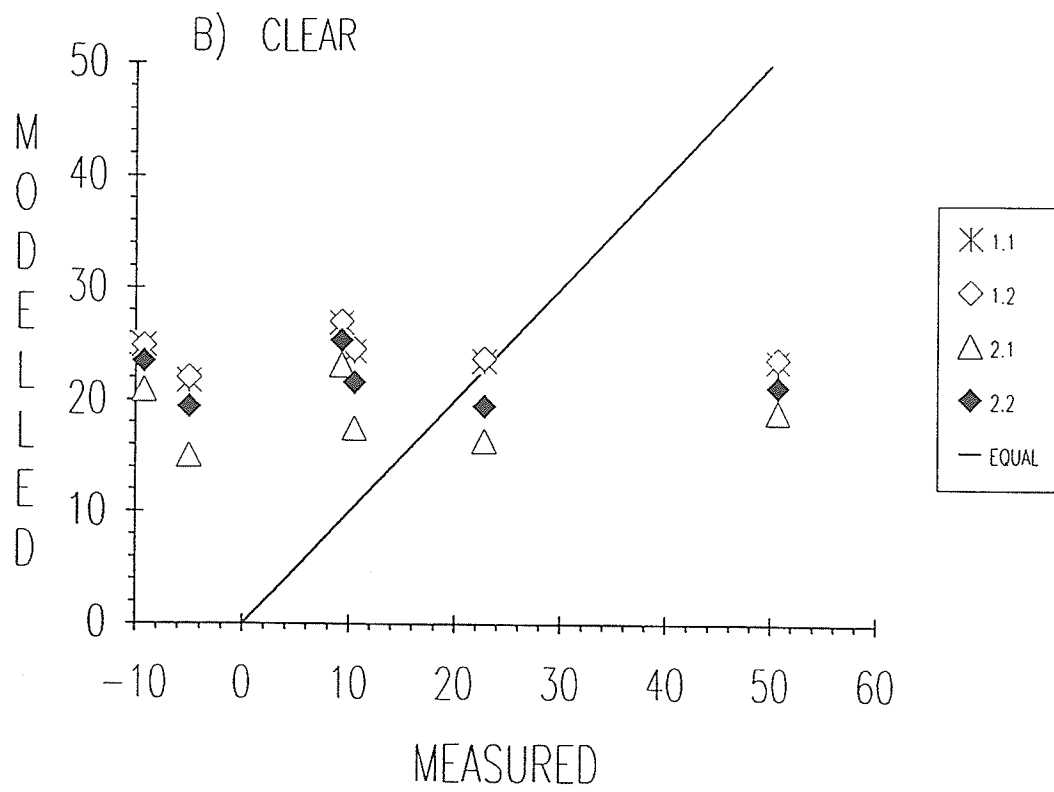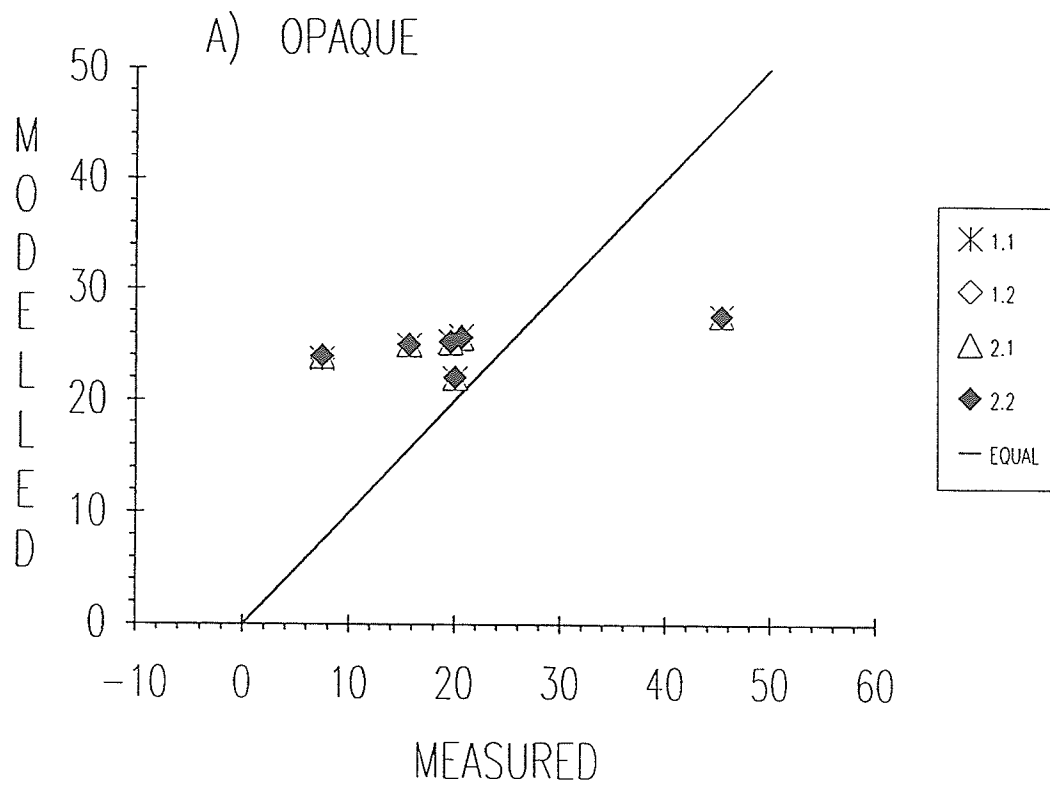
Figure 20. Second instar Colorado potato beetle feeding rates ($mm^2 \cdot day^{-1}$).
    Predictions by model version (ordinate) plotted against mean value
    measured in field trial. A) Clear-shade cages;   B) Opaque-shade
    cages
    <u>Legend codes</u>:
        Diagonal line represents 1:1 agreement.
        Binomial codes refer to model versions (see text for details).
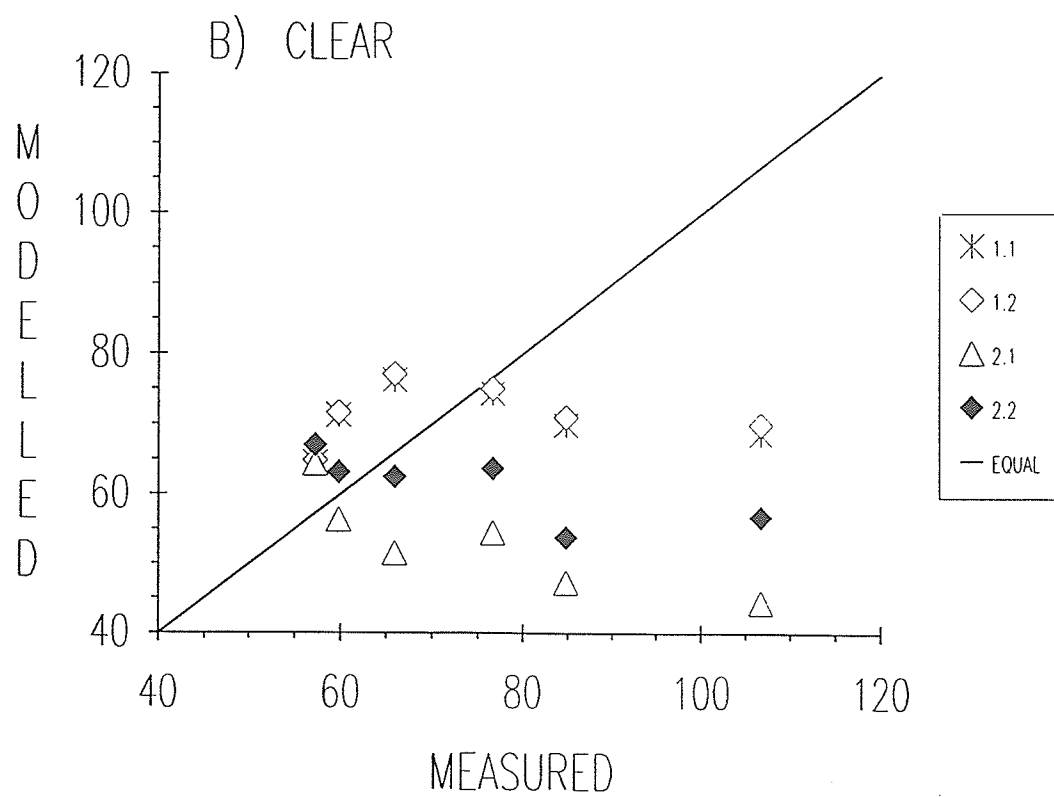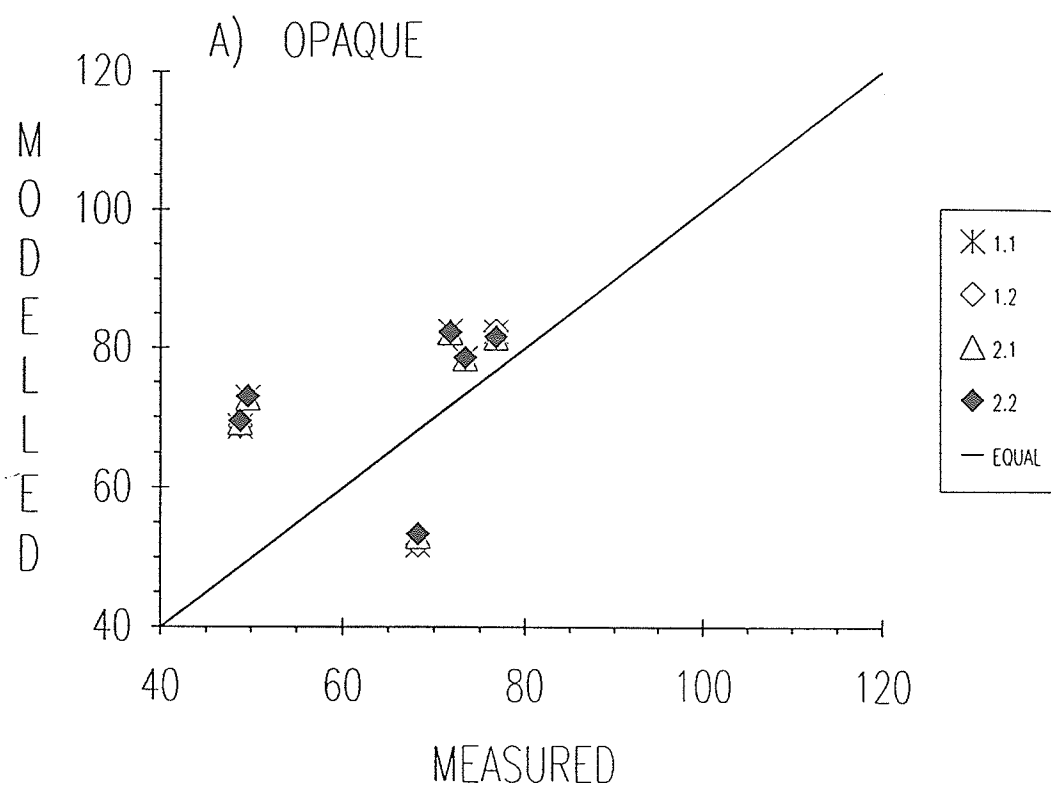
A) OPAQUE

B) CLEAR

Figure 21. Third instar Colorado potato beetle feeding rates ($mm^2 \cdot day^{-1}$).
Predictions by model version (ordinate) plotted against mean value
measured in field trial.   A) Clear-shade cages;   B) Opaque-shade
cages
<u>Legend codes</u>:
Diagonal line represents 1:1 agreement.
Binomial codes refer to model versions (see text for details).
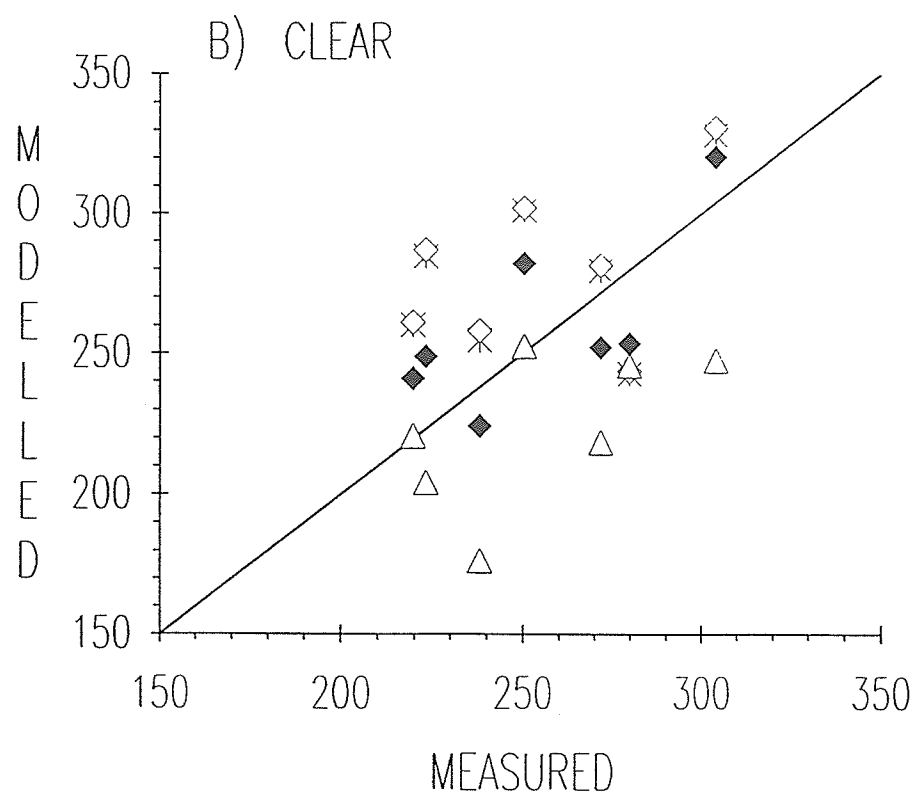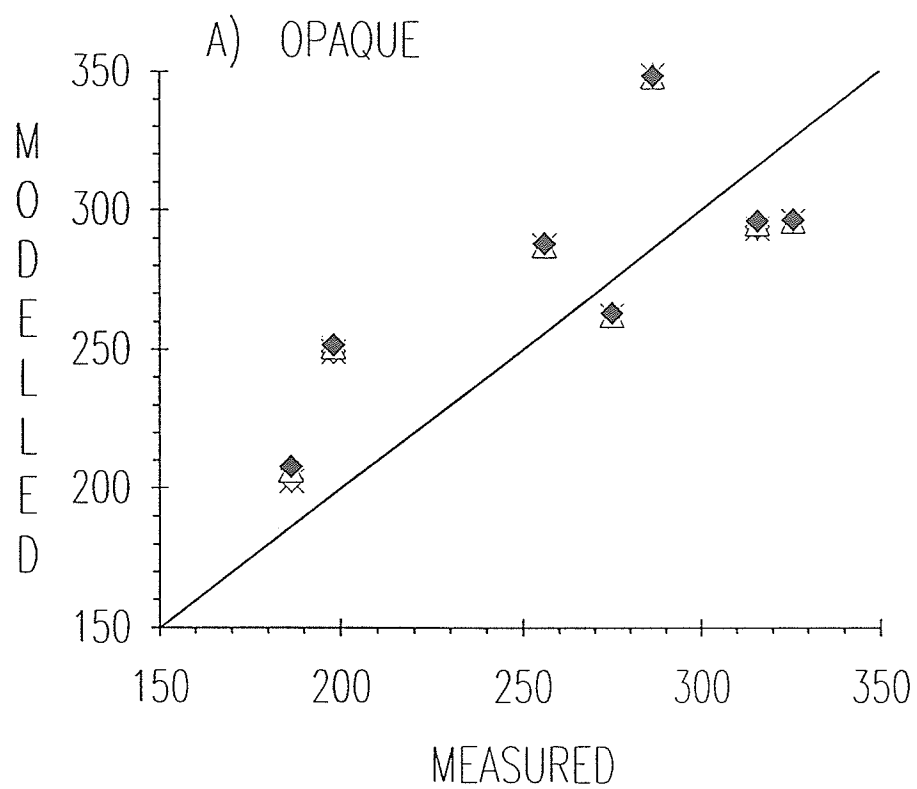
A) OPAQUE

B) CLEAR

Figure 22. Fourth instar Colorado potato beetle feeding rates ($mm^2 \cdot day^{-1}$).
Predictions by model version (ordinate) plotted against mean value
measured in field trial.
A) Clear-shade cages; B) Opaque-shade cages
<u>Legend codes</u>:
Diagonal line (EQUAL) represents 1:1 agreement.
Binomial codes refer to model versions (see text for details).

A) OPAQUE

B) CLEAR

163
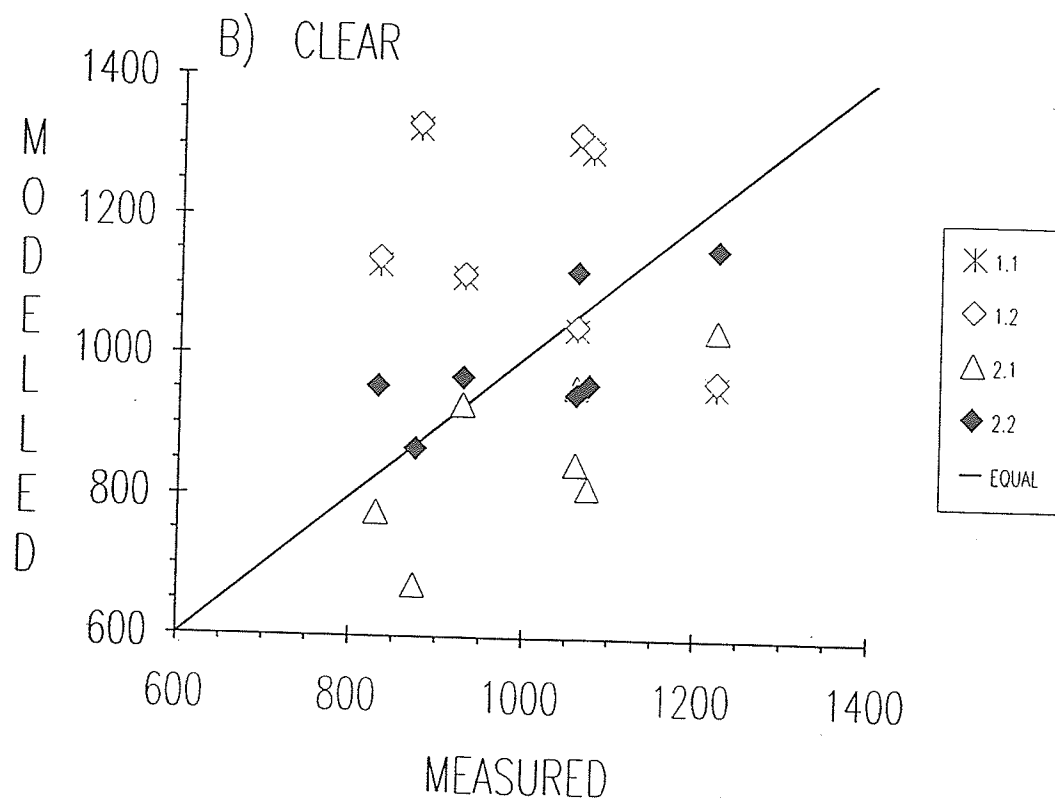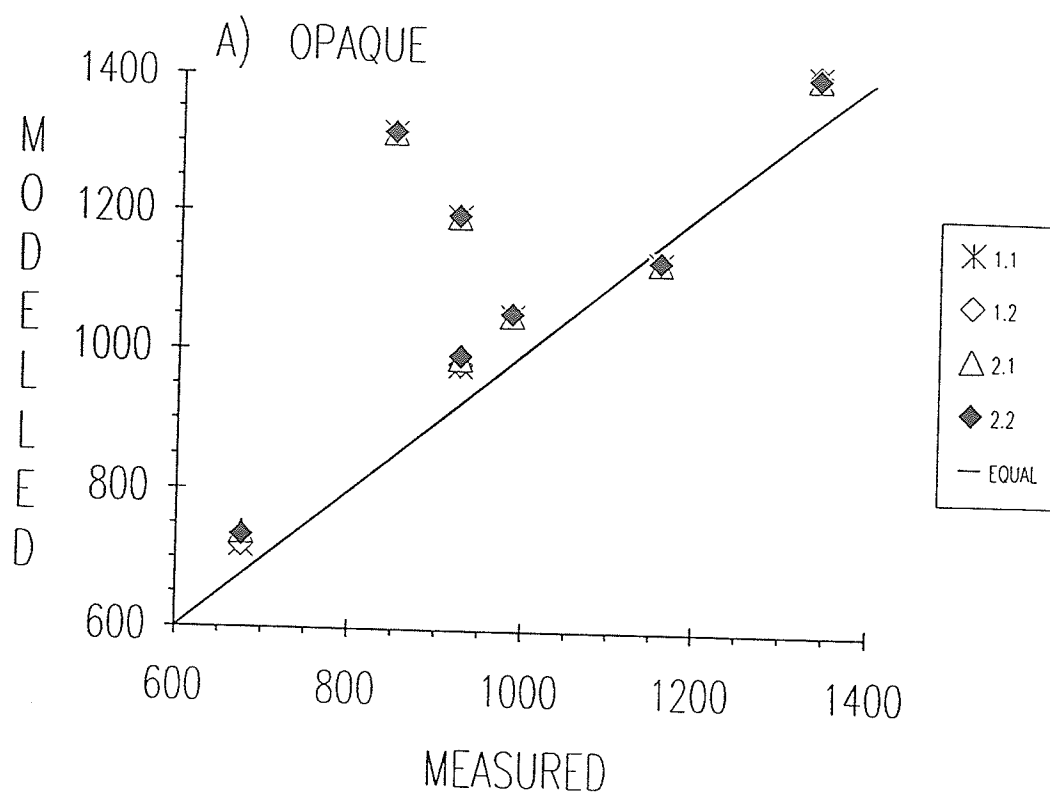
Figure 23. Hourly feeding rates of fourth instar Colorado potato beetle larvae on two days in 1991, simulated using actual macroclimatic data. Four thermoregulatory strategies compared. All models include the effect of insolative heating on body temperature. A) 25 July; B) 31 July

Legend codes:

2.1: Larvae spend 50% of time on top of the leaflet

2.2: Larvae respond to insolation as modelled using equation 12 (Section III, Chapter B)

ALL TOP: Larvae remain on top of the leaflet at all times

ALL UNDER: Larvae remain under the leaflet at all times.

A) 25 JULY

B) 31 JULY
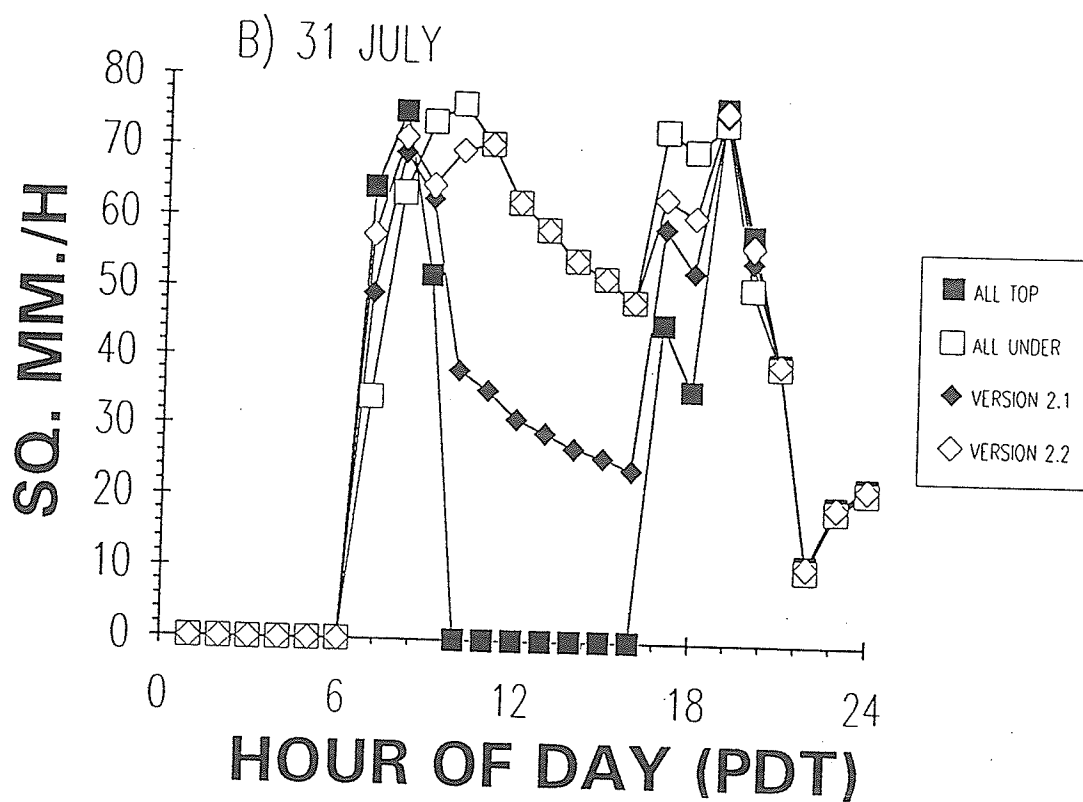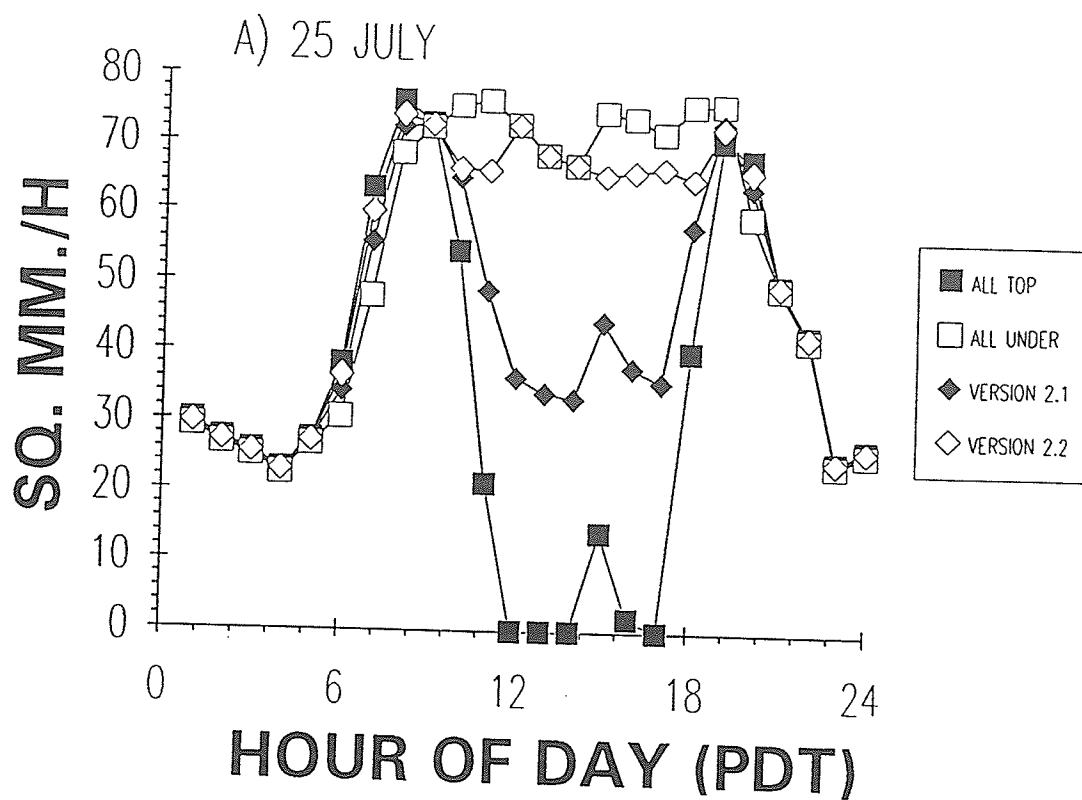
Figure 24. Hourly feeding rates of fourth instar Colorado potato beetle
larvae over 14 days in 1991, simulated using actual macroclimatic
data, using model version 2.2. Solid line joins mean response.
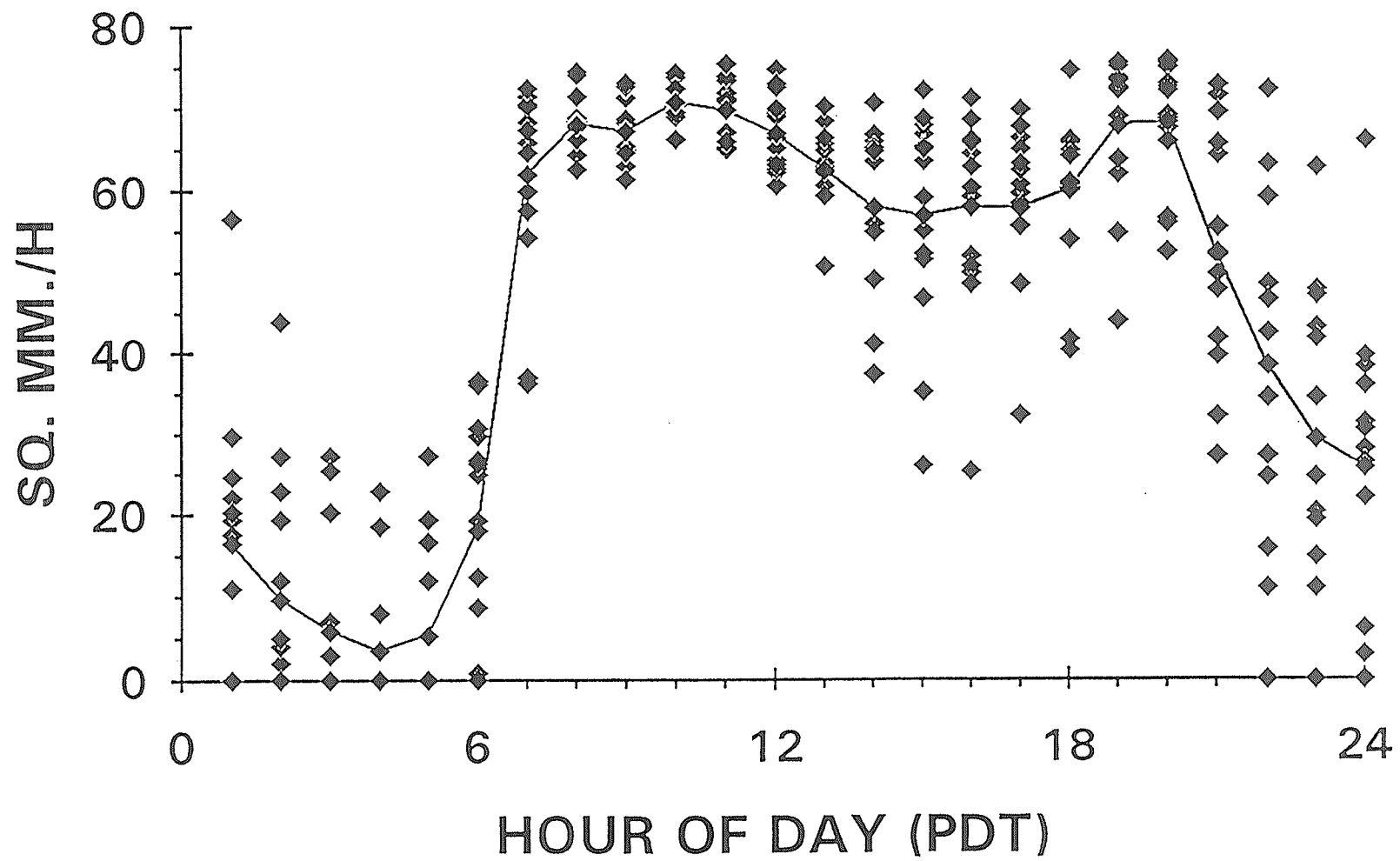
Section III. Chapter D)
    DEVELOPMENTAL RATES OF LARVAL COLORADO POTATO BEETLES UNDER FIELD
    CONDITIONS AND ASSEMBLY OF A MODEL SIMULATING THIS PROCESS

ABSTRACT

Four similar models of development of larval Colorado potato beetles are assembled and tested under conditions of naturally varying temperature and insolation. All model versions are founded on the assumption that development is driven by body temperature. Model versions include or disregard the effects of microhabitat choice and the possible effect of insolative heating, in all four possible combinations. The version which includes microhabitat choice and possible insolative heating performed best, although larvae consistently developed approximately 9% faster than predicted. Estimation bias may occur because the developmental rate functions used in the models pertain to constant temperatures, whereas development of Colorado potato beetle larvae may continue under brief exposure to temperatures which are lethal on chronic exposure.

INTRODUCTION

Insect development : temperature relationships are generally characterized by comparing responses of specimens reared under a series of constant temperatures, but the application of such relationships to conditions in which temperatures vary, has met with limited success even in closely controlled laboratory conditions (Hagstrum and Milliken 1991). In general, the process of applying constant-temperature data to field conditions has entailed three simplifying assumptions, necessitated by the limited resolution of the available meteorological data; these are (1) that developmental rate is adequately described by a linear function of temperature above a developmental threshold (the degree-day approach); (2) that macrometeorological temperature data can be used to drive this function, and (3) that the effects of solar heating and behavioral thermoregulation are negligible. Each of these assumptions is invalid. The linear relationship between development and temperature in poikilotherms has long been known to break down at extreme temperatures (Pradhan 1946). Macrometeorological data are measured in the shade and bear limited resemblance to temperatures experienced by the insects. The impact of insolative heating and thermoregulation are not negligible (May 1979, 1981, 1982; this thesis, Section III. Chapter B). The following case will illustrate the problem in Colorado potato beetle.

Three research groups have used the degree-day approach to predict Colorado potato beetle population trends under field conditions; the results have been mixed. In one trial (Walgenbach and Wyman 1984)

developmental times as predicted from constant-temperature data agreed well with those observed under field conditions. Two other groups (Tauber et al. 1988; Groden and Casagrande 1986) observed that Colorado potato beetle development under field conditions was faster than predicted. The former group observed a systematic error of up to ≈ 35% (mean ≈ 12%); the latter did not state the bias. These studies may have had different results because they used different linear developmental rate functions (both threshold and slope) in their models. The disagreement in estimates of these functions occurs because the inherent nonlinearity of the response makes estimation of the parameters sensitive to the choice of temperatures used in their determination.

Groden and Casagrande (1986) were able to reduce the disagreement between predicted and observed developmental rates in first instar larvae to < 6.5% by using a simple correction for thermoregulation developed by May (1981); whether the approach was successful in other instars was not revealed. The relative success of this correction illustrates the weakness of ignoring thermoregulation in temperature-driven phenology models.

Clearly, the degree-day approach to modelling poikilotherm phenology under natural conditions, is limited by the invalidity of the assumptions. An alternative approach is required by which to apply constant-temperature developmental rate data to field conditions. The optimal approach may be to integrate the non-linear constant-temperature developmental rate function over the fluctuating temperature cycle (Eubank et al. 1973). This approach has generally met with limited success even under laboratory conditions where temporal temperature variations are controlled (Hagstrum

and Milliken 1991). Its utility under field conditions is limited by the temporal resolution of the temperature data, which is commonly available only as daily mean, maximum and minimum, and is further complicated by the thermoregulatory abilities of the insect. The study reported here uses this approach to model the developmental rate of Colorado potato beetle larvae under field conditions, while attempting to incorporate the influence of insolative heating and behavioral thermoregulation of the outcome.

This study had two stages. In the first, Colorado potato beetle developmental rates are measured under conditions of naturally-varying temperature in a field experiment. In the second stage, a model is developed which predicts Colorado potato beetle larval developmental rates under natural conditions. The predictive model synthesizes constant-temperature developmental rate functions (Section II, Chapter B) with functions which estimate microclimatic temperatures from macroclimatic temperature, insolation, and cloud cover data (Section III, Chapter A). Different versions of the model evaluate the impact of insolative heating and behavioral thermoregulation (Section III, Chapter B). The model versions were tested by comparing predictions to field measurements.

MATERIALS AND METHODS

FIELD EXPERIMENT

Development of free-ranging Colorado potato beetles was measured on small potted plants under natural conditions in Winfield, British Columbia (50° 02' N, 119° 24' W) from June to August 1991. 'Russet Burbank' plants were grown from 50 g seed pieces, in field soil in 210 mm x 210 mm plastic

pots; when used, the plants were ≈ 40 cm in diameter and were mutually isolated. Consequently, plants were small enough that few larvae were missed during census, and larvae could not move among plants.

Sixteen egg masses (454 eggs) on leaflets were obtained from an outdoor insectary (Section III, Chapter B). The number of eggs in each mass and the time were noted. The leaflet was trimmed to a small piece centred on the egg mass and attached to the underside of a leaflet on a potted plant, using a straight pin. One egg mass was attached per plant. Egg masses were attached to plants in three release groups. Six masses (182 eggs) were pinned to the plants on 12 Jun; four masses (122 eggs) were attached on 03 Jul; and six masses (150 eggs) were attached on 28 Jul. In this trial, all larvae from an egg mass are called a cohort.

Each plant with an egg mass was inspected at least daily. At each inspection, the numbers each instar and the time were noted. In each cohort, each larval instar was considered to be bounded by the times at which 50% of surviving larvae had moulted into the instar (median moult-in) and 50% had moulted into the following instar (median moult-out). Time plots of cumulative proportion moult-out of each instar were prepared for each cohort. Median moult-in and moult-out were estimated from these plots by linear interpolation; because of limitations to precision, these estimates were rounded to 1/4 day.

DEVELOPMENTAL RATE MODEL

The model of development of free-living larvae had the same structure as the feeding rate model assembled in Section III, Chapter C, except that instar-specific constant-temperature developmental rate

functions (Section II, Chapter B) were substituted for the feeding rate functions. All temperature and insolation estimation functions were structured to pertain to free-living, rather than caged, larvae.

Assumptions The fundamental assumptions of this model are (i) that larval developmental rate is affected only by body temperature, and (ii) that this rate is unaffected by previous experience; and (iii) that body temperature and developmental rate respond immediately to changes in ambient temperature. Much of the modelling process is a test of which body temperature estimate is best.

The model is an assemblage of relationships derived in earlier sections; equation numbers are retained. Refer to Fig 16 for a flowchart outlining the structure of the developmental rate models. Note that for each iteration of the algorithm, all calculations listed here were performed specifically for each hour (h), day (d), and position (p) (above or below leaflet) using parameters specific to each variable. Where possible, subscripts are omitted for clarity in the following summary.

Constituent information The model is based most fundamentally on hourly macroclimatic measurements of:

1) Theoretical insolation on a horizontal surface before atmospheric attenuation (I_0) calculated using the astrometeorological estimator (Robertson and Russelo 1968).

2) Airport temperature (MACRO).

3) Proportion of sky clear of clouds (CLARITY), as calculated from cloud cover (total opacity) estimates.

Hourly macroclimatic temperature and cloud cover data were collected from the Kelowna municipal airport approximately 5 km south of the experimental site.

Driving variables The model is driven by microclimatic variables derived from the macroclimatic measurements via empirically-derived relationships. These are:

4) External photometer reading P, estimated from the astrometeorological estimator and proportion of sky free of clouds by the relationship

$$P \quad = \quad I_0 \cdot [0.1569 + 0.3576(\text{CLARITY})] \qquad (5)$$

5) Photometer reading above and below uncaged leaflets, as estimated from external reading using the empirically derived scalar multiplier (μ), specific to position (Table 4, Section III. Chapter A):

$$P_{c,p,h,d} = \mu_{c,p} \cdot P_{h,d} \qquad (6)$$

6) Microclimate air temperatures (MICRO), calculated from macroclimate temperatures and estimated external photometer reading by the relationship

$$MICRO = MACRO + \frac{K_{c,p}}{1 + \exp(-(\alpha_{c,p} + \beta_{c,p} \cdot P_{h,d}))} - \Gamma_{c,p} \qquad (4')$$

This is modified from the equation given in Section III, Chapter A, by substituting (MICRO - MACRO) for DIFF, and rearranging. The parameter estimates are specific to position above or below leaflet; values are listed in Table 5 (Section III, Chapter A).

Behavioral variables In alternative versions of the model, the effects of insolative heating on body temperature and microhabitat choice, were added to the model singly or together.

7) Hypothesized impact of insolation on body temperature was modelled by incrementing microclimate air temperature by a quantity related to microclimate insolation. The operative quantity is

$$T^*_{c,p} = MICRO + 0.0838 \cdot P_{c,p} \qquad (9)$$

8) Behavioral response to T^* (proportion (U) under the leaflet) was modelled as:

$$U = 0.211 + \frac{0.804}{1 + \exp(-(10.9570 + 0.2912 \cdot T^*))} \qquad (12)$$

Where $T_b = T^*$ or MICRO, measured on the upper surface of the leaflet.

9) The developmental increment (stadia^{-1}) by each instar (j) in each hour was calculated in each microhabitat using the function derived by Logan et al. (1976).

$$r_j(T) = \frac{\Psi\left[e^{\rho T} - e^{\left(\rho T_{max} - \frac{(T_{max}-T)}{\Delta}\right)}\right]}{24} \qquad (2')$$

The prime in the equation designation indicates that this is slightly modified from equation (2) (Section II, Chapter B), i.e. the divisor 24 converts rate estimates from per day to per hour. T = MICRO - 17° or T^* - 17° (refer to Section II, Chapter B, or Logan et al. (1976) for justification of this axis rescaling). Instar-specific parameter values obtained in constant-temperature trials (Ψ, ρ, T_{max}, and Δ) are given in table 5, Section II, Chapter B. The value of $r_j(T)$ is constrained to be non-negative, i.e. development ceases when $T \geq T_{max}$.

Model versions   Initial tests of the model compared four versions, which included or excluded microhabitat choice (equation 11) and the hypothesized effects of insolative heating (equation 8) in all possible combinations.   In version 1.1, body temperature was assumed to equal microhabitat air temperature ($MICRO_p$) as calculated using equation (5). Microhabitat choice was ignored: i.e. larvae were considered to be evenly dispersed above and below the leaflet.

In version 1.2, body temperature was calculated as in version 1.1, and microhabitat choice was modelled using equation 11. This response was assumed to be cued by temperature on top of the leaflet.

In version 2.1, body temperature was assumed to equal T^*, which was calculated separately above and below the leaflet (equation 8). Microhabitat choice was ignored; larval dispersion was as in version 1.1.

In version 2.2, body temperature was calculated as in version 2.1, and microhabitat choice was modelled as in version 1.2.

Procedure   The model iterated hourly.   For each version, at each iteration, larval body temperature (MICRO or T^*) was calculated separately for microhabitats above and below the leaflet.   Developmental rates in each microhabitat were estimated from these calculated body temperatures. The estimate of larval development was calculated as the mean of the microhabitat values, weighted by the proportion of larvae estimated to be in each microhabitat.   Hourly developmental rate estimates were summed to estimate daily development.

Simulations were performed using model versions 2.1 and 2.2, and two additional thermoregulatory strategies: "ALL TOP", in which all larvae remain on the upper leaflet surface at all times; and "ALL UNDER", in which larvae remain below the leaflet at all times.

RESULTS AND DISCUSSION

FIELD EXPERIMENT

Sample time plots of total numbers observed per instar are shown in Fig 25 A - C. Disappearance rate (presumably mortality) was very high in egg masses 1 to 6 (set out 12 Jun): of 182 eggs, only 4 survived to prepupation. Ants (Formica neoclara (Emery) [Hymenoptera: Formicidae]) from a nearby colony were observed on the plants. F. neoclara is a predatory species, which has been used in biological control of insect pests (Paulson and Akre 1992). Plants bearing egg masses 7 to 16 were moved away from the ant nest, and the disappearance rate was lower, although still substantial: of the 272 eggs, only 45 remained to prepupation. Reasons for disappearance are unknown.

A sample time plot of cumulative proportion moulted out of instar j (= [#larvae in instar (j+1)]/[#larvae in instars (j) and (j+1)]) is presented in Fig. 26. This plot demonstrates that despite the reduction in sample size due to larval mortality, stadium estimates remain possible.

Although the timing of ecdysis of single larvae can be estimated only to 1/2 day (i.e. midway between the inspections bracketing moult) the average time of ecdysis of the cohort was usually measured more precisely than this, because the event was spread over several observations. Thus, the decision to round the time of moult to 1/4 day seems appropriate.

MODEL VERSION ASSESSMENT

Observed stadia for each instar and cohort are presented with model version estimates in Appendix 5. Note that days were divided into quarters for estimation of time of moult; two decimal places are required to convey this information in the appendix, but this does not reflect estimation precision. In most cases, the model versions predicted stadia greater than observed values.

Mean temperatures during the development of each cohort from eggs to prepupation, as estimated from macroclimatic temperatures, and by the body temperature estimation algorithms of the four model versions, are summarized in appendix 6.

D_v for the four model versions is plotted against date in Fig. 27. Mean $\pm$ standard deviation of D_v for the four model versions are presented in Table 13. This table also contains a table which compares mean D_v (paired t-tests), and the variance of the D_v (F-tests between pairs of models). In both sets of tests, the performance of model versions 1.1 and 1.2 are similar, but differ significantly from versions 2.1 and 2.2, which also differ from each other.

Model versions 1.1 and 1.2 performed similarly because the potential effects of behavioral thermoregulation on development are minimal if insolative heating does not occur. In Fig. 27, the data points from model versions 1.1 and 1.2 are seldom separable at the resolution of the graphics. These two versions both have mean D_v near 1, but a large S.D./mean ratio (≈ 0.2). The performance of these versions changes systematically over time (Fig. 27); both underestimate developmental rate early and late in the season, and overestimate it during mid-season. The

ultimate establishment of a mean D_v near unity is coincidental. The seasonal bias renders these versions undesirable.

Versions 2.1 and 2.2 show no seasonal change in estimation bias. Both underestimate developmental rates (Figs 26 and 27), but have consistent estimation bias, and a small S.D./mean ratio (<0.08) (Table 13). Thus, these versions are more precise, and because the bias is consistent, post hoc correction is relatively uncomplicated. Of these, version 2.2 has significantly greater precision and lower estimation bias than model version 2.1. Model version 2.2 will be adopted for the rest of the thesis. This model produces a biased estimate of developmental rate ($\approx$ -9%). Fig. 28 demonstrates that the bias is similar for all instars. The choice of version is the same as in the assessment of feeding rate models.

Sources of error

Several plausible explanations exist for the observed systematic errors in estimation by the various model versions. The most obvious are the effects of ignoring microhabitat choice and the possible effects of insolative heating in the estimation process. These error sources are the same as in the feeding rate model, and their possible impact has been discussed in detail in the chapter pertaining to that model (Section III, Chapter C); additional discussion here will focus only on possibilities which are specific to the present model, or which clarify uncertainties noted in that chapter.

The estimation bias of versions 1.1 and 1.2 is primarily seasonal. This result is consistent with neglect of the elevation of body temperature by insolative heating. During the relatively cool early and

late season, insolative heating would benefit larvae by elevating body temperature into a more optimal range and accelerating development. During mid-season, the effect might be detrimental, elevating body temperature to a range in which development slows. The seasonal bias trend in model versions 1.1 and 1.2 mirrors this seasonal trend in insolation effect. These model versions are clearly deficient.

The estimation bias of model versions 2.1 and 2.2 appears independent of season; this indicates that the portion of the model which estimates the effect of insolative heating, which is common to the two versions, is successful in accounting for the effects of seasonal changes in this factor. Part of the estimation error by version 2.1 is probably attributable to neglect of the effects of microhabitat choice, which mitigate the effect of insolative heating.

Thus, comparison of seasonal bias in estimation by the four model versions is consistent with the hypothesis raised in Section III, Chapter B, that T^* is body temperature, and that microhabitat choice is a behavioral thermoregulation response.

Comparison of developmental rate estimates from versions 2.2 and 2.1 suggests that the impact of microhabitat choice on this rate appears to be independent of the time of the season. This observation may be due to the closely linked developmental rates of model versions 2.1 and 2.2, which differ only in their treatment of larval behavior. Limits to the amount by which microhabitat choice can increase developmental rate, certainly limit the amount by which the developmental rate estimates of these model versions can differ over the season. The temporal gap in the data (Fig

27), which occurs because the British Columbia population is bivoltine, might also impede detection of any such trend.

Although model version 2.2 performs best, modelled development is slower than observed. Thus the model performance is slightly better than those of Groden and Casagrande (1986) and Tauber et al. (1988), but inferior to that of Walgenbach and Wyman (1984), all of which were based on the much simpler degree-day process. Despite the greater detail involved in the estimation process used here, an estimation error remains. Several non-exclusive error sources are plausible. One possibility is that the process of estimating microclimate temperature is biased; this possibility was raised in the discussion of the feeding rate model (Section III, Chapter C). If error in microclimatic temperature estimation is occurring, it cannot exceed the magnitude of the estimation error in the feeding rate models, because the feeding and developmental rate models have the same temperature-estimation algorithm. The bias in the present studies is much greater than in the feeding rate trials; this eliminates the microclimate temperature estimation error as the primary source of the bias in the developmental rate models.

Another possibility is that the developmental rate curves derived under constant temperatures in Section II, Chapter B, which were used in the estimation process, are inadequate to describe developmental rates at temperatures which exceed T_{max}. The developmental rate functions derived in Section II, Chapter B extrapolate beyond the range of the data; the dangers of such extrapolation are well known, but unavoidable in this case. In addition, the developmental rate functions used here pertain to constant-temperature conditions, and so give little guidance where

temperatures briefly exceed those which are lethal on chronic exposure. Colorado potato beetle eggs continue to develop for "more than 3 h" during exposure to 35°C, a temperature which is lethal under long-term exposure (Logan et al. 1985). That larval development would respond similarly seems reasonable. The rate equations used in all model versions estimate developmental rate to be zero when temperatures exceed the upper lethal limit; the results of Logan et al. (1985) suggest that this assumption may be invalid, but in the absence of developmental rate data obtained under fluctuating conditions, it is also unavoidable.

A further possibility is that temperature fluctuations themselves influence developmental rates, independent of the temperatures. This effect has been observed frequently, although it is by no means universal. Where it does occur, the magnitude and direction of the effect are often dependent on the mean temperature chosen, relative to developmental thresholds and optima (e.g. Butler and Lopez 1980; Messenger and Flitters 1959; Mellors and Allegro 1984), and on the amplitude (e.g. Siddiqui and Barlow 1973; Lamb and Gerber 1985), and frequency of the oscillations (e.g. Behrens et al. 1983). In Colorado potato beetles, compared to rates at constant temperatures, variable temperatures accelerate larval development when the mean temperature is ≤ 22.5°C, but slow development at higher mean temperatures (Chlodny 1975). Chlodny's data do not allow conclusions about the effects of naturally varying temperature regimes on Colorado potato beetle development, but the possibility that rate acceleration is due directly to the temperature oscillations, should be examined directly.

MODELLED DIEL DEVELOPMENTAL RATE PATTERN. Simulation results are very similar to those in the feeding rate model; only conclusions which are different or further illuminating will be discussed in detail. Simulation results were similar for all instars; only those for instar 4 will be presented. Of the 14 daily simulations, two representative examples are provided (Fig. 29). As in the feeding rate models, the thermoregulatory strategy "ALL TOP" and that modelled by version 2.1 are inferior to the other two strategies, owing to larval inability to optimize their thermal niche by microhabitat choice. The diel developmental rate patterns resulting from "ALL UNDER" and the strategy modelled by version 2.2 are similar. On most days (e.g. Fig. 29 B), developmental rate is maximal near dawn and dusk, and falls slightly in the late afternoon. Developmental rate in the thermoregulatory strategy "ALL UNDER" exceeds that in the strategy modelled by version 2.2, for most of each day. "ALL UNDER" was generally the superior of the two strategies; over the 14 days of the simulation, "ALL UNDER" produced the greatest developmental rate 10 times. However, in most cases the difference was small; overall the average developmental rate resulting from the strategy modelled by version 2.2 was 98.5% of that modelled by "ALL UNDER".

The difference in modelled daily developmental rate increments between version 2.2, and "ALL UNDER" is a result of summation of comparative advantages and disadvantages over the entire day. The strategy modelled by version 2.2 provides a consistent advantage over "ALL UNDER" in the early morning by accelerating the increase in body temperature. During the hottest part of the day, the larval distribution and hence developmental rate, predicted by model version 2.2 is identical

to "ALL UNDER". The modelled developmental rate advantage attained by "ALL UNDER" results from superior performance during the periods between dawn or dusk, and the hottest part of the day.

These model conclusions are very sensitive to the characteristics of the component functions, in particular regarding developmental rate at high temperatures. Note that evidence was cited earlier that Colorado potato beetle larvae may continue to develop during brief exposure to temperatures which are lethal on chronic exposure. The present model assumes that development ceases under such conditions, and thus almost certainly underestimates development at temperatures slightly greater than the nominal upper limit for developmental arrest. If so, actual developmental rate would not drop as quickly as the modelled rate at temperatures above this limit. Model version 2.2 is more sensitive to this source of error than is "ALL UNDER" because the body temperature of larvae above the leaflet will climb into this range more frequently than that of larvae which remain under the leaflet. Hence, the developmental rate deficit under the thermoregulatory strategy modelled by version 2.2, compared to that of "ALL UNDER" may be an artifact of an inapplicable developmental rate model, rather than a reflection on a suboptimal thermoregulatory strategy. This possibility is also consistent with the explanation proposed earlier for the consistent bias in estimation of developmental rate by model versions 2.1 and 2.2.

Results of all 14 developmental rate simulations for model version 2.2 are overlain in Fig 30. For clarity, a single symbol is used to depict all simulated rates, regardless of the date. The mean response is represented by a solid line. Over the 14 days included in this

simulation, the mean hourly feeding rate by fourth instar Colorado potato beetles during daylight hours was 0.011 stadia·h^{-1}. According to the model of development under constant temperatures (Section II, Chapter B), maximal hourly development by fourth instar Colorado potato beetles is ≈ 0.0135 stadia·h^{-1}; thus during daylight hours, the thermoregulatory strategy modelled by version 2.2 appears to maintain developmental rate at ≈ 80% of maximal, except during exceptionally warm periods. Of course, this conclusion is a consequence of the thermal niche preference submodel (Section III, Chapter A) which is an important component of this model version. Independent verification of this prediction is required. The modelled diel developmental rate pattern typically peaks during crepuscular periods. The pattern is similar to that produced by the feeding rate model (Fig. 23, Section III, Chapter C), except that the modelled midday rate decrease is greater than that in the feeding rate trial; this difference may be another consequence of the possible inapplicability of the developmental rate functions to temperatures exceeding T_{max}.

Model version 2.2 is the most computationally complex model of development by Colorado potato beetle larvae under field conditions, that has been presented to date. Despite this complexity, the performance of the model is not markedly superior to simple degree-day models. The advantage of the present approach is that by examining the processes which may influence developmental rate under field conditions, the model yields insight into the potential sources of error; the degree-day approach provides no such feedback.

For example, the present approach has revealed the apparent importance of microhabitat choice and insolative heating in obtaining reasonable rate estimates. It has also revealed that the assumption that larval development under variable conditions is equivalent to that under constant temperature conditions, is dubious, and has revealed that a study of larval developmental response to short periods of exposure to temperatures which are lethal on chronic exposure, appears necessary.

Although model version 2.2 produces a developmental rate estimate which is in error by about -9%, the error is consistent, and operationally, the version can be modified to specify that larvae moult when the modelled stadium is 91% complete.

Table 13. Comparison of proportion of instar modelled to be complete (D_v) by the model versions, at observed median moult . Triangular matrices of pairwise comparisons of mean D_v (paired t-tests) and variance of D_v (F-tests). N = 38 in all cases.

Version	D_v mean	S.D.	Summary of pairwise comparisons[a] $P(>F)$[b] above diagonal and $P(>|t|)$[c] below diagonal.			
			1.1	1.2	2.1	2.2
1.1	1.0113	0.1939	.	ns	***	***
1.2	1.0124	0.1957	ns	.	***	***
2.1	0.7647	0.0678	***	***	.	*
2.2	0.9113	0.0470	**	**	***	.

[a] ns, p > 0.05; *, P ≤ 0.05; **, P ≤ 0.001; ***, P ≤ 0.0001

[b] (greater s^2)/(smaller s^2). Both denominator and numerator have 37 degrees of freedom.

[c] Two-tailed t-tests of mean difference in D_v between pairs of model versions. In all cases, df = 76

Figure 25. Temporal trend in number of Colorado potato beetle larvae on
           plants, by instar.
           A) Cohort 3; egg mass pinned to plant 12 Jun.
           B) Cohort 8; egg mass pinned to plant 03 Jul.
           C) Cohort 12; egg mass pinned to plant 29 Jul.

           Symbols:
           E   , eggs;
           1   , instar 1;
           2   , instar 2;
           3   , instar 3;
           4   , instar 4;
           PP   , prepupa.

A)
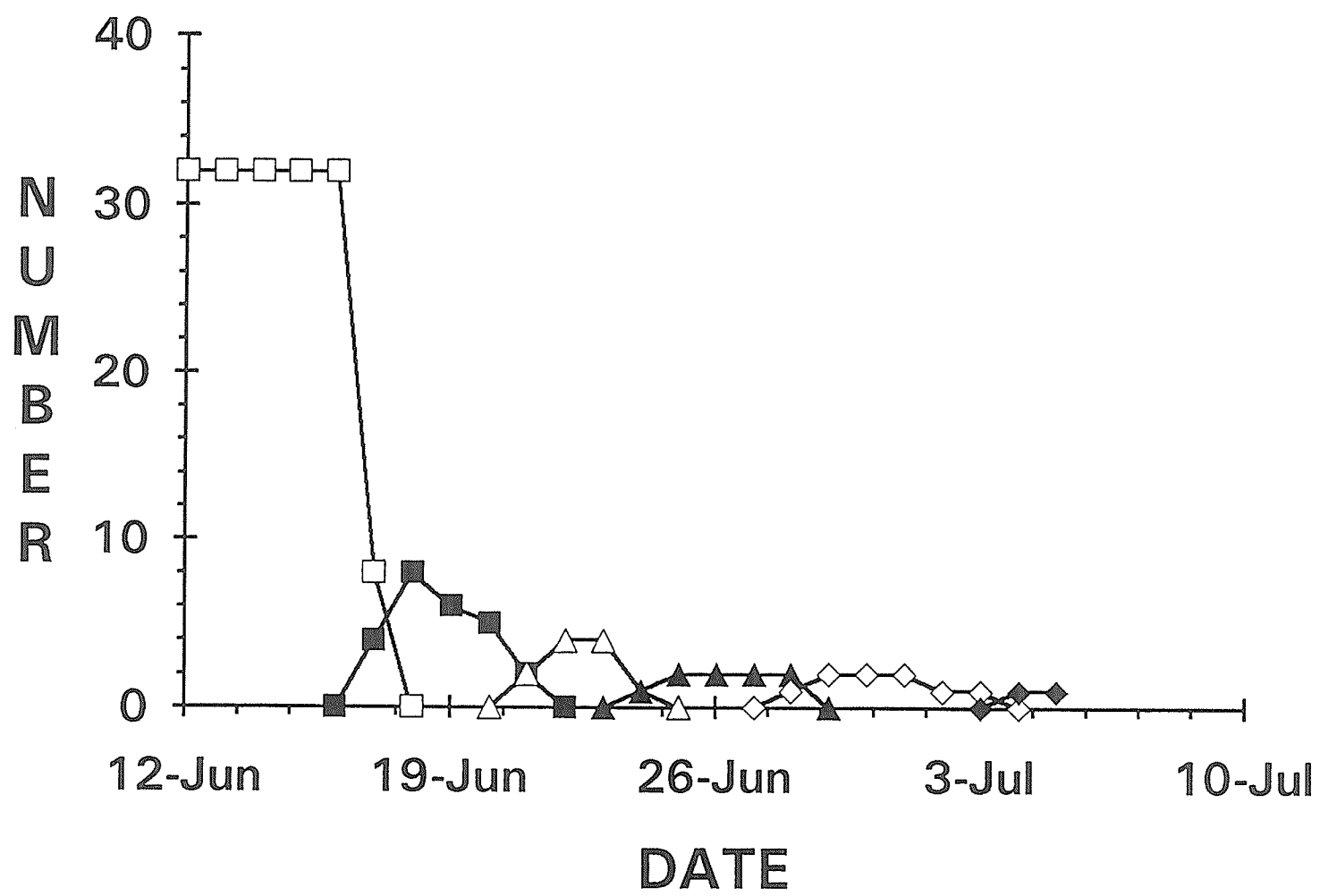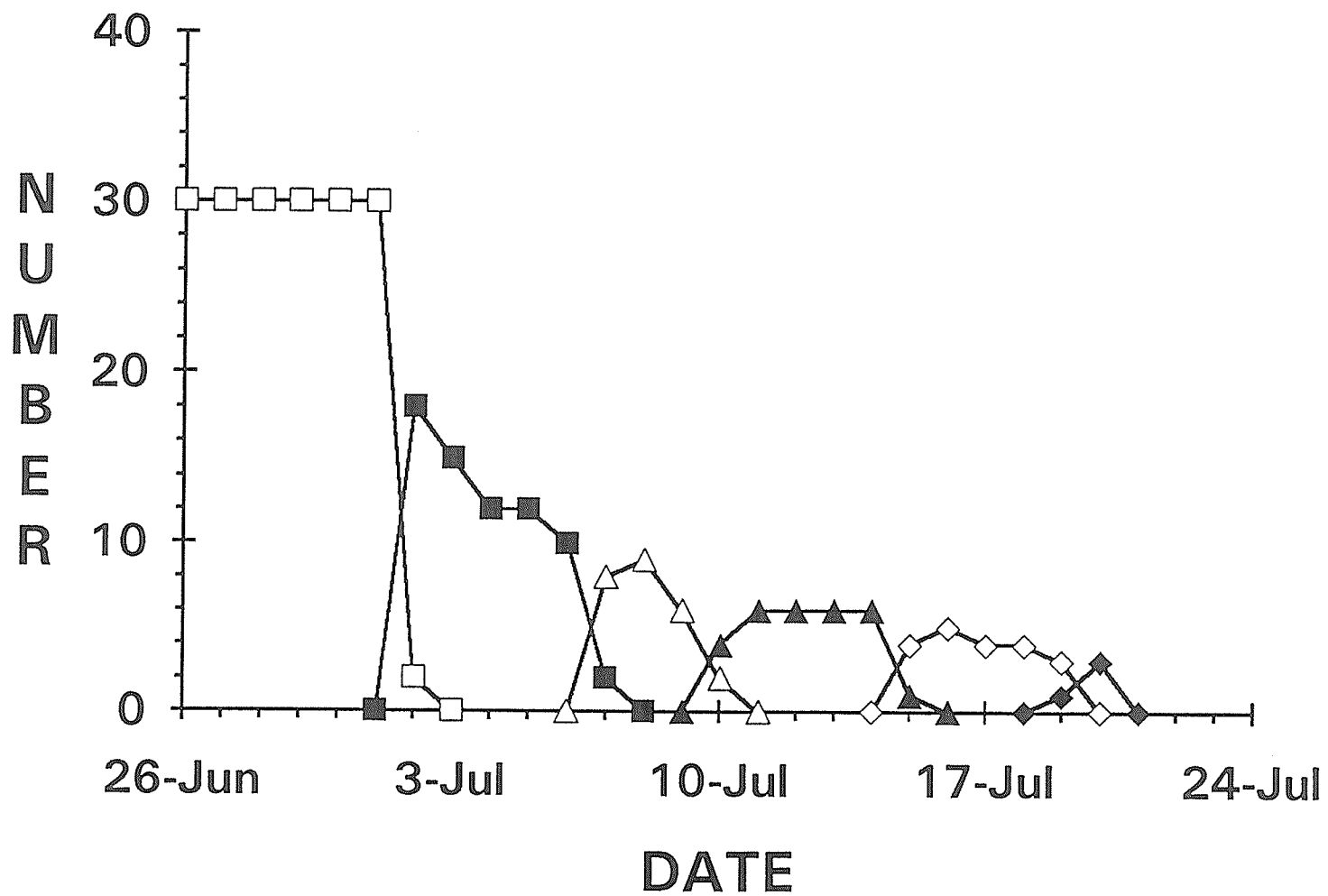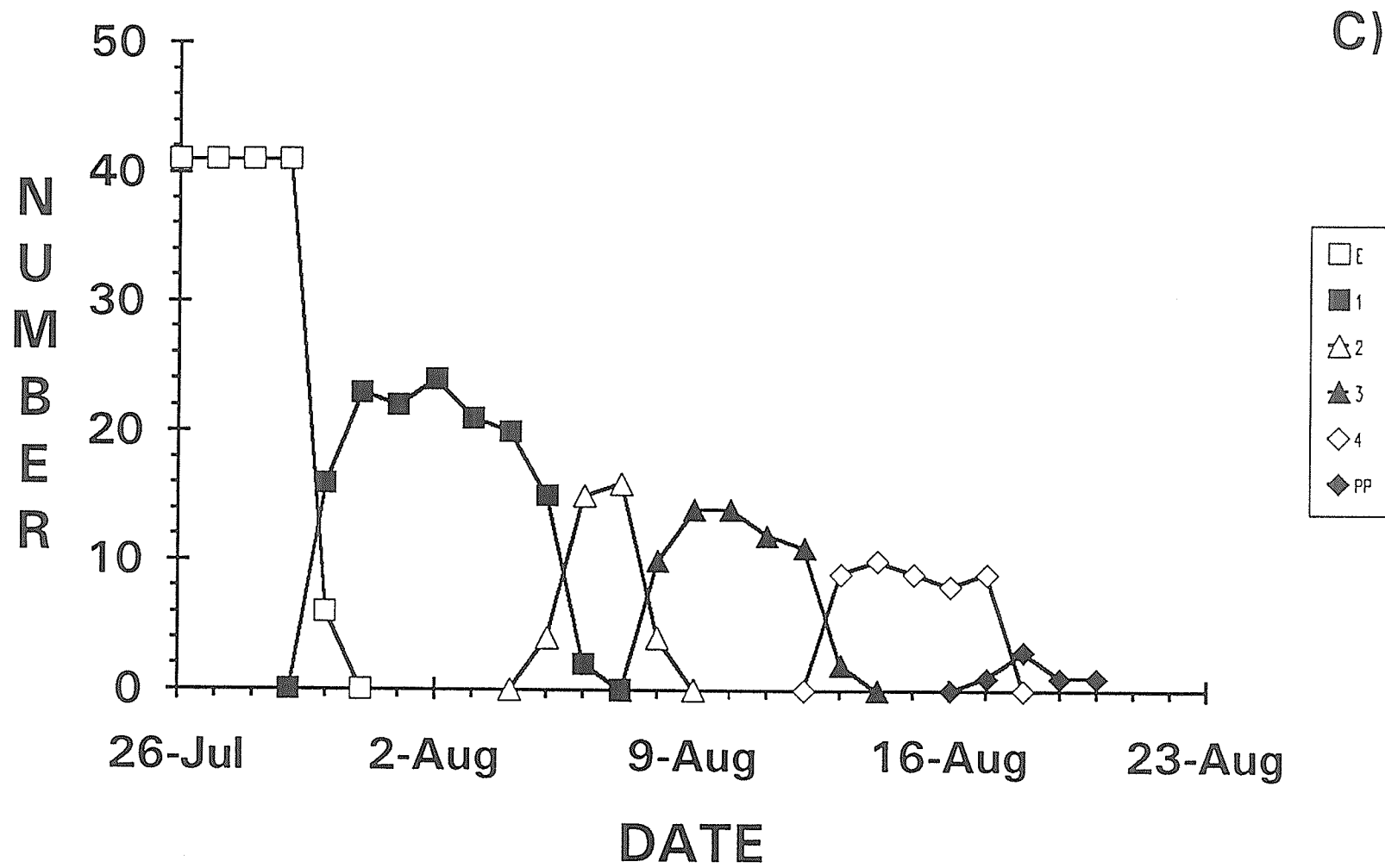
Figure 26. Sample plot of cumulative proportion moulted to next instar,
      vs time.   Cohort 3 , pinned to plant 12 Jun.
      <u>Symbols</u>:
      E to 1 , proportion moulting from eggs to instar 1.
      1 to 2 , proportion moulting from instar 1 to instar 2.
      2 to 3 , proportion moulting from instar 2 to instar 3.
      3 to 4 , proportion moulting from instar 3 to instar 4.
      4 to PP, proportion moulting from instar 4 to prepupa.
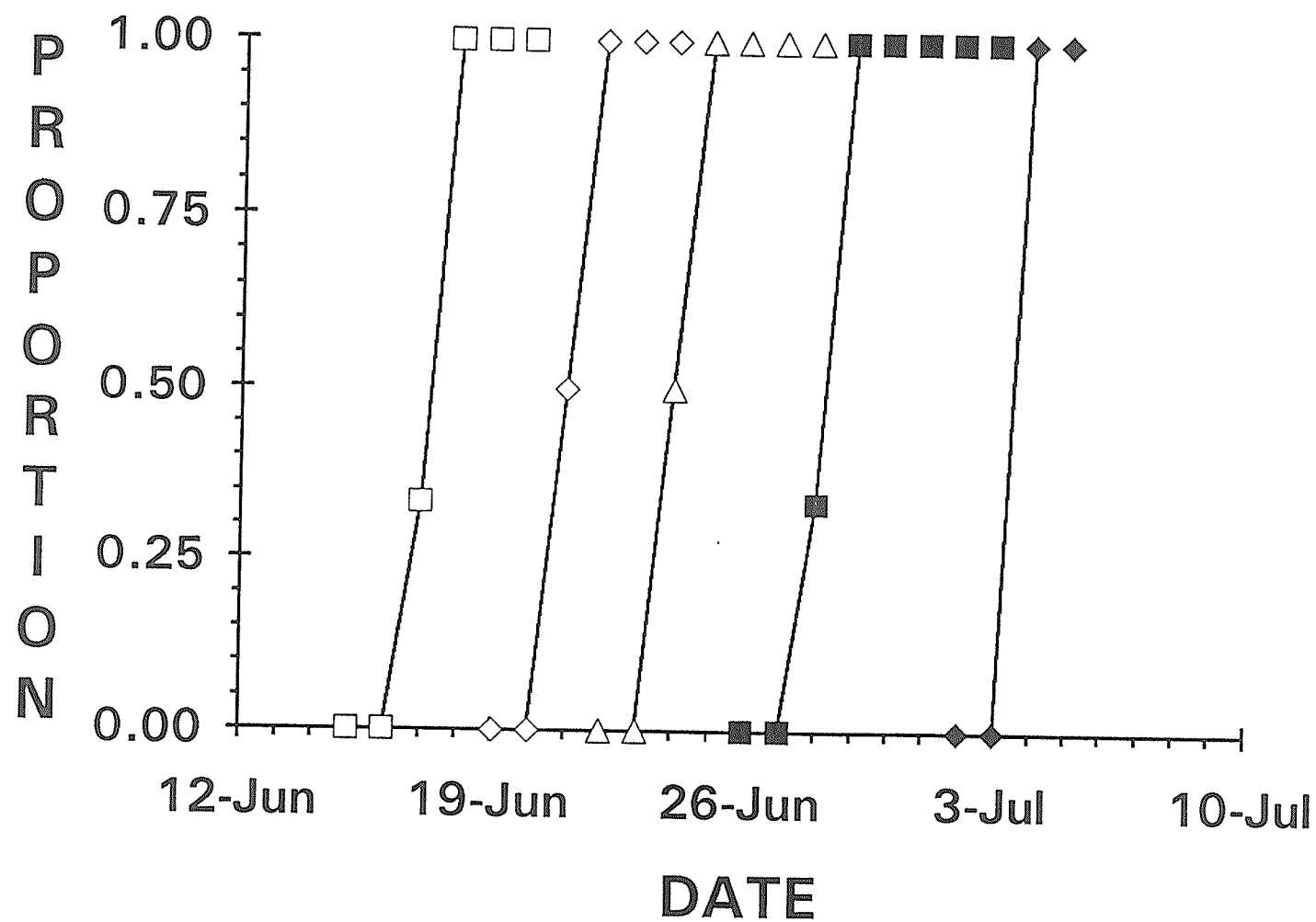
Figure 27. Temporal trend in proportion of instar development modelled to
be complete (D_v) at observed median moult, by model version.
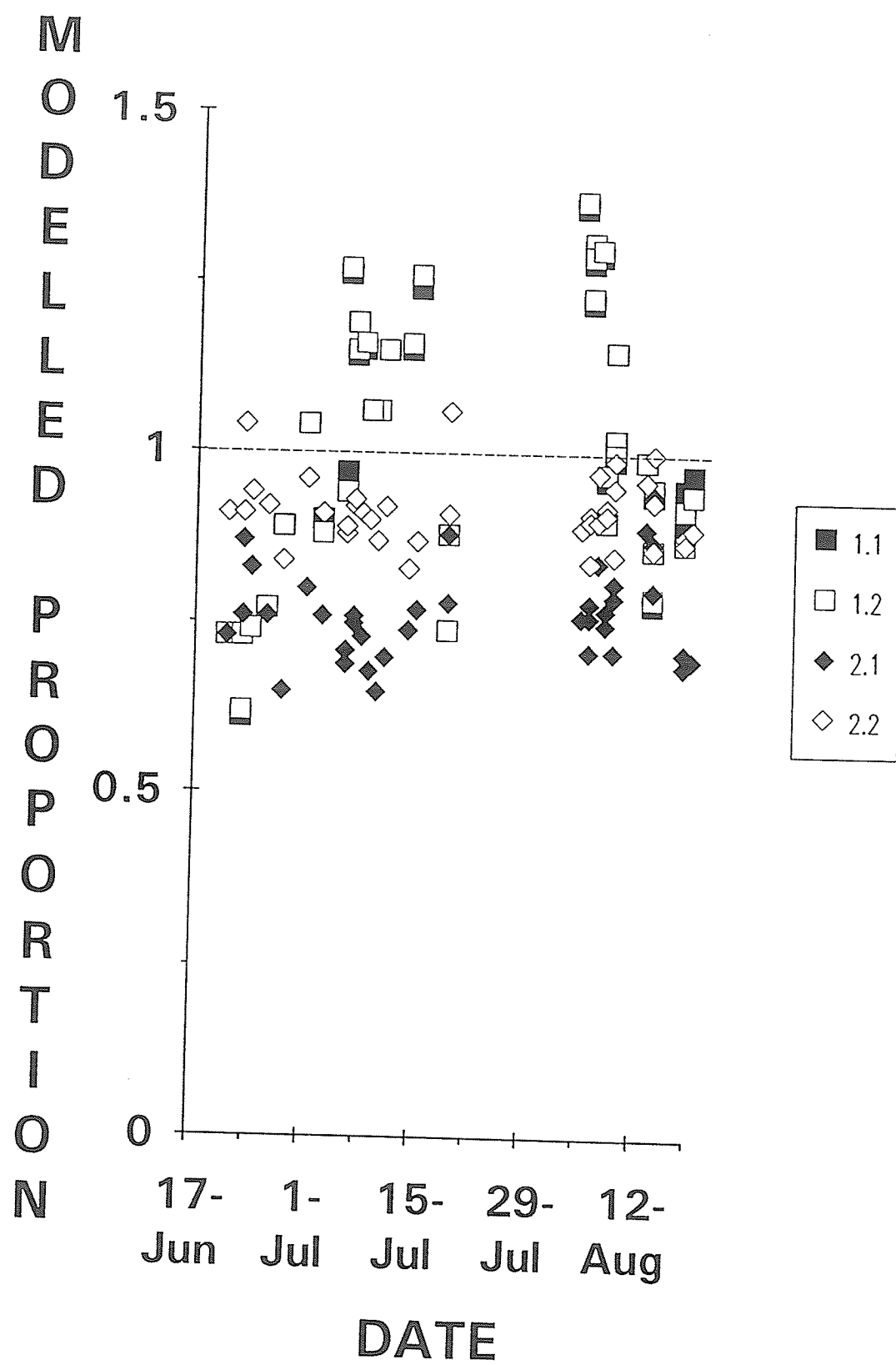
Figure 28. Temporal trend in proportion of instar modelled to be complete
(D_v) at observed median moult of each instar, by model version 2.2

L1, First instar

L2, Second instar

L3, Third instar

L4, Fourth instar
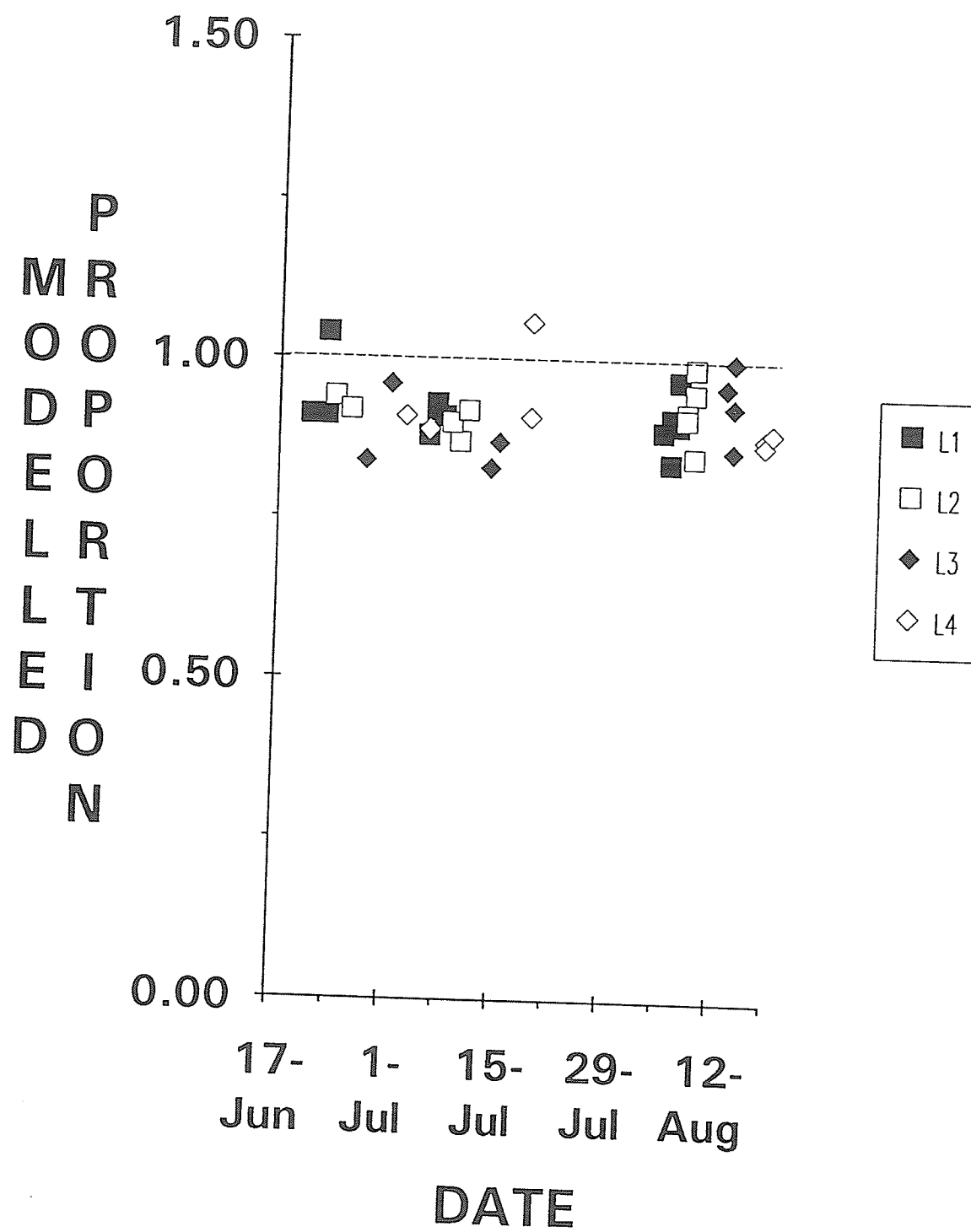
Figure 29. Colorado potato beetle instar 4. Simulated hourly development
rate under four thermoregulatory strategies.
A) 25 Jul 1991; B) 30 Jul 1991

ALL TOP   , larvae remain on upper leaf surface at all times.
ALL UNDER   , larvae remain under leaf at all times
VERSION 2.1 , larvae spend 50% of time under leaf
VERSION 2.2 , larvae choose position according to equation (12)

A)

B)
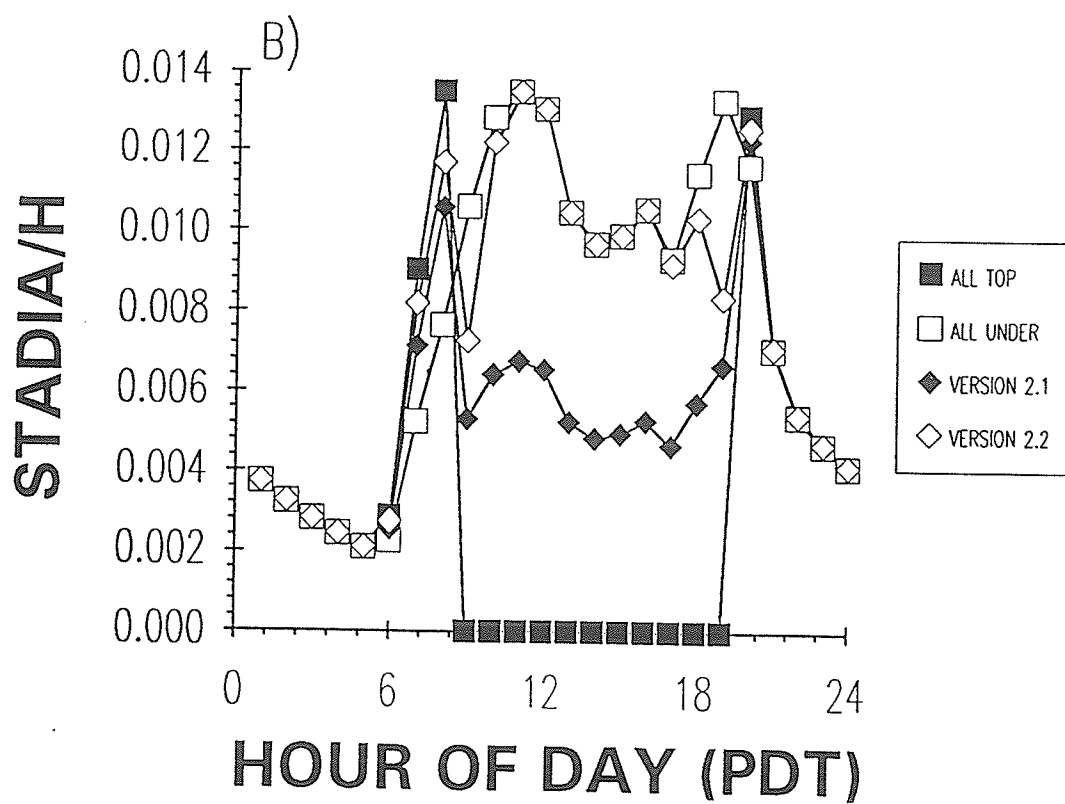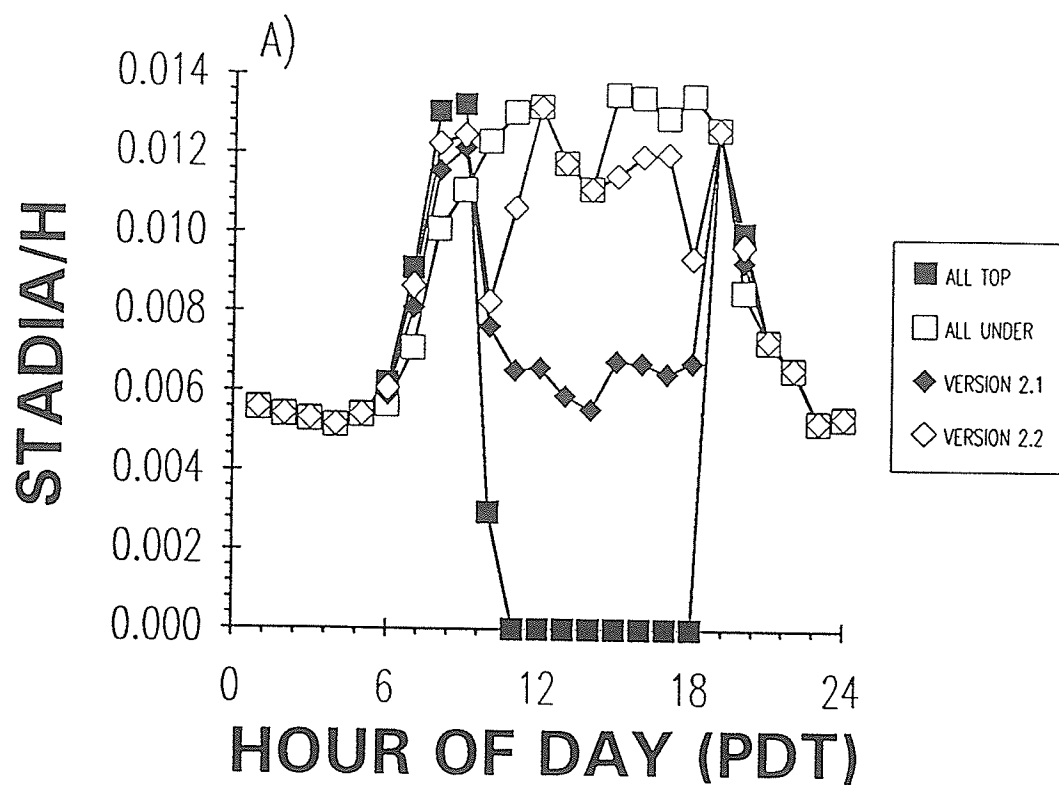
Figure 30. Colorado potato beetle instar 4. Simulated hourly development over 14 days in July 1991, Kelowna, B.C., plus mean response.
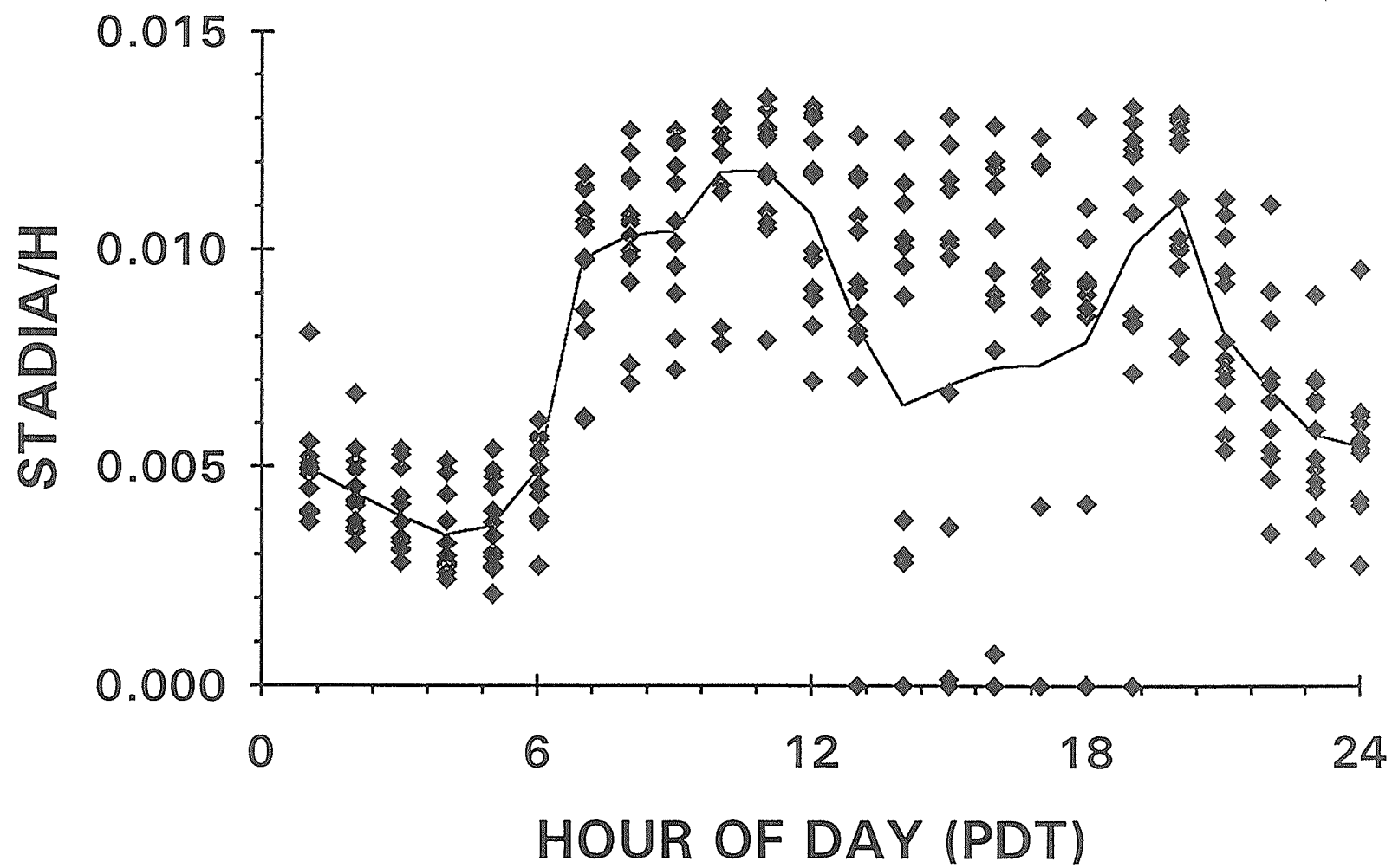
SECTION IV. ECONOMIC THERMAL BIOLOGY OF COLORADO POTATO BEETLES IN
SOUTHERN MANITOBA

Section IV. Chapter A)
     TWO DESTRUCTIVE METHODS OF ESTIMATING FRESH LEAFLET MASS OF POTATO
     PLANTS (<u>SOLANUM</u> <u>TUBEROSUM</u> L.)

ABSTRACT

Leaf area of plants may be estimated by weighing the leaves and relating area to mass. In this chapter I compare the accuracy, precision, and cost of two methods of estimating leaflet mass of potato plants. In the 'ratio' method leaflet mass estimates are derived by comparison of dry/fresh mass ratios of leaflet samples, stem samples, and of the entire above-ground parts of the plant. In the 'extrapolation' method, samples of the above-ground portions of the plant are taken and the mass of leaflets, as a proportion of sample mass, is used to estimate the mass of leaflets on the entire plant. The methods are equally accurate and precise (r^2 of regressions of predicted on actual leaflet masses: ratio method, 0.98; extrapolation method, 0.99). The ratio method requires less time except for relatively small plants. The ratio method can be appended to measurements of tissue dry-mass. Both methods can be applied to all plants that can be processed to consist of only two tissues.

INTRODUCTION

In studies of tuber production of potato plants (<u>Solanum</u> <u>tuberosum</u> L.) in the presence (Ferro <u>et</u> <u>al</u>. 1983; Shields and Wyman 1984; Wellik <u>et</u> <u>al</u>. 1981) or absence (e.g. Ng and Loomis 1984; MacKerron and Waister 1985) of defoliation, some estimate of leaf area is often necessary. Normally, this must be estimated from the mean leaf area of a sample of plants. Methods which have been used to estimate leaf area of potato plants include direct measurement of all leaves (Shields and Wyman 1984), or extrapolating from the areas of a few leaves (Epstein and Robinson 1965; Hare 1980). Some authors have used fresh mass (Sandford and Ladd 1986) or dry mass (Ng and Loomis 1984) of the foliage and stems as a covariate. Seldom has the precision or accuracy of the estimate been given, and in some cases the correlation of the measured variable and leaf area has not been explored.

To study the effects of defoliation on potato plants, it was necessary to find a cost-effective method of leaf area estimation. The method used was to determine the mass of the leaves, and to calibrate this mass to leaf area (Watson 1937). The purpose of this paper is to compare the accuracy, precision and cost of two methods of estimating the leaf mass of potato plants. The calibration of leaflet mass to area in potatoes will be explored Section IV, Chapter B.

MATERIALS AND METHODS

The haulm of a potato plant consists of one or more vines growing from a seed tuber. Vines consist of stems, flowers, fruits and compound leaves; each leaf consists of a petiole, a rachis and several leaflets. Each leaflet consists of a lamina attached to a rachis by a petiolule (Usher 1970). In this study the petiole and rachis are considered stems and the petiolule is considered part of the leaflet.

In the ratio method, the leaflet mass of potato haulms was estimated by comparing the dry/fresh mass ratios of leaf, stem and haulm. The derivation of the method follows. Total fresh masses of leaflets and stems on a given haulm are F_1 and F_s, respectively; the fresh mass of the haulm is F_h. Total dry masses are D_1, D_s and D_h. Dry/fresh mass ratios are defined as R_1, R_s and R_h. If all flowers and fruits are removed such that the haulm consists only of leaflets and stems, then

$$F_h = F_1 + F_s$$

and

$$D_h = D_1 + D_s$$

by definition, $D_h/F_h = R_h$,

therefore

$$D_h = R_h F_h \quad \text{(etc.)}$$

and

$$R_h F_h = R_1 F_1 + R_s F_s$$

$$R_h F_h = R_1 F_1 + R_s (F_h - F_1)$$

$$R_h F_h - R_s F_h = R_1 F_1 - R_s F_1$$

$$F_h (R_h - R_s) = F_1 (R_1 - R_s)$$

therefore,

$$\hat{F}_L = F_h \cdot \frac{R_h - R_s}{R_L - R_s} \tag{14}$$

Given the fresh mass of the haulm, and estimates of the dry/fresh ratios, an estimate of the fresh mass of leaflets can be obtained from equation 14. This method is tested here for the first time.

In the 'extrapolation method', the leaflet mass of the haulm was extrapolated from that of a haulm sample of known mass:

$$\hat{F}_L = F_h \cdot \frac{f_L}{f_h} \qquad (15)$$

where the circumflex denotes an estimate and lowercase 'f' denotes a sample mass. This method is based on the assumption that the proportion of leaflet mass in a sample of haulm is an unbiased estimator of that of the entire haulm. Other authors have used this, or a similar method (e.g. Epstein and Robinson 1965; Wellik et al. 1981). The two methods are algebraically identical (appendix 7).

Leaflet Mass Estimation Methods

Potato cultivation. These trials were performed in 1988 using Russet Burbank potato plants. All plants used to test the ratio method and 5 of those used to test the extrapolation method were harvested from field plots on the University of Manitoba campus. These plots were 7 m x 5 m; plants were seeded 0.42 m apart in rows 0.84 m apart. Plants used for leaf area estimation were chosen randomly and harvested at intervals of about 3 days starting 5 weeks after plant emergence.

Five of the plants used to test the extrapolation method were grown from cuttings planted singly in Cornell mix in 113.5 litre opaque plastic bags. These were grown in a growth chamber for 4 weeks at a diel cycle of 14:10 (l:d) h at about 25°C, and were then moved outdoors where they grew

under natural conditions for about 6 weeks more. Plants were harvested in random order over 5 days.

Preliminary processing. The first stages in processing haulms were the same for both methods. Each haulm was cut at ground level, sealed in a large plastic bag and stored at 5°C until processed. Storage time was usually less than 2 days, and never exceeded 4 days. After storage, all flowers, fruits and roots were picked off, leaving only leaflets and stems.

Ratio method. After preliminary processing, all leaflets were picked off at least two vines from each haulm until at least 175 g of leaflets was obtained. To ensure that the frequency distribution of leaflet size in the sample was similar to that of the whole plant, all selected vines were defoliated completely. The mass of leaflets obtained was usually well over 175 g. The leaflets were mixed thoroughly, and three subsamples of about 50 g were drawn by taking 5-6 g of leaflets from each of at least eight different locations within the large sample. The stems which remained after defoliation of the vines were cut with pruning shears into pieces about 5 cm long. Three subsamples, each of about 100 g, (about 15 pieces) were drawn by a method similar to that used to draw the leaflet subsamples. Leaflets and stems remaining after subsampling were combined with the remainder of the haulm. Throughout this study, all masses were determined to 0.1 g on a Mettler PE3000 top-loading balance.

Each leaflet or stem subsample was put individually into a '5 lb. hardware' paper bag. The remaining haulm from each plant was divided into portions, each approximately 1 kg; each portion was put into a '20 lb. hardware' paper bag. Bags were moved to a fan-ventilated room ($\approx$ 35°C and

pan evaporation of 23.4 ± 1.3 mm day^{-1}), and air-dried for at least 8 days. Preliminary trials showed that 8 days in the room ensured that the haulms had dried to constant mass.

Dry tissues were weighed, and the ratio of dry to fresh mass was determined for each subsample of each tissue. For each haulm the estimate of dry/fresh mass ratio of leaflets ($\hat{R}_1$) and stems ($\hat{R}_s$) was calculated from the mean of the three dry to fresh mass ratios for that tissue, weighted by the fresh mass of the subsamples. The total dry mass of the haulm was obtained by adding the dry masses of all subsamples to the dry mass of the remainder; R_h was obtained by dividing this sum by F_h. The leaflet mass of the haulm was estimated using Equation 14.

Extrapolation Method. After preliminary processing, each haulm was held in a tight bundle and cut into pieces approximately 10 cm long using a handsaw. The pieces were sorted by hand into samples of approximately 100 g which were as similar in the proportion of leaflets and stems as possible. Three samples were randomly chosen and the mass (f_h) of each was determined. In each sample the stems and leaflets were separated, and the fresh leaflet mass (f_1) was determined. F_h was obtained by weighing the remainder of the haulm and adding this quantity to the sum of sample masses.

Fresh mass of leaflets in a haulm ($\hat{F}_1$) was estimated by summing the leaflet and haulm masses of samples and substituting into Equation 15.

Comparison of Ratio and Extrapolation Methods

Relationship between $\hat{F}_1$ and F_1. To compare the ability of each method to predict the true fresh leaflet mass, 20 haulms were sampled, 10 by each method. After the normal procedures of each method, all leaflets

remaining on each haulm were removed and weighed, and this mass added to the leaflet masses of the samples to determine F_1. For each method, $\hat{F}_1$ was compared to F_1 by least-squares regression. Analysis of covariance (ACOVA) was used to test whether the relationship between estimated and actual leaflet mass detected using the extrapolation method was affected by the methods of growing the plants.

The accuracy of each method individually was determined from the regression parameters. The comparative accuracy of the methods was assessed using ACOVA. The relative strength of the two linear relationships was assessed by comparing their Pearson correlation coefficients; because of the relatively small sample size, an adaptation (Sokal and Rohlf 1981) of Hotelling's (1953) z^* modification of Fisher's Z-transformation (Muirhead 1982) was used.

Comparative cost of estimation. The time required, in seconds (actual time multiplied by the number of workers) to perform each component action of each method, was measured while processing several haulms. For actions in which required time depended on haulm size or sample size, regressions were used to estimate time required to process units of standard size. The time to process haulms by each method was estimated from the respective sums of these times. For the extrapolation method, ACOVA was used to test whether methods of growing the plants affected processing time.

RESULTS

Relationship between $\hat{F}_1$ and F_1. Estimated leaflet mass is plotted against actual leaflet mass in Fig. 31. Each point represents the mean of three estimates of the leaflet mass of one plant.

Using the ratio method, $\hat{F}_1 = 0.0353 + 0.9348F_1$ ($F_{1,8} = 513.3$; $P < 0.0001$; $r^2 = 0.98$; $MSE_r = 0.000868$). The intercept was not significantly different from 0 ($P = 0.11$), so the line was forced through the origin. Without the intercept, $\hat{F}_1 = 0.99995F_1$ ($F_{1,9} = 2107$; $P < 0.0001$; $r^2=0.99$; $MSE_r = 0.00108$). The slope of the regression was not significantly different from 1 either with the intercept ($P = 0.17$) or without it ($P = 0.65$) (Fig. 31a).

The methods of growing the plants for estimation by the extrapolation method had no significant effect on the relationship between estimated and actual leaflet masses (Analysis of covariance, $P = 0.42$); therefore, this factor was ignored. Using the extrapolation method, $\hat{F}_1 = 0.00979 + 0.985F_1$. ($F_{1,8} = 1263$; $P < 0.0001$; $r^2 = 0.99$; $MSE_e=0.000566$). The intercept was not significantly different from 0 ($P = 0.52$), so the line was forced through the origin. Without the intercept, $\hat{F}_1 = 1.0012F_1$ ($F_{1,9} = 5092$; $P < 0.0001$; $r^2 = 0.9982$; $MSE_e = 0.000532$). The slope of the regression was not significantly different from 1 either with the intercept ($P = 0.43$) or without it ($P = 0.80$) (Fig. 31b).

The scatter of data points about the regression lines is similar for the two methods. Hartley's test (Neter et al. 1985) was used to test for homogeneity of variance. For the two regressions of $\hat{F}_1$ on F_1 which include the intercept, the ratio $MSE_r/MSE_e=1.534$ is not significantly different from 1 ($P = 0.28$, df = 8,8). For the regressions forced through the

origin, the ratio $MSE_r/MSE_e = 2.033$ is not significantly different from 1 ($P = 0.15$, df = 9,9). Therefore the variances of the data obtained by the two methods are similar enough to warrant pooling.

Data were pooled to compare the parameters of the regressions of $\hat{F}_1$ on F_1 obtained by the two methods (analysis of covariance); no effect was detected whether the regressions included the intercept or not. If the intercept is included, P(intercepts equal) = 0.31; and P(slopes equal) = 0.32. If the intercept is excluded, P(intercepts equal) = 0.49; P(slopes equal) = 0.32. Therefore, the two methods gave statistically indistinguishable results.

The linear relationships of the two methods show similar strength. If the intercept is included in the regression models, $z^* = 0.8342$, ($P = 0.40$, df = 16); if the regressions are forced through the origin, $z^* = 0.8158$, ($P = 0.41$, df = 18). Therefore, whether the regression of $\hat{F}_1$ onto F_1 includes the intercept term or not, the strengths of the linear relationships are similar.

Comparative cost of estimation. Both methods can be divided into several subprocesses, each of which should be examined separately. Table 14 details the time required to process a single haulm by each method; times required to complete each subprocess are included.

In the ratio method, only the time required to weigh the haulm varied with haulm mass. Assuming 120 s $haulm^{-1}$ moving time (time required to transport haulms to and from the drying room), total time in person·seconds required to estimate leaflet mass by the ratio method (T_r) was 1763.9 + 166.1· (fresh mass (kg) of haulm).

Using the extrapolation method, time required for most subprocesses depended on haulm- or sample mass. These relationships were all unaffected by the method of growing the plant ($p > 0.2$). Separating samples into leaflets and stems was the most time-consuming process. Assuming that three 100 g samples are taken, total time in person·seconds required to estimate leaflet mass by the extrapolation method (T_e) was $1624.9 + 383.6 \cdot$ (fresh mass (kg) of haulm).

The equations describing time to process haulms by each method intersect at $F_1 = 0.64$ kg; above this mass, the ratio method is faster.

DISCUSSION AND CONCLUSIONS

The characteristics of the regressions of $\hat{F}_1$ on F_1 were similar for the two methods. Perfect accuracy of estimation occurs when the regression of $\hat{F}_1$ onto F_1 has intercept = 0 and slope = 1, and shows no systematic deviation from linearity. Both methods gave results which approached this ideal, whether the intercept was included in the model or not, and analysis of covariance revealed no effect of estimation method on these relationships: both methods were equally accurate.

The strength of the linear relationship, as measured by the correlation coefficient, is similar for the two methods. This coefficient is affected by both systematic and random deviation of estimates from the regression line (Neter et al. 1985). Rigorous statistical separation of these two sources of error requires repeated observations at more than one value of F_1; this was not feasible, but inspection of residuals suggested no evident systematic deviation from linearity. This is good ad hoc evidence that in this case the correlation coefficients measure the

precision of the regressions and hence of the methods. Therefore, the two methods appear to be similarly precise, as well as similarly accurate.

Thus, evaluation of the relative merits of the two methods may be based on the cost of estimation, which changes with haulm mass. Assuming 120 s·haulm^{-1} moving time, the extrapolation method is superior for haulms of less than about 0.64 kg mass; above this mass, the ratio method is superior. Moving time varies according to conditions. In the worst case, moving time may reach 300 s·haulm^{-1}; in this case, the ratio method is faster for haulms weighing 1.48 kg or more.

The range in which the extrapolation method is most efficient cannot be extended by the use of smaller samples to speed processing, because potato haulms are heterogeneous. Preliminary investigation revealed that the standard error of $\hat{F}_1$, expressed as a percent of F_1, increases exponentially as sample mass decreases (Lactin, unpublished). Therefore, if smaller samples are used, more must be taken to maintain precision. Reduction in time required to separate leaflets and stems in smaller samples, would be negated by the need for more samples.

To describe the change in mean leaflet mass (or area) of a population of haulms over a growing season, it is best to maximize the number of haulms sampled. Assuming that time is limited, faster methods are preferable. For potato cultivars such as Russet Burbank, in which haulm mass may exceed 5 kg, the ratio method is best; for a cultivar such as Norland in which haulm mass seldom exceeds 2 kg (Lactin, unpublished), the extrapolation method is preferable. For cultivars of intermediate haulm mass, the optimal sampling strategy is based on the anticipated range of haulm masses.

This comparison of relative net costs has assumed that estimation of F_1 occurs separately from other investigations. This is not necessarily true. Whereas the extrapolation method can be used only for leaflet-mass estimation, the ratio method can be appended to measurements of tissue dry-matter content, which are often made for studies of plant growth (e.g. Allen and Scott 1980), or of insect/plant interactions (e.g. Johnson et al. 1986, 1988). If this is done, leaflet mass estimation by the ratio method has little extra cost. The ratio method also has the advantage that dry/fresh mass ratios may be indicative of the plant's physiological condition.

The ratio method has at least two possible disadvantages. Firstly, leaf mass estimates are seriously affected if the leaflet, stem, and haulm samples do not reach the same degree of dryness. If tissues are to be passively air-dried, careful preliminary investigation is needed to determine the adequate drying interval. The second possible disadvantage is that drying takes several days; under some circumstances, this may be unacceptable.

Although this paper has dealt with estimation of leaflet mass of potato haulms, both methods may be applied to other plants which consist only of two tissues, or which can be easily processed to be so. For such plants, and for potato cultivars with growth habits different from those of Russet Burbank, it may be necessary to develop alternative methods of drawing samples.

Table 14. Times in person·seconds (p·sec) of actions involved in estimation of leaflet mass of one potato haulm by the extrapolation or ratio methods.

RATIO METHOD

Action	n	INTERCEPT		SLOPE		
		p·sec		p·sec·(kg haulm)$^{-1}$		
		EST	S.E.	EST	S.E.	
Strip leaves	14	910.7	106.1***	-4.0	164.0	ns
Sample & weigh leaves	14	208.4	45.8***	44.1	27.6	ns
Sample & weigh stems	14	231.6	17.3***	-1.1	10.5	ns
Reweigh dried tissues	14	245.8	5.7***	-3.9	3.4	ns
TOTAL ratio actions	14	1596.6	135.0***	35.1	81.4	ns
+ Time to weigh haulm	7	47.3	17.7*	131.0	39.0*	
+ Moving time	ca. 120					
= TOTAL TIME PER HAULM			1763.9 + 166.1(F_h)			

EXTRAPOLATION METHOD

1) Actions performed on entire haulms

Action	n	INTERCEPT		SLOPE		
		p·sec		p·sec·(kg haulm)$^{-1}$		
		EST	S.E.	EST	S.E.	
Weigh haulm	7	47.3	17.7 *	131.0	39.0 *	
Chop haulm & divide	7	96.6	12.7 ***	109.3	27.8 *	
Select 3 samples	7	180.7	29.5 **	143.3	64.7	ns
PROCESS HAULM	7	324.6	59.4 ***	383.6	106.6 *	

2) Actions performed on samples (total time for three)

Action	n	INTERCEPT		SLOPE		
		p·sec		p·sec·(kg haulm)$^{-1}$		
		EST	S.E.	EST	S.E.	
Separate tissues	13	250.5	118.7 ns	9866.3	1286.0 ***	
Weigh tissues	13	88.0	10.6 ***	-248.3	115.5	ns
PROCESS 3 SAMPLES	13	338.5	117.9 *	9618.0	1277.6 ***	

= TOTAL TIME PER HAULM   (assuming 3 samples of 100g)
= 324.6 + 338.5 + (9618.0*0.1) + 383.6(F_h)
= 1624.9 + 383.6(F_h)

NOTE: p(Parameter=0): ns > 0.05; * ≤ 0.05; ** ≤ 0.01; *** ≤ 0.001

218

Figure 31. Leaflet masses estimated by ratio (a) or extrapolation (b) methods, vs. actual leaflet masses. Regression lines (forced through the origin) and 95% confidence limits of regression lines.

(a) RATIO METHOD

(b) EXTRAPOLATION METHOD

ESTIMATED LEAFLET MASS (kg)

ACTUAL LEAFLET MASS (kg)
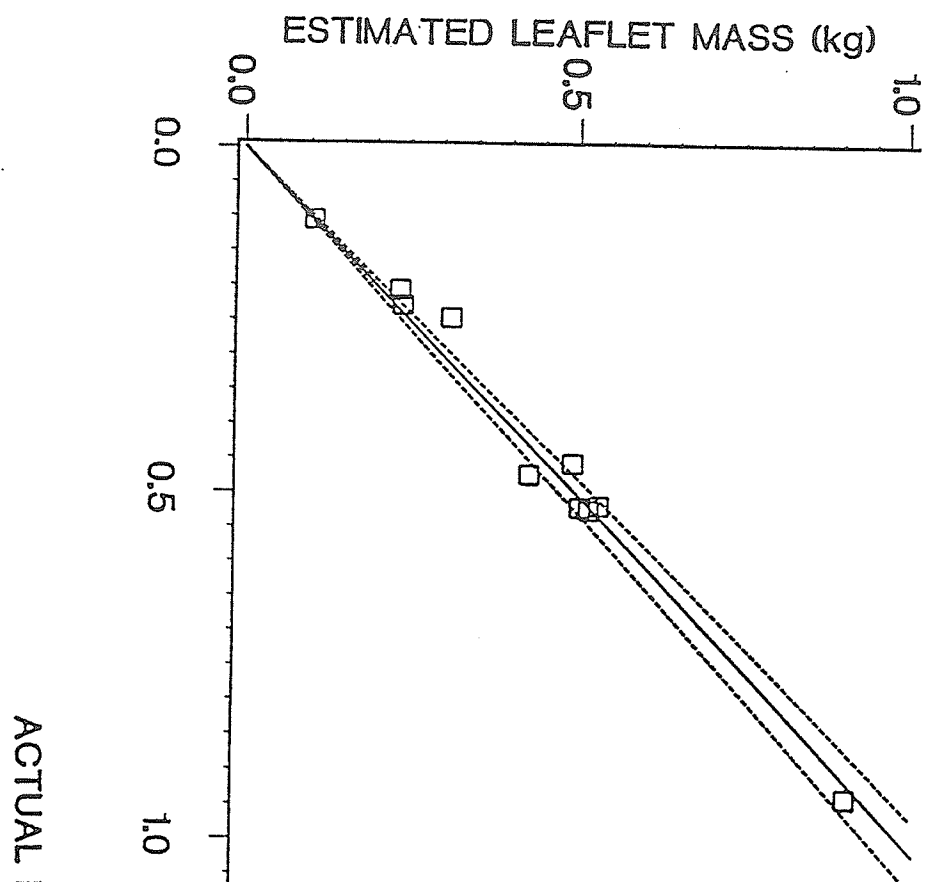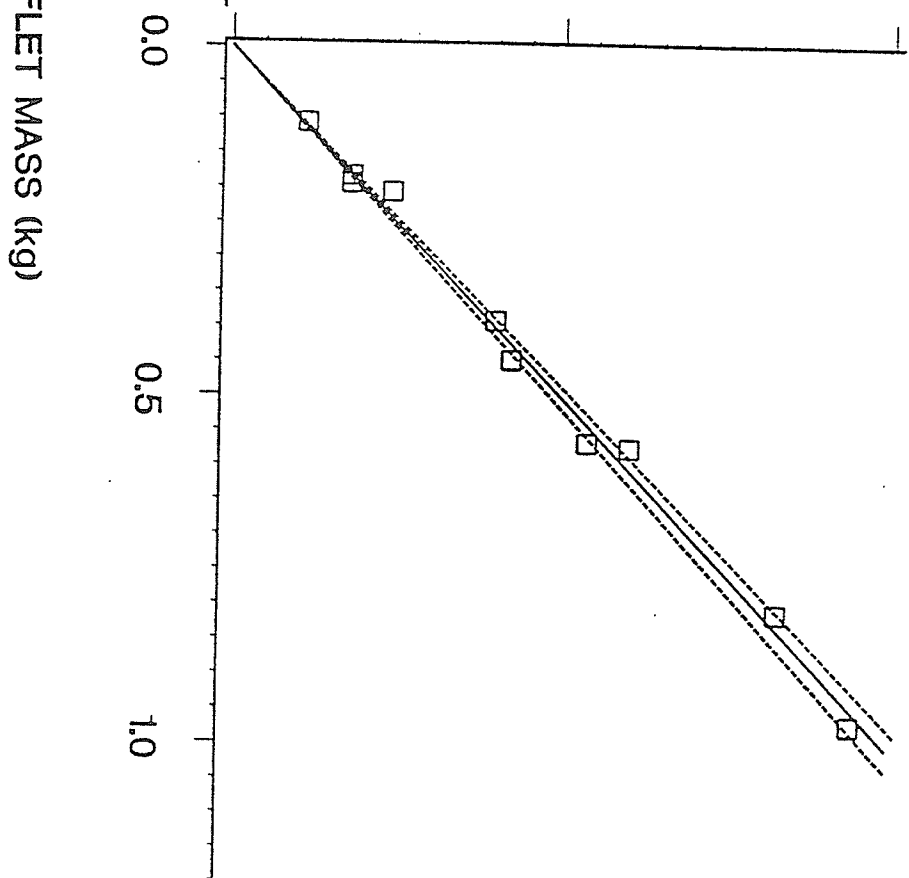
Section IV.   Chapter B)
    ESTIMATION OF POTATO PLANT LEAF AREA

ABSTRACT

The relationship between fresh mass and area was determined repeatedly for Russet Burbank potato leaflets in two fields in two seasons. Each year, one field was infested with Colorado potato beetles, and the other was not.

The relationship of leaflet area to mass was described better by a ratio than by a regression model. The area : mass ratio started at $\approx 20 - 26$ $cm^2 \cdot g^{-1}$ in both fields in both years. In the uninfested fields, the ratio increased at a decelerating rate, then fell in the last week before harvest (1986), or increased steadily until mid-season and then decreased until harvest (1987). In the infested field, the ratio either increased gradually until harvest (1986) or remained relatively constant until six weeks after median plant emergence, and then decreased rapidly as the plants died by defoliation at the eighth week (1987). Except in the infested field in 1987, the leaflet area : mass ratio was ≈ 40 $cm^2 \cdot g^{-1}$ at harvest. In both years, the area : mass ratio in the infested fields was consistently lower than in the uninfested fields, after the second week.

These observations demonstrate that the area : mass ratio cannot be assumed constant, nor to increase linearly, nor to be unaffected by Colorado potato beetle infestation. These conclusions have important consequences to models of potato growth which make any or all of these assumptions.

INTRODUCTION

Because tuber yield of potato plants is strongly related to some function of the integral of leaf area index (i.e. [leaf area]/[ground area]) over time (Bremner and Taha 1966; Allen and Scott 1980), mechanistic models of tuber production require an explicit description of the seasonal change in leaf area. This requirement is particularly important if the model is to be used in predicting the impact of partial defoliation on tuber yield.

In many potato plant growth models, total plant leaf area is a fundamental driving variable (e.g. Ng and Loomis 1984), but is often replaced by total leaf mass, for convenience. In adopting this substitution modellers assume that the area : mass relationship of leaflets is either constant (e.g. Fishman et al. 1985) or changes linearly over time (e.g. Johnson et al. 1988). However, in Russet Burbank potato plants, leaves are initiated over an extended period, and mature independently thereafter (Ng and Loomis 1984). Because the area : mass ratio of leaves changes greatly as they age (Watson 1937), there are grounds to suspect that both assumptions are invalid.

This study was initiated with to characterize the temporal dynamics of the area : mass relationship of Russet Burbank potato leaflets in Southern Manitoba. The impact of infestation by Colorado potato beetle (Leptinotarsa decemlineata (Say) (Coleoptera: Chrysomelidae)) on this relationship was also examined.

Leaf area of potato plants may be estimated by first estimating leaf mass and calibrating this quantity to area, using an area : mass relationship (Watson 1937; Watson and Watson 1953). Extrapolation from samples to plants is error-prone in that any inaccuracy in estimating the area : mass relationship is amplified. Consequently, this chapter also contains an examination of one possible source of estimation error, the effect of sample processing time on the area : mass relationship.

MATERIALS AND METHODS

Experimental fields.

Plant growth and the population mean area : mass relationship of Russet Burbank potato leaflets were followed in two fields in each of 1986 and 1987. In each year, one field was located on the University of Manitoba Department of Plant Science field station at Portage la Prairie, Manitoba (49° 58' N, 98° 18' W) (Portage field); the other was ≈ 70 km away, on the University of Manitoba campus in Winnipeg, Manitoba (49° 54' N, 97° 9' W) (Campus field).

Edaphic characteristics and experimental treatments varied in the two plots. Soil in the Portage field is a Newhorst sandy loam (Michalyna et al. 1972); that in the campus field is a Riverdale floodplain clay (Ehrlich et al. 1953). In the Portage field, naturally occurring populations of Colorado potato beetle (Leptinotarsa decemlineata (Say) (Coleoptera: Chrysomelidae)) caused varying degrees of defoliation; the Campus field was kept virtually free of Colorado potato beetles manually.

The Portage field consisted of a central array of 15 plots, in a 3 x 5 array, surrounded by a buffer 8 m wide. Each plot consisted of 15

rows 0.84 m apart, each containing 15 plants 0.84 m apart. The Campus field was divided into plots consisting of 15 rows 0.84 m apart, each containing 15 plants 0.42 m apart; five such plots were created in 1986 and four in 1987.

Seed pieces weighing $\approx$ 50 g were planted using a single-row seeder in the Portage field on 26 May 1986 and 20 May 1987 and manually in the Campus field on 27 May 1986 and 22 May 1987. In the Portage field, fertilizer (23.1 - 13.5 - 13.5 N-P-K) was applied in-furrow at 400 kg·ha^{-1} in 1986 and 500 kg·ha^{-1} in 1987; no fertilizer was applied to the Campus field.

Sampling protocol.

Three to six plants were selected randomly from each location at intervals from shortly after estimated median plant emergence (18 Jun 1986, 09 Jun 1987) until harvest, or until the field became defoliated by Colorado potato beetles. Plants growing next to gaps in the canopy were rejected and alternatives selected in order to avoid complications resulting from possible unusual growth characteristics in such instances. Haulms of the chosen plants were cut off at ground level and sealed immediately in large plastic bags and stored at 5°C until the next day, when leaf area estimation began.

Leaflet area : mass relationship.

Area and mass were determined for five to ten leaflet samples of $\approx$ 1.5 - 3 g each from each plant. Samples were weighed to 0.1 g on a Mettler PE3000® top loading balance in 1986 and to 0.0001 g on a Mettler AE166® analytical balance in 1987. After weighing, all leaflets from each sample were flattened between a sheet of white paper and a sheet of

transparent plastic and photocopied. Haulms were stored at 5°C for no more than four days before sampling, and leaflets were photocopied within 20 min of removal from the plant.

The total leaflet area of each subsample was measured photometrically from the photocopies, using an Ikegami® computerized image analysis system in 1986 and a computerized image analysis program (METER, Lamari and Bernier 1987) in 1987. The Ikegami system measured areas to the nearest cm^2 with constant absolute precision. METER has relative precision of 1%; absolute precision was always within 1 cm^2. Neither measurement system detected any consistent difference in the areas of the actual leaflet sample and of the photocopied image.

The relationship between area and mass of leaflet subsamples in each field at each sample date was characterized using regression analysis, comparing models with and without the intercept (i.e. simple ratio). **Effect of storage and processing time on estimated leaf area of plants.**

The area and mass of the leaflet samples may change in the interval between removal from the plant and weighing; physiological effects of storage at 5°C may also affect the dynamics of any such change. Both types of change could affect the estimated leaf area of the source plant. Therefore, a trial was designed to assess the effect of these two types of possible error on the area : mass relationship of samples, and on the estimated leaf area of plants.

Three small Russet Burbank potato plants (haulm mass approximately 82 to 125 g), grown in pots under artificial light (14h:10h L:D) were each stored at 5°C for 7 days. At 0, 4 and 7 days after entering storage, three leaflet samples of ≈ 2 g were drawn from each haulm and the mass and

area of each was determined four times. The samples were weighed to
0.1 mg and the time between drawing and weighing samples was noted to the
nearest 5 s. All leaflets from each sample were flattened between a sheet
of white paper and a sheet of transparent plastic, and photocopied.
Leaflets were left between the paper and plastic for $\approx$ 20 min., then
assessed again by removing and reweighing. The samples were then replaced
between the paper and plastic, and photocopied again. Time was noted to
the nearest 5 s at each assessment. This process was repeated three
times, i.e. each sample was assessed four times. Total elapsed time
between initial and final assessments exceeded 1.4 h at each storage
duration; this was considerably greater than the normal maximum of
$\approx$ 20 min (Section IV, Chapter A; Lactin and Holliday 1989); similarly, the
maximum tested duration of storage is nearly twice the normal allowed
maximum storage duration of 4 days. These unrealistically high maximum
values of the two variables were adopted to facilitate statistical
characterization of the response.

To eliminate effects of random variation in sample size, all
dependent variables were converted to a proportion of the value when the
sample was first taken. To determine whether mass, area or the
area : mass ratio changed was significantly influenced by storage duration
and time elapsed since sampling, data were subjected to repeated measures
analysis of variance; orthogonal polynomials were used to test for linear
effects and interactions. Parameters describing the proportional change
in area, mass and the area : mass ratio as functions of storage duration
and time elapsed since sampling, were then estimated by multiple
regression on dependent variable means by plant at each combination of

storage duration and time elapsed since sampling. These regression

parameters were used to determine whether bias occurred in estimation of

leaf area of plants.

Estimation of total leaflet area of field plants.

On each sample date in each field, total leaflet area on each plant

was estimated from total fresh leaflet mass and an area : mass calibration

relationship. Total fresh leaflet mass of each potato plant was estimated

by either the ratio or the extrapolation method (Section IV, Chapter A;

Lactin and Holliday 1989). The methods are practically and theoretically

(Appendix 7) equivalent, so hereafter no distinction will be made between

them.

RESULTS AND DISCUSSION

Leaflet area : mass relationship in field plants.

Table 15 presents parameters for the regressions of leaflet area on

leaflet mass, with and without the intercept term, for each sample day in

each field. Because this analysis entailed 33 independent regressions

(comparisons), the experiment-wise error rate was protected at $\alpha_e \leq 0.10$

by setting the comparison-wise rate at $\alpha_c = 0.00319$ (Sidak 1967). The

intercept of the regression of leaflet area on leaflet mass met this

significance criterion only once out of 33 comparisons; this frequency is

consistent with type-I error. Therefore, it is reasonable to ignore the

intercept term in the calibration of leaf area to leaf mass and adopt a

simple area : mass ratio.

Figure 32 illustrates that leaflet area : mass ratio changes over

time and differs among fields. The ratio started at $\approx 20 - 26$ $cm^2 \cdot g^{-1}$ in

both fields in both years. In the uninfested Campus fields, this ratio either increased at a decelerating rate, then fell in the last week before harvest (1986), or increased steadily until mid-season and then decreased until harvest (1987). In the infested Portage fields, the area : mass ratio either increased gradually until harvest (1986) or remained relatively constant until six weeks after median plant emergence, and then decreased rapidly as the plants died by defoliation at the eighth week (1987). Except in the infested field in 1987, the leaflet area : mass ratio was ≈ 40 $cm^{2} \cdot g^{-1}$ at harvest. In both years, the area : mass ratio in the infested fields was consistently lower than in the uninfested fields, after the second week after plant emergence.

Effect of storage and processing time on estimated leaf area of plants.

Table 16 suggests that both area and mass of leaflet samples changed with both storage duration at 5°C and time elapsed between drawing and weighing samples. Effects of storage duration result from random variation in the size of the sample drawn; this irrelevant variation is eliminated by the rescaling of dependent variables to a proportion of the value when the sample was first taken. Total mass of the plants (remaining tissues plus total sample mass) did not change with storage duration.

Results of the repeated measures analysis of variance are summarized in Table 17. Linear orthogonal polynomials indicated that sample mass changed with duration of storage, but that sample area and area : mass ratio did not. All of these quantities showed highly significant change with time elapsed since the sample was drawn, and with the interaction of storage duration and time elapsed since sampling. Regressions and

polynomials did not differ among plants. Inspection of the data indicated that higher-order polynomials were inapplicable.

Regression results (Table 18) indicate that both mass and area of leaflet samples decrease significantly with duration of storage at 5°C, and as time elapses after the samples are taken, and this decrease is faster as duration of storage increases. Sample mass decreases faster than does area; consequently the area : mass ratio increases (Table 18).

Calculations based on the parameters in Table 18, using the worst allowed combination of duration of storage at 5°C (4 days) and time elapsed between drawing and measuring samples (20 min) indicate that the area : mass ratio changes by +2.4% and that plant leaf area (biased ratio x biased mass) is underestimated by 1.3%. The bias in estimation of area : mass ratio is much less than the change in this ratio detected in the field (Table 15, Fig. 32); therefore the latter change is real. The proportional bias in the estimate of plant leaf area which results from change in sample characteristics during handling, is much less than the proportional standard error of the estimate of plant leaf area, and is thus negligible. Normally, the change in area : mass ratio might be less than 1.3%, because plants are not processed repetitively.

Estimation of total leaflet area of field plants.

Estimated mean leaflet area per plant in each field in each year are plotted in Fig. 33. Seasonal trends in mean total leaf area per plant differed in the two fields. In the Campus fields, mean total leaf area per plant attained a clear peak near mid-season, and then diminished until harvest. A gap in the data precludes certain placement of the leaf area peak in 1986. In the Portage fields, mean total leaf area per plant

increased until the penultimate sample in 1986, but in 1987 the field was completely defoliated before any clear peak was attained; the sudden decline in area : mass ratio just preceding this time (Table 15) may be related to dehydration of the plants just before death.

CONCLUSIONS

The differences in the characteristics of the fields, coupled with the lack of replication and randomization of the infestation and fertilization treatments, allow only qualitative conclusions to be drawn from this study. Nonetheless, important conclusions emerge from the trends observed.

The area : mass ratio of Russet Burbank potato leaflets changed systematically over the growing season (Table 15). Only a small part of the change could be an artifact of increased time required to process samples, concomitant with seasonal increase in plant size. The observed change in the area : mass ratio is consistent with a gradual temporal change in the age structure of the leaflet population, resulting from sequential initiation and independent maturation of leaves (Ng and Loomis 1984), coupled with age-dependent change in their area : mass ratio (Watson 1937).

This observed trend in the area : mass ratio has three immediate implications. First, when estimating leaf area of potato plants by extrapolating from samples, the calibration of area to mass is required on each sample date. Second, potato growth models in which the leaf area : mass relationship is assumed constant (e.g. Fishman et al. 1985; Johnson et al. 1986), or is modelled as a linear trend over time (Johnson et al. 1988) require refinement. Third, the differences between fields

and years indicates that a better understanding of the determinants of area : mass ratios will be needed to incorporate accurate leaf area:mass relationships into general models of potato growth.

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Table 15. Parameters of regressions of area on mass of leaflet samples from potatoes of cultivar Russet Burbank. Each regression was performed independently of all others.

DATE	DAE[a]	REGRESSION						SIMPLE RATIO		
		Intercept (cm²)			Slope (cm²·g⁻¹)			Slope (cm²·g⁻¹)		
		Est	S.E.	P	Est	S.E.	P	Est	S.E.	P
					Campus Field 1986					
23Jun	05	2.1	1.0	0.0541	23.7	0.43	0.0001	24.4	0.27	0.0001
30Jun	12	-0.6	21.8	0.9802	27.1	3.18	0.0001	27.0	0.55	0.0001
07Jul	19	23.3	27.0	0.3977	24.6	4.56	0.0001	28.5	0.63	0.0001
14Jul	26	50.9	16.7	0.0054	26.7	3.09	0.0001	35.9	0.66	0.0001
21Jul	33	31.0	23.1	0.2504	30.6	5.91	0.0066	38.5	1.23	0.0001
20Aug	63	11.5	12.2	0.3560	39.6	3.78	0.0001	43.1	0.69	0.0001
01Sep	82	10.8	17.3	0.5396	39.6	5.73	0.0001	43.1	0.83	0.0001
08Sep	89	-3.2	10.1	0.7555	41.3	3.49	0.0001	40.2	0.64	0.0001
					Campus Field 1987					
09Jun	00	1.6	0.8	0.1719	20.3	0.81	0.0016	21.9	0.34	0.0001
16Jun	07	-2.5	25.4	0.9240	25.9	6.36	0.0035	25.3	0.88	0.0001
19Jun	10	-10.0	7.6	0.2204	27.5	2.33	0.0001	24.5	0.45	0.0001
29Jun	20	4.8	9.2	0.1183	27.8	2.31	0.0001	31.5	0.42	0.0001
10Jul	31	6.0	10.0	0.1174	33.1	2.89	0.0001	37.6	0.60	0.0001
21Jul	45	9.5	14.5	0.5169	45.6	4.70	0.0001	48.6	0.59	0.0001
04Aug	56	17.3	10.4	0.1067	43.1	3.67	0.0001	49.1	0.55	0.0001
17Aug	69	-19.2	6.9	0.0095	53.6	2.50	0.0001	46.7	0.42	0.0001
28Aug	80	23.7	12.6	0.0700	33.4	4.93	0.0001	42.6	0.72	0.0001
11Sep	94	6.6	19.9	0.7446	40.6	7.87	0.0001	43.2	0.59	0.0001
					Portage Field 1986					
25Jun	07	1.8	1.6	0.2828	25.2	0.79	0.0001	26.0	0.44	0.0001
09Jul	21	-5.5	7.1	0.7544	26.8	2.69	0.0001	26.0	0.61	0.0001
16Jul	28	52.2	25.4	0.0538	19.5	3.72	0.0001	27.1	0.53	0.0001
23Jul	35	10.9	15.0	0.4742	32.3	2.62	0.0001	34.2	0.46	0.0001
06Aug	49	33.6	25.6	0.2120	29.2	4.89	0.0001	35.6	0.78	0.0001
20Aug	63	72.9	17.5	0.0002[b]	19.8	4.01	0.0001	36.2	0.93	0.0001
03Sep	77	0.7	7.8	0.9327	41.0	2.30	0.0001	41.2	0.39	0.0001
10Sep	84	13.8	12.2	0.2641	34.7	3.96	0.0001	39.1	0.70	0.0001
17Sep	91	4.7	13.4	0.7305	37.4	4.49	0.0001	38.9	0.64	0.0001
					Portage Field 1987					
10Jun	01	-7.1	6.9	0.3746	22.7	2.99	0.0047	20.2	1.84	0.0004
17Jun	08	-4.8	5.0	0.3665	21.2	1.66	0.0001	19.8	0.74	0.0001
24Jun	15	29.5	12.5	0.0340	10.8	3.11	0.0042	18.1	0.49	0.0001
01Jul	22	1.1	13.6	0.9383	23.6	2.86	0.0001	23.8	0.48	0.0001
22Jul	43	15.5	10.2	0.1453	16.8	2.85	0.0001	21.1	0.56	0.0001
29Jul	50	8.2	15.5	0.6158	9.2	4.52	0.0815	11.5	0.76	0.0001
05Aug	57	.	.	.	.	.	.	8.1	.	.

[a] Days after date of 50% plant emergence.

[b] Significant at experimentwise error rate of 0.10

Table 16. Change in mean mass and area of leaflets samples vs. days duration of storage at 5°C before processing (DURAT) and minutes elapsed between drawing and weighing samples (ELAPSE). In all cases, n = 9 (3 plants x 3 samples)

DURAT	MEASURE	ELAPSE		SAMPLE MASS (g)		SAMPLE AREA (cm^2)		RATIO[a]	PLANT MASS[b]
		Mean	S.E.	Mean	S.E.	Mean	S.E.		
0	1	0.0	0.00	2.31	0.13	102.0	6.73	44.2	110.8
0	2	24.2	2.22	2.23	0.12	102.0	7.01	45.7	
0	3	51.6	1.13	2.17	0.12	100.1	6.10	46.1	
0	4	87.8	4.39	2.10	0.11	99.2	6.31	47.2	
4	1	0.0	0.00	2.13	0.08	94.1	4.31	44.2	110.9
4	2	28.0	0.97	1.99	0.07	93.8	4.23	47.1	
4	3	64.6	2.05	1.89	0.07	91.1	3.94	48.2	
4	4	122.6	4.13	1.76	0.06	88.2	3.68	50.1	
7	1	0.0	0.00	2.14	0.14	97.3	7.24	45.5	110.8
7	2	35.2	1.02	1.93	0.13	93.1	6.57	48.2	
7	3	71.0	4.17	1.81	0.12	91.3	6.79	50.4	
7	4	123.9	5.85	1.65	0.14	87.9	6.24	53.3	

[a] (sample area)/(sample mass)

[b] Mean plant mass (g) (remainder plus sum of sample weights to date)

Table 17. Summary of results of repeated measures analysis of variance testing effects of storage duration (DURAT, days) and time elapsed since sample was drawn (ELAPSE, min) on area, mass, and area : mass ratio of leaflet samples. Significance levels of first order orthogonal polynomials from repeated measures analysis of variance.

VARIABLE	AREAS	MASS	RATIO
DURAT	0.2995	0.0203	0.1005
ELAPSE	0.0001	0.0001	0.0001
DURAT*ELAPSE	0.0733	0.0815	0.6043

Table 18. Coefficients of multiple regressions of proportional change in area (cm^2), mass (g) and area:mass ratio of potato leaflet samples, vs. duration in storage (DURAT) and time elapsed (ELAPSE) since drawing sample and making measurement.

DEPENDENT VARIABLE	DURAT[a]	ELAPSE[b]	ELAPSE*DURAT[c]	$F_{3,32}$	r^2
AREA	-1.23×10^{-3}	-2.94×10^{-3}	-5.63×10^{-5}	19.3	0.64
MASS	-2.23×10^{-3}	-9.17×10^{-4}	-6.65×10^{-6}	130.7	0.92
AREA/MASS	1.59×10^{-2}	4.12×10^{-4}	9.33×10^{-5}	64.0	0.86

[a] Days in plastic bag at 5°C; Parameter units: (change in variable)·day^{-1}

[b] Seconds elapsed between initial measurement and measurement. Parameter units: (change in variable)·min^{-1}

[c] Parameter units: (change in variable)·min^{-1}·day^{-1}

Figure 32. Seasonal change in area:mass ratio of leaflets in plants from
    two fields in two years. Bars denote one standard error.
    Portage field was naturally infested with Colorado potato beetles;
    Campus plots were uninfested. Dates of median plant emergence were
    18 Jul 1986 and 19 Jul 1987.

<u>Symbols</u>:   Open diamonds,   Portage field 1986
                Filled diamonds,   Portage field 1987
                Open triangles,   Campus field 1986
                Filled triangles,   Campus field 1987
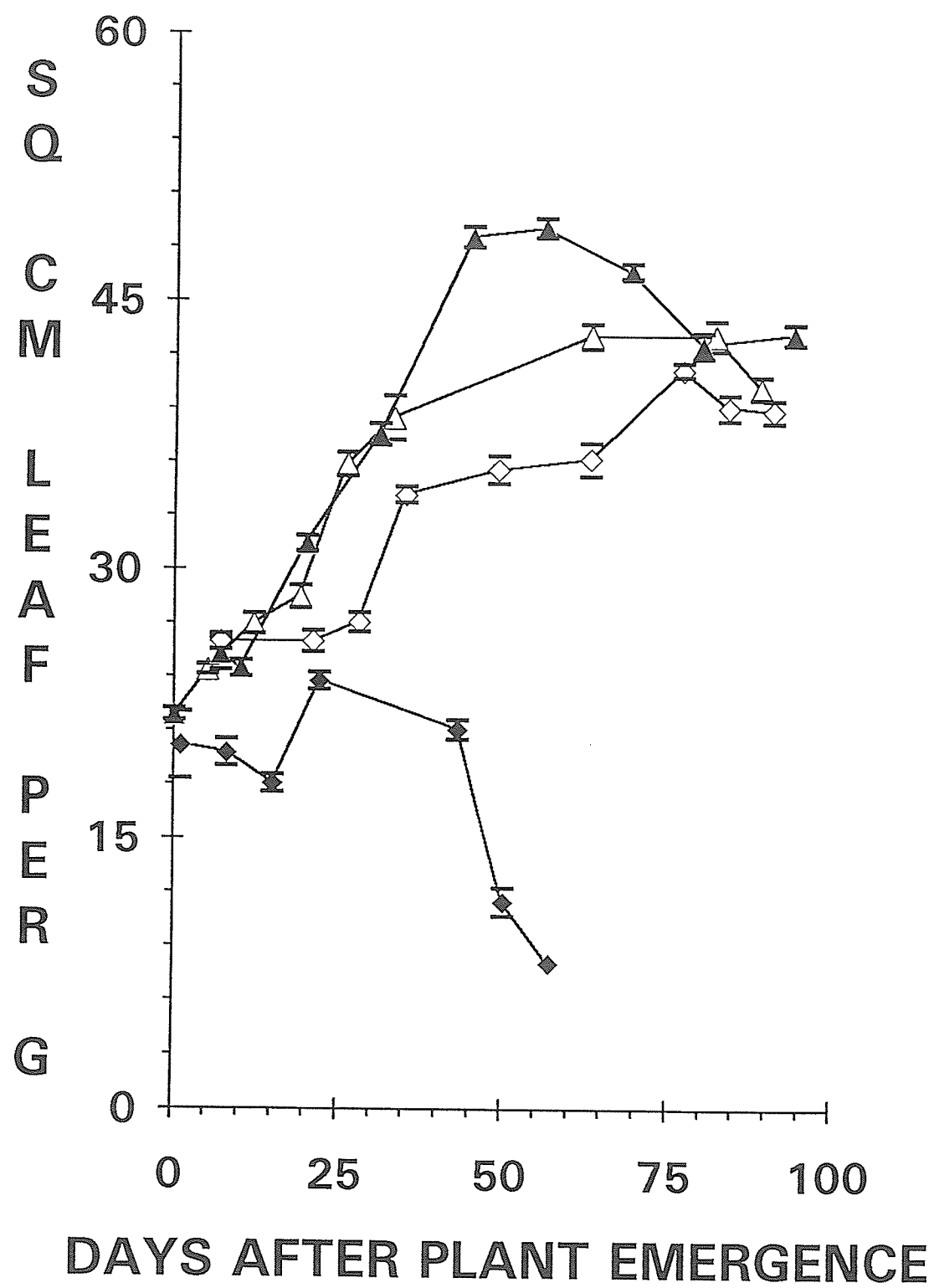
Figure 33.   Seasonal change in mean leaf area ($m^2 \cdot plant^{-1}$) $\pm$ 1 S.E.
    Standard errors of leaf area estimate per plant by date and field
    were estimated as S.E. of plant mass times point estimate of the
    ratio of leaflet area to leaflet mass for that date and field.
    Closed symbols: Portage field; filled symbols: Campus field.
    Dates of median plant emergence were 18 Jul 1986 and 19 Jul 1987.
    A) 1986
    B) 1987
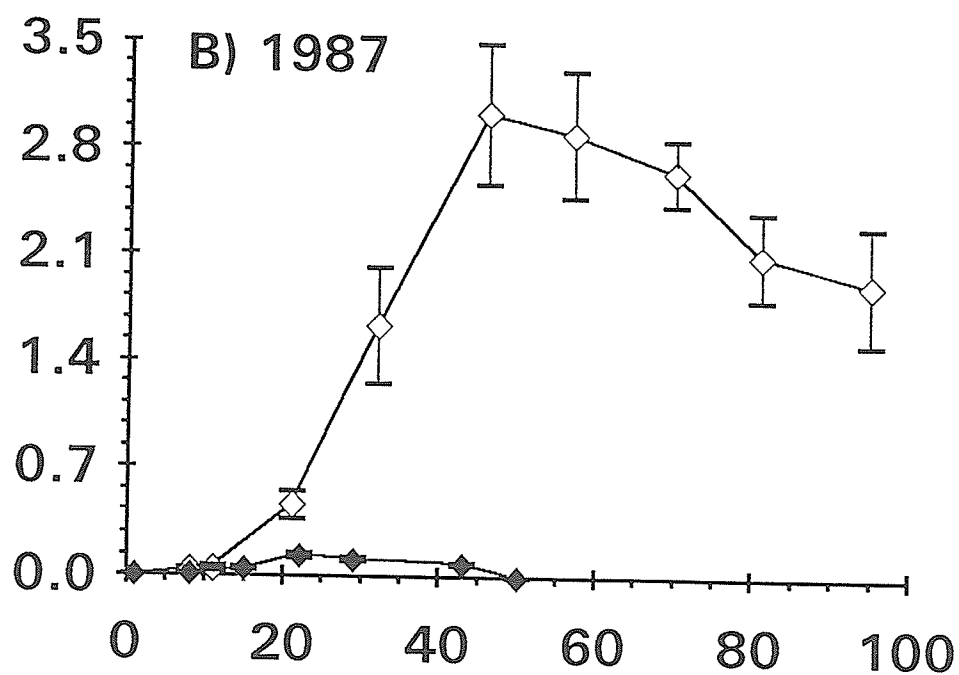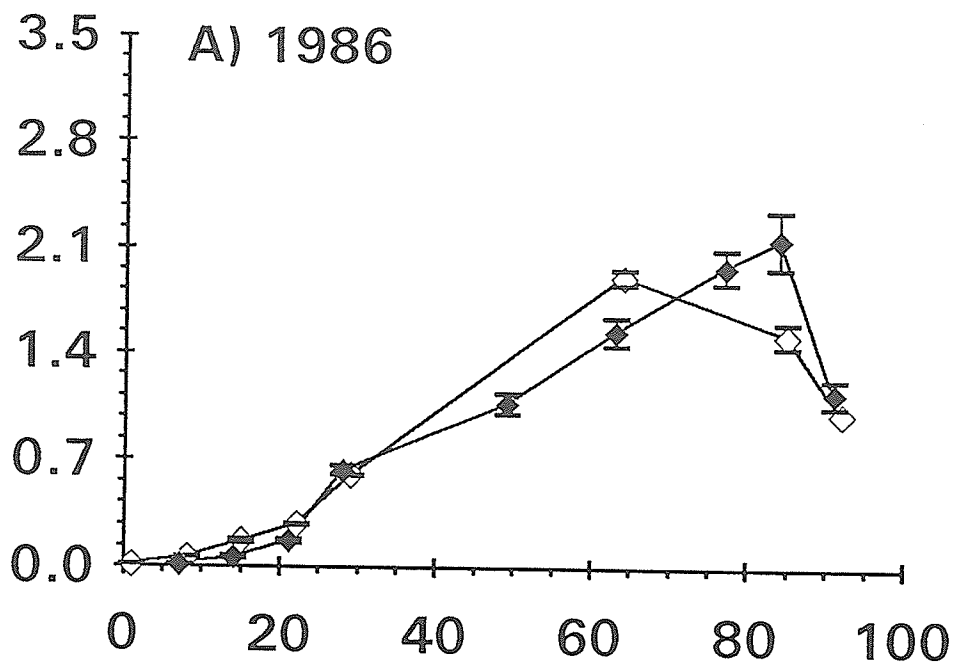
Section IV. Chapter C)
    VALIDATION OF MODELS OF FEEDING AND DEVELOPMENT BY COLORADO POTATO
    BEETLE LARVAE UNDER VARIABLE CONDITIONS IN FIELD CAGES IN SOUTHERN
    MANITOBA.

241

ABSTRACT

Populations of Colorado potato beetle larvae and adults on caged 'Russet Burbank' potato plants were adjusted weekly to a range of multiples of the mean number per plant in a naturally infested field. Detailed weekly records of population change were kept, and leaf areas were determined for each plant at harvest. These data were used to test models of temperature dependent development and feeding, which were developed in earlier chapters.

The performance of the developmental rate model was evaluated by comparing observed phenological trends to those predicted by the model. The model simulated population changes on a one week time scale. Modelled numbers consider only Colorado potato beetles which were larvae on the first day of the simulation. All larvae which started a simulation in the first or second instar reached the third or fourth instars, respectively, by the end of the simulation. Those which started in the third instar reached either the fourth instar or, more usually, the prepupal stage. All larvae which started the simulation in the fourth instar attained the prepupal stage.

The developmental rate model predicted more third instars and fewer fourths than were observed. The difference may result from relative sampling bias against third instars, or from errors in the functions which constitute the model.

The performance of the feeding rate model was assessed by summing daily feeding rate estimates on the caged plants and comparing this sum to

the difference in leaf area at harvest between infested and uninfested plants. This differences always exceeded the total leaf consumption estimate and they increased as estimated leaf consumption increased. The discrepancy is consistent with current understanding of potato plant growth, in which leaf area loss feeds back to reduce leaf growth. It could also result from the bias in estimation of developmental rates.

INTRODUCTION

Numerous authors (Tauber et al. 1988; Groden and Casagrande 1986; Walgenbach and Wyman 1984; Logan et al. 1985; Ferro et al. 1985; Tamaki and Butt 1978) have measured Colorado potato beetle development or feeding rate or both, at constant temperatures, but only the first three groups tested predictions from constant-temperature trials, under variable conditions. In all cases, the test applied only to developmental rates. Tauber et al. (1988) observed that development under field conditions was faster than predicted, as did Groden and Casagrande (1986) before applying a correction for behavioral thermoregulation (May 1981). Walgenbach and Wyman (1984) observed good agreement between observed and predicted rates.

Tauber et al. (1988), Groden and Casagrande (1986), and Walgenbach and Wyman (1984) all assumed a linear relationship between temperature and developmental rate, whereas this relationship is actually distinctly nonlinear (e.g. Logan et al. 1976). This simplification may explain the discrepancies in the results. A predictive algorithm which explicitly addresses the nonlinearity of the response is desirable.

There are no published studies in which feeding by Colorado potato beetles has been measured under naturally varying temperature conditions. This lack of information has necessitated the assumption that data collected under laboratory conditions apply to variable-temperature conditions (e.g. Dripps and Smilowitz 1989; Senanayake and Holliday 1990), but this assumption remains to be validated. Considering that defoliation is a very important cause of yield loss in potato plants (Takatori et al. 1952; Snyder and Michelson 1958; Murphy and Goven 1962; Beresford 1967;

Hare 1980; Cranshaw and Radcliffe 1980; Wellik et al. 1981) this gap in the knowledge should be filled.

Models of development and feeding rate were derived in Sections III C and D, which recognize the non-linear temperature-dependence of the responses, plus the effects microhabitat choice and the possible effects of insolative heating on body temperature (Section III, Chapter B). These models were partially verified under a spatiotemporally limited set of naturally varying conditions. The best measure of a model's generality is its predictive capacity under conditions well removed from those in which it was developed. Therefore, the main purpose of this chapter is to test these models under conditions of natural temperature variation, in circumstances well-removed geographically ($\approx$ 800 km), temporally (4 - 6 years) and seasonally (0 - 3 months) from the conditions under which the models were derived.

Limitations to knowledge on population processes of Colorado potato beetles circumscribe the type of validation currently possible. The models of field development pertain only to larvae, so it is only feasible to model the phenology of Colorado potato beetles which were larvae at the beginning of the simulation. Under field conditions, oviposition occurs over an extended period, and so new larvae are produced continuously. Without information on the time of oviposition, it is not possible to specify the time at which these larvae hatch, nor the time of subsequent moults. Thus, continuous oviposition in the field results in "noise" which obscures the observed phenological change, which is the signal used in evaluation of the development model.

To account for this noise under conditions in which oviposition proceeds naturally, a validated model is required which describes the time course of egg production. This model requires detailed information on: 1) the age- and temperature-dependence of egg production by adults; and 2) the temporal change in mean age distribution of adult population, which in turn requires detailed information on the time course of emergence from the soil for the spring and summer generations, and on age-dependent mortality in the adult population. None of this information is yet available for Manitoba populations, and so this approach is not yet possible.

Given currently available information, the developmental rate model can be tested only under conditions in which the effects of oviposition can be controlled. Thus I chose to test the model using population data from a cage trial, in which eggs were removed weekly. Larvae resulting from subsequent oviposition can be identified with certainty because they lag behind in development by at least the duration of the egg stage (> 3.5 days under constant optimal temperatures: Section I, Chapter A), compared to individuals which were larvae at the time the eggs were laid.

MATERIALS AND METHODS

This trial involved an experiment on caged 'Russet Burbank' potato plants. On each plant, numbers of adults and of each instar were adjusted weekly to one of a range of fixed multiples of the mean weekly population of that life stage as determined in a naturally infested field. These manipulations resulted in a range of infestation intensities, and final leaf areas. In each growing season, the Colorado potato beetle field

census occurred on Wednesday, insect numbers on plants collected (see below) were assessed on Thursday, and populations on the caged plants were adjusted on Friday.

The performance of the developmental rate model was assessed by comparing predicted phenological trends to those observed in the weekly census of the caged plants. The performance of the feeding rate model was assessed by summing daily feeding rate estimates on the caged plants and comparing this area to the difference in leaf area at harvest between infested and uninfested plants.

Estimation of weekly mean field population

Reference fields of potatoes (cv. 'Russet Burbank') were planted at the University of Manitoba Department of Plant Science field station at Portage la Prairie, Manitoba on 16 May 1985, 26 May 1986, and 20 May 1987 Fields consisted of 53 rows, 1 m apart and $\approx$ 65 m long. Fertilizer (23:14:14 [N:P:K]) was applied in-furrow at 500 kg·ha^{-1} in 1985 and 1986, and at 400 kg·ha^{-1} in 1987. Estimated dates of 50% plant emergence were 12 Jun 1985, 18 Jun 1986, and 09 Jun 1987.

Colorado potato beetles infestations occurred naturally in the reference fields. Populations were monitored by visual inspection and by whole-plant bag sampling (Byerly et al. 1978). The whole-plant sample bag, sampling method and details of sample processing were described in Senanayake and Holliday (1988), who worked with potato cv. 'Norland'; in the present study the bag was larger (1.5 m tall by 3.2 m in circumference) to accommodate the larger 'Russet Burbank' plants.

Samples were taken each week between plant emergence and harvest, from a 37 row by 49 m area in the centre of the field. Plants in the

sampled area were seeded 0.84 m apart (twice the normal spacing for 'Russet Burbank' plants in Manitoba) to facilitate whole plant bag sampling. Plant spacing does not affect the number of Colorado potato beetles per plant (Senanayake and Holliday 1988).

The sampled area was divided into 15 plots, each of 11 rows by 11 plants. To avoid the possibility that plants growing next to gaps in the canopy might harbor unrepresentative numbers of Colorado potato beetle larvae, a sampling protocol was developed which ensured that such plants could not be sampled. Only plants 2, 4, 6, 8 and 10 in rows 2, 4, 6, 8 and 10 were designated sampling candidates; these were numbered sequentially from 1 to 25. An independent random permutation of the numbers 1 to 25 was generated for each plot. In each week, one sampling candidate was harvested by whole plant bag sampling in each plot. Candidates were sampled in the order listed in the random permutation. If the sampling candidate chosen was absent or adjacent to a gap in the canopy, the next candidate in the permutation for that plot was substituted, and the frame-shift was maintained in that plot thereafter.

One plant per plot was sampled repeatedly over the season, by visual inspection. This plant was inspected leaf by leaf, and the numbers of egg masses, larvae of each instar, and adults were noted.

Each week, the mean numbers per plant of adults, eggs, and each instar were calculated for each sampling method. The means from bag sampling, defined as "field density" for that life stage on that week, were the basis for the populations maintained on the caged plants.

Manipulation of Colorado potato beetles populations in cages.

The caged plants used were located in plots on the University of Manitoba campus. 'Russet Burbank' seed pieces ($\approx$ 50 g) were sown on 27 May 1986, and 22 May 1987 at 2 m spacing in rows 3 m apart. No fertilizer was applied, and weeds were removed by hand. (This experiment was also tried in 1985, but because of problems associated with refinement of the procedure, results from that year are not presented.)

In each year, the experimental area consisted of seven rows. Rows consisted of 9 and 11 plants in 1986 and 1987, respectively. The outer rows, and the end plants in all other rows, were unused buffer plants. Of the remaining plants, some were selected as experimental units; these were enclosed in 1.22 m x 1.22 m x 1.0 m tall wood-framed cages covered by white 'Tergal' fabric, 28 mesh$\cdot$cm^{-1}.

Methods of selecting experimental plants differed among years. In 1986 all caged plants were in the planted array. Rows were considered to be blocks. Within a week after plant emergence, the six plants in each row which were considered most similar in size, were caged and treatments were assigned among them in a randomized complete block design. This procedure ensured within-block homogeneity; any differences in plant size among rows became the block effect.

In 1987, an infestation of red-backed cutworms (<u>Euxoa</u> <u>ochrogaster</u> (Guenée) (Lepidoptera: Noctuidae)) dictated that only three experimental blocks could be placed in the designated experimental area. Irregular plant emergence precluded blocking by rows; plants were instead blocked by size as follows. On 09 Jun 1987, $\approx$ 1 week after plant emergence, maximum dimensions of the haulms on all emerged plants were measured along three

mutually perpendicular axes, and the size of each was estimated by determining the volume of a prolate half-spheroid with these dimensions. Plants were assigned to three blocks of six plants whose estimated volumes were as similar as possible. Two additional experimental blocks were placed in a nearby plot of 'Russet Burbank' potato plants, in which potatoes had been planted at 0.45 m x 0.9 m spacing on the same day as those in the experimental array. Plants were chosen randomly from among those not within 2 m of either the plot edge or any previously-selected plant. These were measured and assigned to blocks by volume as just described. To allow caging, all other plants were cleared from a 2 m x 2 m square centred on each plant so chosen.

A further complication to the experimental protocol occurred in 1987. In that year, Colorado potato beetle populations were earlier than in previous years, and defoliated the reference field by 05 Aug, the eighth week after plant emergence. The Colorado potato beetle population declined to zero thereafter. For the remaining 5 weeks until harvest, Colorado potato beetle numbers on caged plants after 05 Aug 1987 were based on 1986 field densities, one week later in the season. This frame shift was chosen based on inspection of the comparative timing of the 1987 and 1986 population curves.

Each week, on each caged plant, the numbers of Colorado potato beetle adults and larvae of each instar were adjusted to one of a range of fixed multiples of field density. Multiples were 4.0, 2.0, 1.0, 0.5, and 0.0 in 1986 and 2.0, 1.0, 0.5, 0.25, and 0.0 in 1987. Two plants with infestation of 0.0 times field density were included per block.

Each week, all caged plants except one of the controls in each block, were inspected visually. The cage was tipped off the plant, and the numbers of adults, and each of instar on the plant were determined. Egg masses were removed when encountered. The population of each instar was adjusted to the required multiple of field density. Detailed records were kept of the number of adults and larvae on each plant at the beginning and end of each week, and of the numbers of insects of each stage which were added to or removed from each plant. Inspection always extended from ≈ 1200 h to ≈ 1600 h C.D.T. Colorado potato beetles are rather sessile, so escapes were not a problem. Insects used were obtained from a reservoir plot ≈ 100 m from the experimental area, and were held in a cooler without ice until needed (≈ 1 h).

Caged plants which became completely defoliated were harvested within one week; the remainder were harvested when commercial potato producers began to do so (19 Sep 1986, 11 Sep 1987). Leaf areas of most plants were estimated at harvest, using methods detailed in Section IV, Chapters A and B. Because of limitations to time and human resources, final leaf areas of plants receiving 0.5 times field density was not estimated in 1987.

Simulations

Colorado potato beetles were assumed to have the choice of two microclimates in the cage: in shade and in sun. Functions by which to estimate conditions in these microclimates were derived in August 1992 by measuring temperature and insolation above and below selected leaflets on

a 'Russet Burbank' potato plant in one of the field cages described above. This plant was contained in a 40 litre pot, which was buried to the brim.

Macroclimate data consisting of hourly temperature and opacity (tenths of sky covered by cloud) was obtained from the Environment Canada Weather office at the Winnipeg International airport, ≈ 15 km from the experimental site. Hourly estimates of insolation intensity at the top of the atmosphere were obtained using the astrometeorological estimator (Robertson and Russelo 1968).

Temperature and insolation in the microclimates above and below the leaflets in the cages were estimated using methods described in Section III, Chapter A, using data provided in appendix 8. A nonlinear (asymptotic) function (equation 4') was used to estimate microclimate temperature (MICRO) above and below leaflets within the cages, from macroclimatic temperature (MACRO) and measured insolation (P).

$$MICRO = MACRO + \frac{K_{c,p}}{1 + \exp(-(\alpha_{c,p} + \beta_{c,p} \cdot P_{h,d}))} - \Gamma_{c,p} \qquad (4')$$

Parameters and variables are explained in Section III, Chapter A. Parameter values were estimated by iterative nonlinear regression (PROC NLIN, SAS Institute 1988) as outlined in Section III, Chapter A), and were as follows. Above the leaflet: $K = 6.461$, $\alpha = -1.360$, $\beta = 0.0278$ and $\Gamma = 0.000$ ($F_{1,14} = 2844$, $P \le 0.0001$; $r^2 = 0.99$). Below the leaflet: $K = 7.650$, $\alpha = -0.700$, $\beta = 0.0200$ and $\Gamma = 1.101$ ($F_{1,14} = 2070$; $P \le 0.0001$; $r^2 = 0.99$).

Measured insolation intensity above and below cages leaflets ($P_{c,p,h,d}$) were estimated from measured insolation outside the cage ($P_{h,d}$)

using equation 6. The function used to estimate $P_{h,d}$ was provided in Section III, Chapter A.

$$P_{c,p,h,d} = \mu_{c,p} \cdot P_{h,d} \qquad (6)$$

Above the leaflet, $\mu = 0.576 \pm 0.0086$ ($F_{1,31} = 449$; $P \leq 0.0001$; $r^2 = 0.99$). Below the leaflet, $\mu = 0.144 \pm 0.0024$ ($F_{1,31} = 3525$; $P \leq 0.0001$; $r^2 = 0.99$).

The model version (coded 2.2) which incorporates the possible effect of insolative heating and behavioral thermoregulation on body temperature, was assembled as detailed in Section III, Chapters C and D, incorporating these field-cage specific parameters. This model was used to estimate development and feeding rates of the Colorado potato beetles in the cages.

All simulations started and ended at 1400 h C.D.T. on Friday, the midpoint of the interval during which larvae were placed on the plants. Hourly feeding or development increments were calculated simultaneously for each instar, from temperature, opacity, and insolation at the top of the atmosphere, as outlined in Section III, Parts C and D, respectively. All functions were iterated hourly, but the output exceeded the memory of the computer, so to make the process computationally tractable, the hourly increments were pooled into 1 day increments.

1) Developmental rates The model was initialized weekly with the numbers of larvae of each instar on plants receiving each treatment, and each simulation ran for one week. At the beginning of the simulation, each larva was assigned to one of four cohorts (one for each instar) and the simulated development of these cohorts were followed through the week. Because initial tests of the model (Section III, Chapter D) revealed that

it consistently underestimated developmental rate by $\approx$ 9%, each instar was assumed to last 0.91 stadia (vs. 1.0 for an unbiased model).

At the start of each weekly simulation, all larvae were assumed to be at the midpoint of their stadium and the development counter for each cohort was initialized at 0.455 stadium before accumulation of the first developmental increment. On the first day of the simulation, one half of the calculated daily developmental increment was added to the development counter; thereafter, the full daily increment was added to this counter daily, until the final day, on which one half of the daily estimated increment was added. The use of half increments on the first and last days is consistent with the population assessments occurring between 1200 and 1600 h, the warmest part of the day. When the developmental counter for a given cohort reached or exceeded 0.91, all larvae in the cohort were promoted to the next instar and the cohort's development counter was reinitialized to 0. Any daily developmental increment in excess of the amount required for moult from an instar was converted to a proportion of the day's development rate increment in that instar, and the same proportion of the day's developmental increment for the newly-attained instar was added to the reinitialized development counter after moult. Cohorts which became prepupa were removed from the simulation, because prepupae are subterranean and are not observed in the normal census. Modelled numbers of larvae of each instar were output on the last day of each week. These were compared to observed numbers.

2) Feeding rates   The larval feeding rate simulation proceeded simultaneously with the developmental rate simulation. Each day, the

numbers of each larval instar, as output by the developmental rate model, were converted to feeding increments.

Although the first and second instars observed at the end of the week could not result from the larvae in the cage at the beginning of the week, and were thus irrelevant to the test of the developmental rate model, they did feed. Feeding by these larvae was obtained by assuming that these larvae were at the midpoint of the stadium at week's end, running the developmental rate model backward until the larvae returned to the egg, then summing the appropriate feeding rate increments.

Because the test of the model involves comparing the consumption estimate to the difference in final leaf area at harvest with respect to uninfested control plants, adult feeding should not be neglected. An estimate of adult feeding was obtained by trapezoidal approximation using adult populations at the beginning and end of each week, and a feeding rate estimate of 500 $mm^2 \cdot day^{-1} \cdot adult^{-1}$, i.e. approximately the mean rate over temperatures calculated from data given by Ferro et al. (1985). I considered that any attempt at greater precision, for example by incorporating temperature-dependence in the estimate, would be indefensible because of the age-dependence of adult feeding (Tamaki and Butt 1978), coupled with uncertainty regarding age distribution of the adult population in the cages.

Feeding rate increments of larvae and adults were summed over the season to estimate total leaf area consumption on plants of each treatment. Estimated consumption was compared to the difference between leaf areas of infested and uninfested plants at harvest.

RESULTS AND DISCUSSION

Field population trends

Data describing seasonal trends in Colorado potato beetle field density in the reference fields in the three years, as determined by whole plant bag sampling and visual assessment, are given as means and standard errors for each instar in Table 19. An illustration of the typical yearly trend in numbers of adults, eggs and larvae, is provided in Fig. 34. For clarity, age groups are presented in separate panels, and standard error bars are not included. The number of eggs is estimated by multiplying the number of egg masses by 30 eggs·mass^{-1}, the average number of eggs per mass, as observed in several studies (e.g. Harcourt 1971; Lactin, unpublished data).

Both sampling methods detected peak numbers of each instar which exceeded peak numbers of the preceding instar. Senanayake and Holliday (1988) observed a similar trend. Where stadia are similar, as in instars 1 to 3 (Section II, Chapter A; Section III, Chapter D), peak sample densities should be the same for the instars if no mortality occurs, or should decrease if mortality does occur. The increasing peak heights suggest that both sampling methods are less than perfectly efficient for these instars, and that this inefficiency is greater for smaller instars. Walgenbach and Wyman (1984) also noted difficulty in detecting first and second instar larvae.

In 1985 and 1986, a small peak of adults in the spring was followed by peaks of eggs and larvae of each instar, followed by a peak of summer adults which exceeded the spring peak. Small second peaks of first and

second instars occurred in both years, but this second generation was not completed. In 1987, peak numbers of adults and larvae each instar were earlier than in 1985 and 1986, and the plants were completely defoliated by the eighth week after 50% plant emergence, after which the pest population also died out. The observed population trends corroborate the results of Cole (1951) in that Colorado potato beetles are univoltine in Southern Manitoba.

Population estimates by the two sampling methods differed in all instars, but the relationship between the estimates by the two methods was linear and relatively consistent. Parameter estimates of regressions of visual counts on whole-plant bag sample counts are given in table 20. Depending on instar, visual sampling detected only 74.5 to 84.7% as many larvae as did whole plant bag sampling. This result is similar to that of Senanayake and Holliday (1988), who found that visual sampling detected only ≈ 69% as many larvae as did whole-plant bag sampling.

Simulation results

Developmental rate

General results of the simulation model were relatively consistent. All larvae which started the week's simulation in the first or second instar reached the third or fourth instars, respectively, by the end of the simulation. Those which started the week in the third instar reached either the fourth instar or, more usually, the prepupal stage. All larvae which started the simulation as fourth instars reached the prepupal stage.

Modelled numbers consider only Colorado potato beetles which were larvae on the first day of the simulation. Observed Colorado potato beetle numbers on caged plants at the end of each week included

substantial numbers of first and second instar larvae; these most likely descended from eggs laid by adults during the week, a process not considered in the simulation algorithm. The presence of first and second instar larvae is irrelevant to the purpose of this section, which is to compare estimated and observed population changes among larvae which were on the caged plants at the beginning of the week. Therefore, these instars are ignored hereafter. Eggs laid during the simulation would require 7.2 days to reach instar 3 even where temperature remained constant at the optimum for development (Section II, Chapter A), thus none of the observed third instars originated from such eggs.

Plots of modelled numbers of instars 3 and 4 against observed numbers are presented in Fig. 35A and B, respectively. Each point represents the weekly mean number on the five plants receiving a given treatment. Lines representing linear regression of modelled on observed larval numbers, and 1:1 agreement are included. Parameter estimates of the regressions of modelled on observed numbers are presented in table 21. These regressions exclude data from the control cages, in which both modelled and expected numbers are zero; this artifactual agreement is not relevant to the performance of the model.

In instar 3, the regressions of modelled on observed numbers did not differ significantly in the two years. The intercept was significantly greater than 0 in 1986 but not in 1987; the slope of the regression was very similar in the two years, and in both years, it was significantly greater than 1. In instar 4, the regressions of modelled on observed numbers did differ significantly in the two years. The intercepts differed significantly among years (P < 0.05), but the slopes did not.

The intercept was significantly greater than 0 in 1986, but not in 1987. The slope of the regression was significantly greater than 0 in both years; it was significantly less than 1 in 1986, but not significantly different from 1 in 1987. The slopes do not differ significantly between years.

Regression of totals of modelled and observed instars 3 and 4 also differed among years. The intercept was significantly greater than 0 in both years. The slope was significantly greater than 1 in 1987 but not in 1986. Thus, the model predicted approximately the right number of larvae in 1986, but more than the observed number in 1987.

Thus, overall, these regression results indicate that fewer instar 3 larvae are observed than are predicted by the model, that the reverse relationship occurs in instar 4, and that the model predicts either the right number, or slightly too many larvae.

These results have several plausible explanations. First, in the population trend data from the naturally-infested field, the observed peak number of each instar exceed that of the previous instar (Fig. 34; table 20). This result was interpreted to mean that the sampling process is inefficient, and that this inefficiency is greater in earlier instars. This sampling bias probably also occurs on the caged plants, and thus the lower number of observed third instar larvae, compared to that predicted by the model, may be a result of sampling bias against third instars, compared to fourths. This does not seem to be an important possibility, because the total of thirds and fourths is roughly correct; bias would reduce the observed total compared to the modelled value.

Most probably, the source of the disagreement resides within the simulation model. The observed results can be explained if development of the modelled population is slightly slower than that of the actual population, with consequent enrichment of the third instar, relative to the fourth, at the end of each simulation. The most obvious possibility is that the assumption that larvae moult when the development counter reaches 0.91 stadia, might be erroneous. I did not explore this possibility because arbitrarily adjusting parameters in the absence of data, simply to improve the fit of the model, is not defensible.

A related possibility is that the bias may result from the assumption that larvae were at the midpoint of their instar at the start of the simulation. This assumption is probably reasonable on average, but for a specified weekly simulation, it is unlikely to be correct. The scatter of data points around the regression lines (Fig. 34) probably contains a component attributable to the imprecision of this assumption, but to generate the observed bias, this assumption must contain a systematic error. Simulations in which larvae were assumed to be initially at the 25th or 75th percentiles in their development, revealed that this possibility did not explain the bias.

A further possibility is that one or more of the functions which comprise the model may be in error. This possibility was tested in a small number of simulations in which parameter estimates were varied in these functions. The output was relatively insensitive to changes in the parameters of the equations which estimate microclimate temperature and insolation, but was affected by changes in the equation describing behavioral response to T^* (data are not presented). These results are

consistent with the importance of behavioral thermoregulation in determining body temperature and buffering poikilotherms against variation in temperature and insolation (Stevenson 1985).

These alternative possible explanations for the disagreement between the model output and the observations are not mutually exclusive. The possibilities cannot be evaluated with the present information. Definitive assessment of the degree of bias in detection of the various instars would help assess the first possibility.

The only defensible conclusion is that the model predictions of numbers of instars 3 and 4 after each simulation are fairly close to those observed. In its imperfect performance, the model helps suggest where more data are needed.

Feeding rate

Temporal patterns of modelled feeding rate in cages varied among years; Fig. 36 illustrates the trend for plants receiving infestation of 1.0 times field density. A more complete dataset is given in appendix 9. In both 1986 and 1987, two defoliation peaks occurred; these were attributable to larval and adult feeding, sequentially. Corresponding peaks had approximately the same height in both years, but were about one week earlier in 1987 than in 1986.

Fig. 37 gives mean final leaf areas by treatment, and final leaf areas with estimated total larval feeding and estimated adult feeding added, from 1986 and 1987. Standard errors are omitted for clarity; they are listed in appendix 9. In all cases, the difference between final leaf area of control and infested plants exceeds estimated total leaf

consumption, and this discrepancy increases with estimated leaf consumption.

Clearly, observed reduction in potato leaf exceeds the estimated amount of leaf area consumed. At least six explanations are possible for this unaccounted leaf area deficit.

(1) The estimates of larval feeding rates may be low. This is not likely because the estimates have been shown to be realistic under field conditions (Section III, Chapter C).

(2) The error may result from the assumption that the larvae are at the midpoint of their instar at the start of each simulation. In a series of simulations in which larvae were assumed to be initially at the 25th or 75th percentiles in development, total larval leaf consumption changed by less than 10% (data not presented) Thus, this possibility is unimportant.

(3) Estimates of adult feeding may be low. This possibility was tested by increasing the estimated rate to 800 $mm^2 \cdot day^{-1}$. The discrepancy between total estimated feeding and the difference between final leaf area of infested and uninfested plants was eliminated in 1986, but not in 1987. This may be part of the answer, but the arbitrariness of the approach is somewhat unsatisfying.

(4) The bias in the modelled larval distribution to favor third instars over fourths, would translate to an underestimate of feeding.

(5) Feeding lesions may expand after they are inflicted (Lowman 1987), particularly when the Colorado potato beetles feed on young, growing tissue. This possibility should be tested, and cannot be eliminated on present evidence.

(6) Leaf area removal may feed back to reduce subsequent leaf growth by reducing the rate of photosynthate accumulation, and by reducing the ability of the leaves to compete with other tissues for photosynthate. This possibility is consistent with several potato growth models which incorporate feedback loops in tissue growth and photosynthate partitioning (Fig. 1; Ng and Loomis 1984; Fishman et al. 1985; Johnson et al. 1988). Unfortunately, in none of these models has the leaf area estimation submodel been validated, so none can be used to test this conjecture. Considering the potential importance of this effect to tuber production, these submodels should be validated. New rapid methods of measuring leaf area (this thesis, Section IV, Chapters A and B) should expedite this process.

Explanations 5 and 6 are consistent with the observation that the unaccounted leaf area deficit was greater in 1987 than 1986, because the earlier timing of injury in 1987 would increase the possible effects of lesion expansion, and long-term disruption of photosynthate partitioning.

In summary, feeding estimates generated by the model are too low to account for the leaf area reduction in the infested plants. The disagreement between estimated total leaf consumption on one hand, and the difference between leaf area of infested and control plants on the other, is in a direction consistent with current understanding of potato plant growth. Alternatively, it could also be a consequence of the biased performance of the developmental rate model. As with the developmental rate model, the imperfect performance of the feeding rate model helps suggest where more data are needed.

Possible improvements in the models.

As currently formulated, there are limits to the precision of the model estimates. These can be grouped into internal and external types.

Internal limitations pertain to the functions which constitute the predictive model, i.e. the temperature-dependent developmental rate and feeding rate functions, the formulae used to estimate microclimatic temperature and insolation from macroclimatic data, the thermoregulatory behavior model, and the function which defines the apparent effect of insolation on body temperature. Each of these functions might be made more precise through collection of additional data.

I strongly suspect that the constant-temperature developmental rate functions may not apply well to the variable conditions in which the model runs. This possibility was discussed more fully in Section II, Chapter B, and Section III, Chapter D. The necessary assumption that larvae moult when 0.91 stadium has been completed is a consequence of this possible inapplicability. Characterization of developmental response of Colorado potato beetle larvae to varying temperatures, and particularly, to brief exposure to high temperatures, is desirable.

The external limitation is the assumption that larvae at the beginning of the simulation all were at the midpoint of their stadium when the simulations started. This is a crude approximation, but it cannot be circumvented, because the solution of rearing larvae for release would not be cost-effective. Nonetheless, because the model is intended to be used to forecast population trends in naturally occurring Colorado potato beetle infestations, where uncertainties of this type are unavoidable, this approximation is indicative of those which are required in the real

world.   Thus, the precision of the model as currently formulated seems
representative of that obtainable under the conditions in which the model
is intended to be used.

Table 19. Counts of Colorado potato beetle adults, eggs, and larval instars obtained by visual and whole plant bag sampling of Colorado potato beetle populations on 'Russet Burbank' potato plants, 1985 to 1987. (Mean number ± S.E. of life stage per plant. n = 15 plants per sample date.)

Part 1 of 3. 1985

a) VISUAL SAMPLES

DAE[a]	ADULTS		EGGS		LARVAL INSTARS							
					FIRST		SECOND		THIRD		FOURTH	
	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.
7	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
14	0.3	0.2	6.0	4.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
21	0.3	0.2	12.0	5.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
28	0.7	0.3	16.0	8.7	7.3	3.7	1.9	1.7	1.8	1.5	0.7	0.7
35	0.5	0.2	26.0	6.5	7.7	3.8	14.5	4.9	6.8	2.3	7.8	3.0
42	0.4	0.2	6.0	3.2	5.2	2.5	9.4	2.9	14.9	4.1	22.9	6.3
49	0.1	0.1	10.0	4.8	2.3	1.8	9.4	3.5	11.4	3.6	20.7	4.2
56	5.8	1.3	2.0	2.0	1.1	1.1	0.5	0.4	2.5	0.8	10.1	3.4
63	13.9	2.6	0.0	0.0	0.5	0.4	0.5	0.2	0.4	0.2	3.2	0.7
70	22.4	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.3	0.9	0.3
77	18.2	2.5	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.0	0.5	0.4
84	13.4	1.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.2
91	20.1	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1
98	7.9	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1

b) WHOLE PLANT BAG SAMPLES

DAE	ADULTS		EGGS		LARVAL INSTARS							
					FIRST		SECOND		THIRD		FOURTH	
	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.
7	0.5	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
14	0.1	0.1	18.0	9.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
21	0.4	0.2	34.0	14.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
28	0.1	0.1	48.0	13.4	12.2	7.3	2.9	1.5	1.9	1.1	0.9	0.7
35	0.1	0.1	34.0	12.0	9.1	5.6	13.6	6.3	18.6	6.4	15.1	5.8
42	0.0	0.0	8.0	3.5	1.4	1.1	13.8	5.0	12.5	5.2	30.7	9.6
49	0.1	0.1	4.0	2.7	0.3	0.2	6.3	3.7	12.7	4.6	21.8	6.3
56	4.6	1.0	16.0	5.8	0.2	0.1	1.1	0.9	2.1	0.6	6.7	1.8
63	9.0	1.3	10.0	6.3	2.9	2.6	0.7	0.2	1.9	0.6	3.1	0.8
70	15.5	2.1	12.0	4.9	0.1	0.1	0.9	0.3	0.4	0.2	1.5	0.3
77	11.3	1.5	0.0	0.0	0.0	0.0	0.2	0.2	1.3	0.5	0.0	0.0
84	7.8	1.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.2
91	8.4	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.2
98	4.3	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.0

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[a] Days after 50% plant emergence

Table 19 (cont'd). Counts of Colorado potato beetle adults, eggs, and larval instars obtained by visual and whole plant bag sampling of Colorado potato beetle populations on 'Russet Burbank' potato plants, 1985 to 1987. (Mean number ± S.E. of life stage per plant. n = 15 plants per sample date.)

Part 2 of 3. 1986

a) VISUAL SAMPLES

									LARVAL	INSTARS		
DAE	ADULTS		EGGS		FIRST		SECOND		THIRD		FOURTH	
	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.
14	0.2	0.1	28.	8.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
21	0.5	0.2	44.	11.7	1.7	1.6	0.1	0.1	0.0	0.0	0.0	0.0
28	0.5	0.2	28.0	8.5	7.1	2.8	6.9	2.6	5.3	1.8	0.5	0.2
35	0.3	0.1	6.0	3.2	8.5	3.7	10.3	2.9	13.0	4.3	7.2	2.6
42	0.4	0.2	8.0	3.5	12.6	4.9	11.4	3.7	12.4	4.1	15.7	2.5
49	0.6	0.2	26.0	10.9	1.3	0.8	2.9	1.1	5.8	1.4	23.1	5.3
56	5.7	1.1	32.0	10.7	7.3	2.8	4.3	1.1	3.5	0.9	9.7	1.7
63	12.6	1.9	8.0	4.6	2.7	1.4	5.3	1.4	3.8	1.0	3.7	0.9
70	24.7	3.2	6.0	3.2	0.8	0.4	2.0	0.6	1.5	0.7	4.1	1.2
77	25.0	3.4	4.0	2.7	1.6	1.4	1.0	0.4	1.3	0.4	1.5	0.4
84	15.3	2.3	2.0	2.0	0.6	0.6	0.3	0.2	1.1	0.5	1.5	0.5
91	13.3	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.2	0.8	0.3
98	3.6	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1

b) WHOLE PLANT BAG SAMPLES

									LARVAL	INSTARS		
DAE	ADULTS		EGGS		FIRST		SECOND		THIRD		FOURTH	
	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.
14	0.6	0.3	12.0	4.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
21	0.6	0.2	24.0	6.7	1.4	1.0	0.0	0.0	0.0	0.0	0.0	0.0
28	0.8	0.3	44.0	10.9	6.7	2.8	1.3	0.9	1.0	0.4	0.1	0.1
35	0.3	0.2	28.0	8.5	7.0	2.8	11.1	3.9	14.9	4.9	3.5	1.8
42	0.1	0.1	20.0	10.4	5.7	3.1	14.0	5.0	16.7	4.3	12.9	3.5
49	0.2	0.1	14.0	8.2	5.9	3.9	9.3	4.4	10.9	4.2	24.9	6.0
56	4.3	0.9	56.0	17.5	6.3	3.3	1.1	0.6	4.8	1.9	8.9	2.7
63	13.4	2.1	46.0	11.3	3.7	1.9	1.7	0.6	2.0	0.6	3.4	0.6
70	26.9	3.1	12.0	4.9	1.7	1.3	1.5	0.8	2.6	1.3	2.3	0.6
77	25.8	3.4	2.0	2.0	1.1	0.5	0.9	0.3	2.5	0.7	1.9	0.6
84	13.5	1.9	0.0	0.0	0.1	0.1	0.8	0.6	0.5	0.3	0.6	0.2
91	5.4	1.1	8.0	8.0	0.0	0.0	0.1	0.1	1.0	0.3	0.8	0.2
98	0.6	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Table 19 (cont'd). Counts of Colorado potato beetle adults, eggs, and larval instars obtained by visual and whole plant bag sampling of Colorado potato beetle populations on 'Russet Burbank' potato plants, 1985 to 1987. (Mean number ± S.E. of life stage per plant. n = 15 plants per sample date.)

Part 3 of 3. 1987

a) VISUAL SAMPLES

| | | | | | LARVAL INSTARS | | | | | | |
| | ADULTS | | EGGS | | FIRST | | SECOND | | THIRD | | FOURTH | |
DAE	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.
12	0.6	0.2	78.0	16.8	0.7	0.7	0.0	0.0	0.0	0.0	0.0	0.0
19	0.3	0.2	78.0	17.3	13.9	5.4	8.9	2.2	9.2	4.1	0.3	0.2
26	0.7	0.2	54.0	16.1	7.7	2.4	9.0	2.9	10.1	3.2	15.3	2.8
33	0.1	0.1	6.0	4.3	8.5	4.1	19.5	7.8	9.9	1.8	12.5	1.8
40	0.7	0.2	12.0	4.9	2.7	1.7	6.5	2.2	13.8	4.7	16.5	3.3
47	9.9	2.5	8.0	4.6	0.1	0.1	1.3	0.7	2.3	1.0	9.6	3.0
54	8.0	2.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.2
61	0.7	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

b) WHOLE PLANT BAG SAMPLES

| | | | | | LARVAL INSTARS | | | | | | |
| | ADULTS | | EGGS | | FIRST | | SECOND | | THIRD | | FOURTH | |
DAE	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.
12	0.4	0.2	76.0	20.9	1.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0
19	0.5	0.2	56.0	8.2	13.5	3.4	10.6	4.3	16.0	6.0	2.4	2.4
26	0.6	0.2	40.0	12.0	11.8	6.1	13.9	3.8	8.7	2.8	18.6	6.6
33	0.5	0.2	24.0	9.4	5.7	2.4	6.7	2.8	14.0	4.9	22.4	5.3
40	0.7	0.3	60.0	27.2	10.0	4.1	12.6	3.5	13.6	2.5	27.7	4.2
47	5.9	2.0	4.0	4.0	1.9	1.1	3.9	3.0	3.9	2.4	6.1	2.1
54	3.9	1.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.2
61	0.4	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Table 20. Parameter estimates ($\pm$ S.E.) of regressions of mean visual counts on whole plant bag sample counts, for age classes of Colorado potato beetle on 'Russet Burbank' potato plants.

AGE CLASS	REGRESSION WITH INTERCEPT						REGRESSION WITHOUT INTERCEPT			r^2
	INTERCEPT			SLOPE			SLOPE			
	EST	S.E.	p(EST=0)	EST	S.E.	p(EST=1)	EST	S.E.	p(EST=1)	
1[1]	1.026	0.910		0.715	0.144		0.837	0.095		0.78
2	1.413	1.107		0.713	0.147		0.847	0.104		0.74
3	0.767	0.744		0.684	0.0818	**	0.745	0.0564	***	0.88
4	1.127	0.660		0.728	0.0535	***	0.785	0.0430	***	0.93
Adults	1.369	0.627	*	1.075	0.0745		1.168	0.0646	*	0.91

NOTE: All slopes significantly greater than 0.
* $p \le 0.05$
** $p \le 0.01$
*** $p \le 0.001$

---

[1] 1 = first instar, ...4 = fourth.

Table 21. Parameter estimates of regressions of numbers per instar predicted by developmental rate model, on observed numbers. (ns, not significant; *, $p \leq 0.05$; **, $p \leq 0.01$; ***, $p \leq 0.001$).

INSTAR 3

	INTERCEPT			SLOPE		P(SLOPE=)		F	df	r^2
						0	1			
1986	1.86	0.71	*	1.65	0.17	***	***	89.4	1,46	0.66
1987	0.21	0.78	ns	1.64	0.19	***	***	73.2	1,45	0.62

INSTAR 4

	INTERCEPT			SLOPE		P(SLOPE=)		F	df	r^2
						0	1			
1986	2.29	0.69	**	0.78	0.05	***	***	272.9	1,46	0.86
1987	-0.71	0.82	ns	0.87	0.08	***	ns	125.7	1,46	0.73

TOTAL LARVAE

	INTERCEPT			SLOPE		P(SLOPE=)		F	df	r^2
						0	1			
1986	4.02	1.20	**	1.01	0.07	***	ns	223.2	1,46	0.83
1987	-1.55	1.20	ns	1.22	0.09	***	*	195.4	1,46	0.81

TESTS OF YEAR EFFECTS

	P(intercepts equal)	P(slopes equal)
Instar 3	0.1206	0.9477
Instar 4	0.0064	0.2907
Instars summed	0.0016	0.0711

Figure 34.   Time trend in mean numbers of Colorado potato beetles per plant in insecticide-free plot, Portage la Prairie 1985. Estimates by whole plant bag sampling.

    a) eggs (EG) and adults (AD)
    b) first (L1) and second (L2) instar
    c) third (L3) and fourth (L4) instar
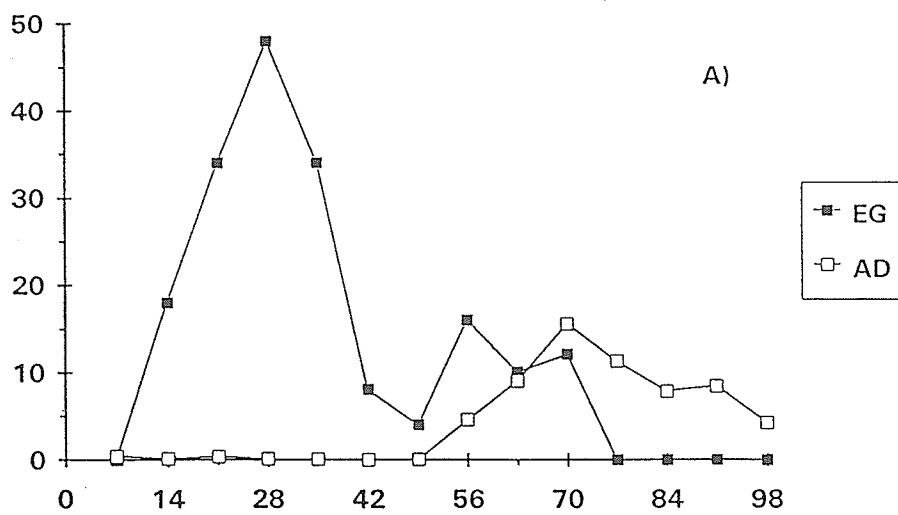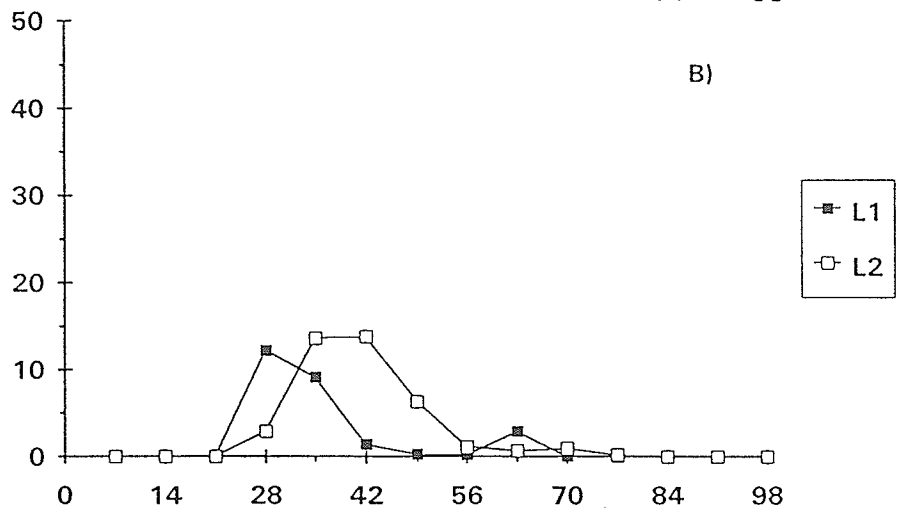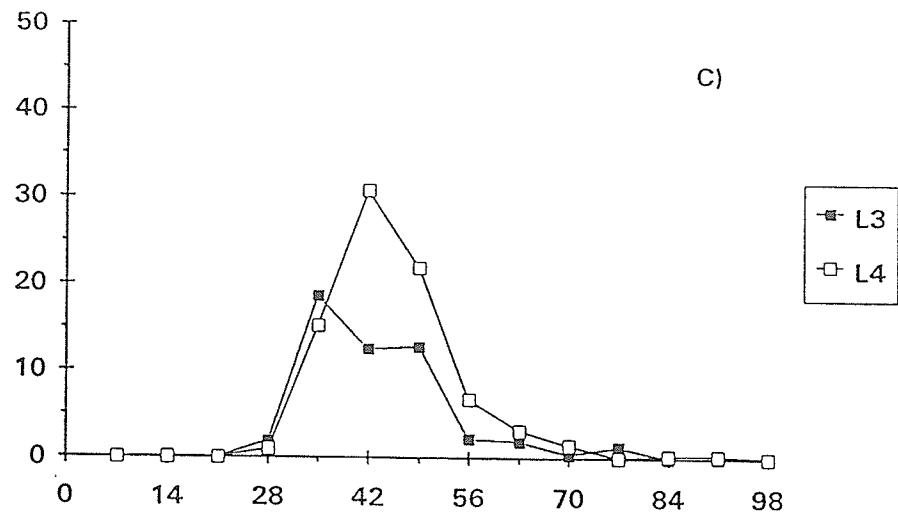
Figure 35. Comparison of modelled and observed numbers of Colorado potato
beetle larvae on caged plants, University of Manitoba campus. Each
point represents the weekly mean of five plants.
A) third instar
B) fourth instar

Filled squares = 1986; open squares = 1987;
Broken lines = regression lines, labelled with year; Solid line =
1:1 agreement

A) INSTAR 3

B) INSTAR 4

MODELLED NUMBER
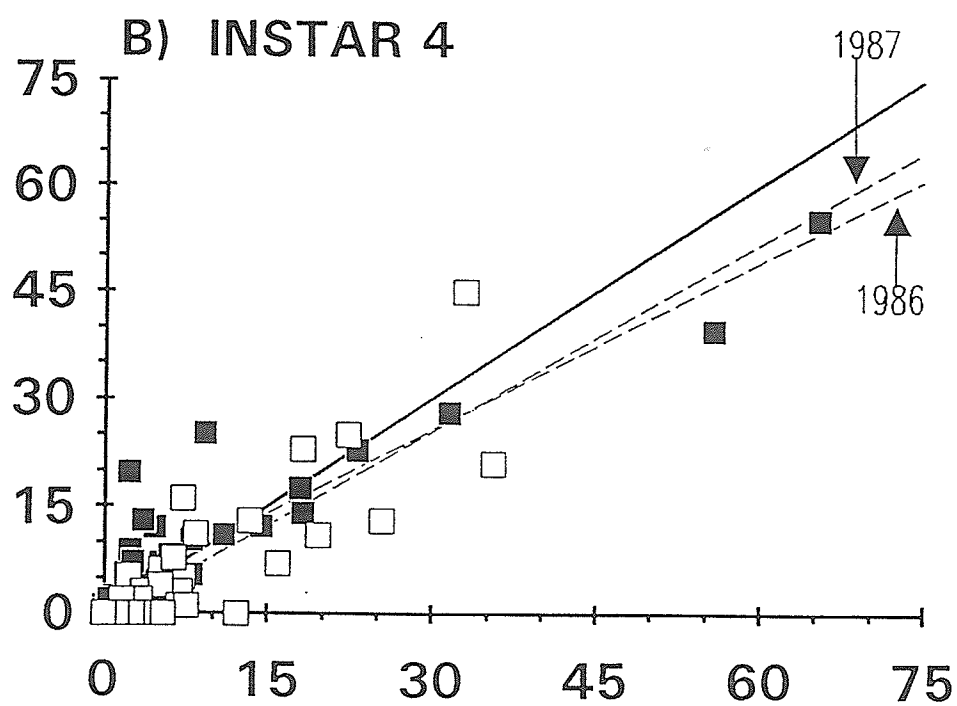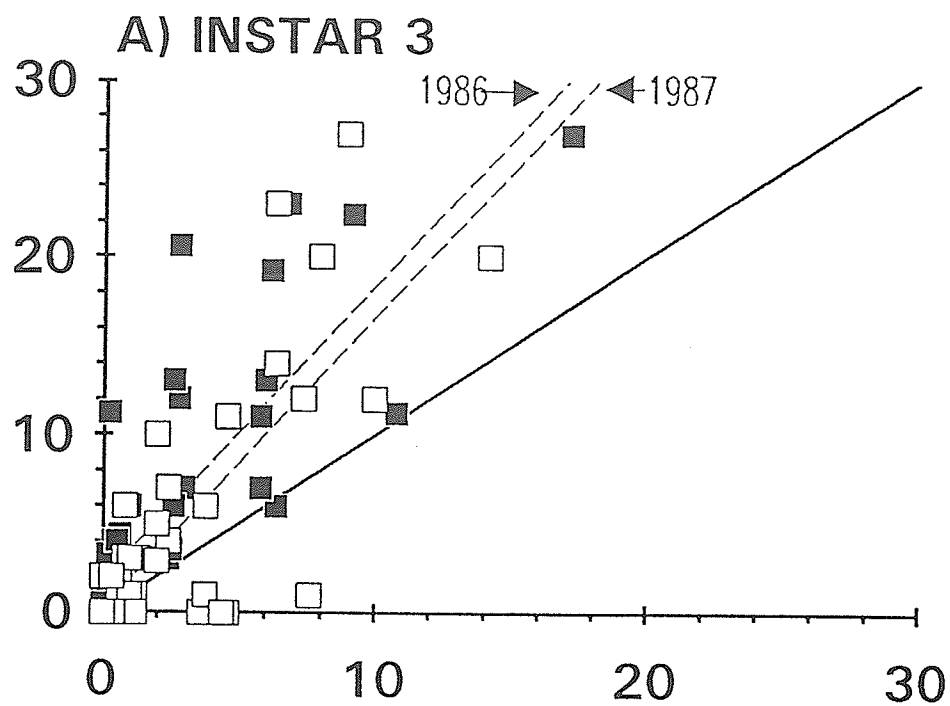
COUNTED NUMBER

Figure 36.   Seasonal pattern of estimated feeding by Colorado potato
     beetles on caged plants, at field density = 1.0. "Field density" is
     defined in the text.
     A) 1986; B) 1987
     <u>Symbols</u>:   square, larval feeding;
                   diamond, adult feeding.
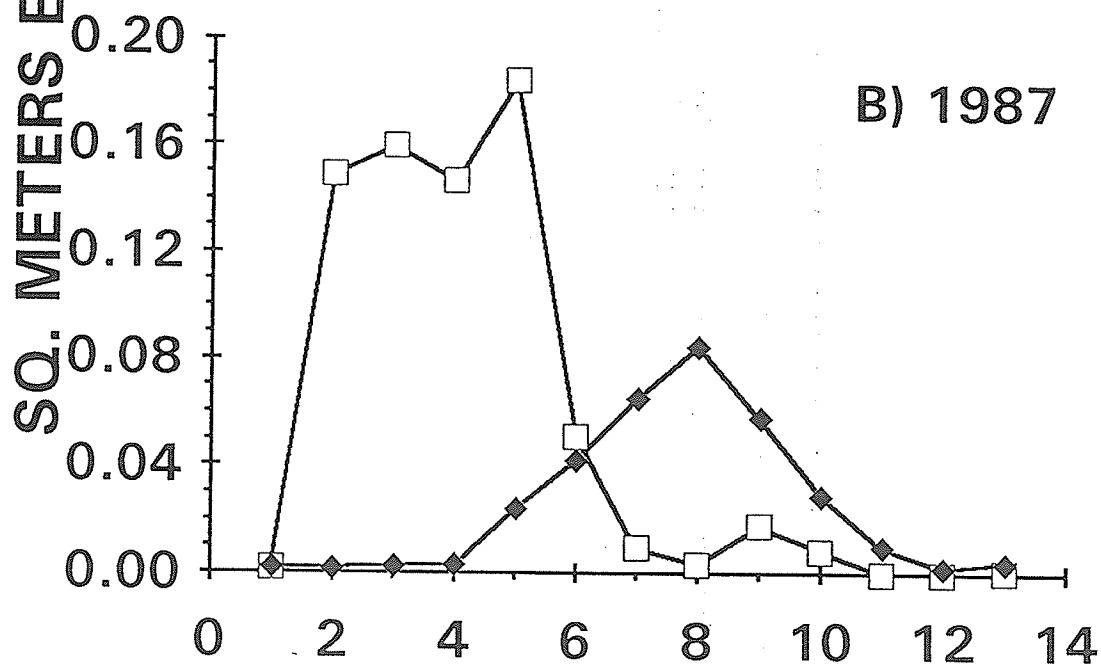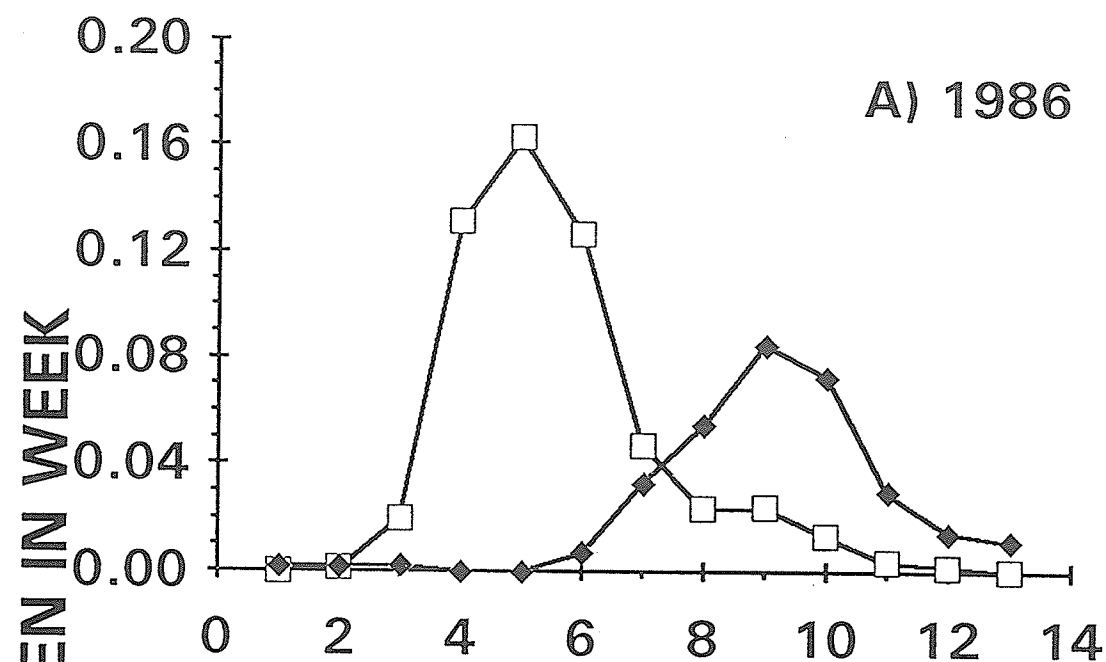
Figure 37.   Mean estimated leaf area at harvest, plus estimated larval
     feeding and estimated adult feeding.;   all values in m². "Field
     density" is defined in the text.

A) 1986; B) 1987.
Symbols: closed square,   final leaf area;
             open square,   final leaf area plus larval feeding;
             diamond,   final leaf area plus larval feeding
                               plus adult feeding.
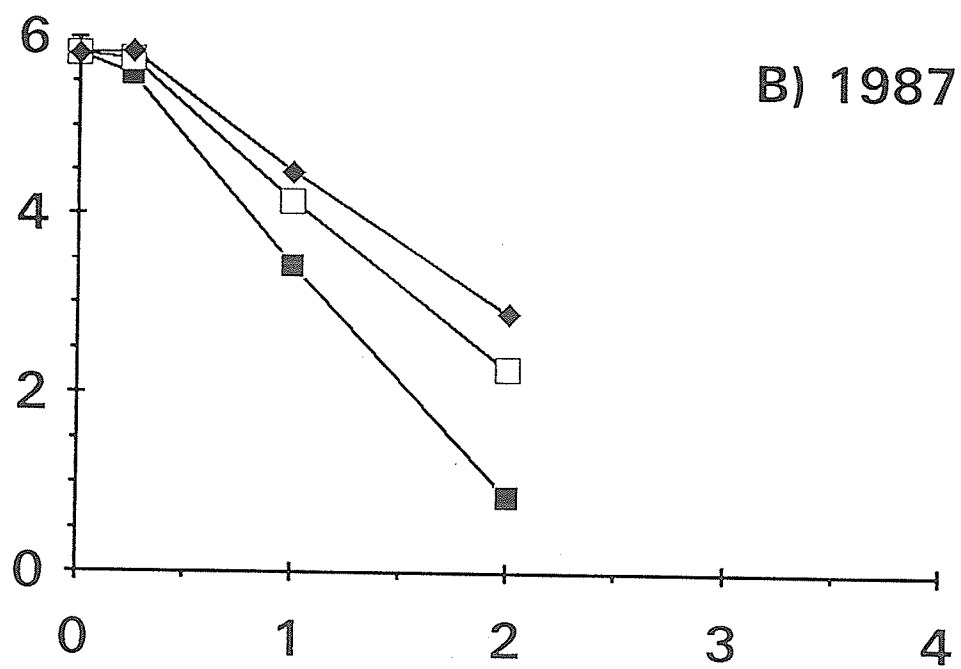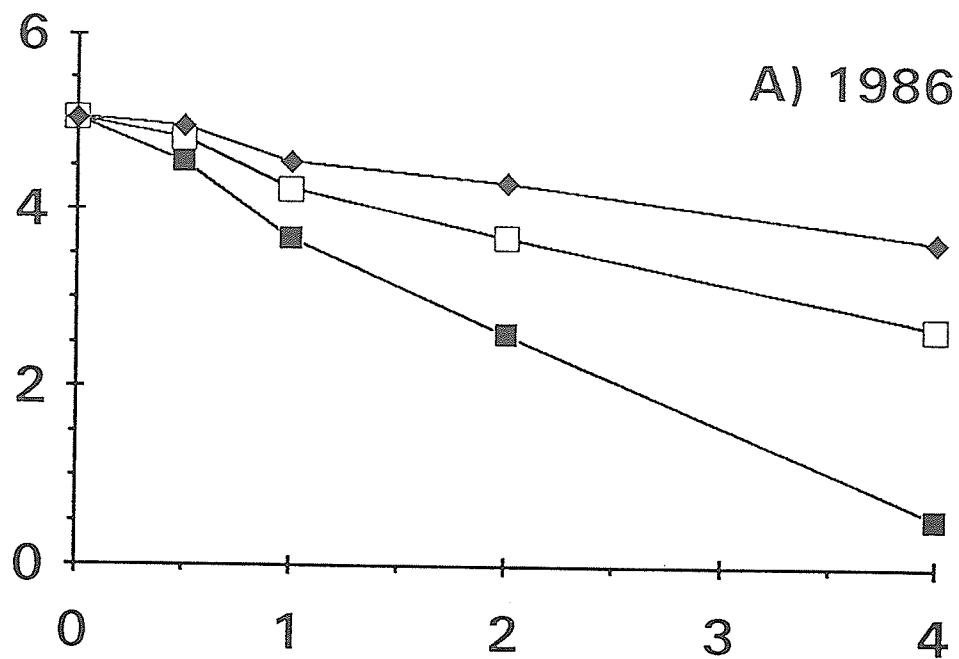
Section IV, Chapter D
    ECONOMIC INJURY LEVELS FOR COLORADO POTATO BEETLE ON 'RUSSET
    BURBANK' POTATOES IN SOUTHERN MANITOBA

ABSTRACT

Numbers of Colorado potato beetle larvae and adults were adjusted on caged 'Russet Burbank' potato plants to provide a range of infestation intensities. Marketable tuber yields were determined for each plant. Yield loss at which pest control was economically justifiable ranged from 1.5% to 7.5% depending on the ratio of control costs to expected yield value. Economic injury level estimates were derived by interpolation into linear regressions of percent yield loss on several measures of Colorado potato beetle infestation.

Several sets of economic injury level estimates were derived, each based on a measure of infestation in the fourth or fifth week after plant emergence. The values were higher when the regression included the intercept term than when it did not. The following estimates were calculated using regressions which include an intercept.

Where only adults and instars 3 and 4 are counted, economic injury level estimates range from 5.0 to 10.3/plant in week 4 after plant emergence, and from 6.0 to 13.0/plant in week 5. Where adults and all larvae are counted, economic injury level estimates range from 7.4 to 15.5/plant in week 4, and from 8.9 to 20.3/plant in week 5. These values agree well with published values for cultivars of size and growth habit similar to 'Russet Burbank'. Where regression models do not include an intercept, the economic injury level estimates are from 1/3 to 3/4 the corresponding values calculated using regression models with an intercept.

Relationships between yield reduction and estimated amount of defoliation were inconsistent among years, and hence did not provide a robust basis for estimation of economic injury levels.

INTRODUCTION

Pest control measures are only economically justifiable if their benefit, measured by reduction in yield loss, exceeds their cost. The pest population at which this balance occurs is defined as the economic injury level (Stern et al. 1959). Several methods of comparing costs and benefits have been proposed (e.g. Headley 1972, 1973; Mumford and Norton 1984; Pedigo et al. 1986), but perhaps the simplest is the gain threshold (Stone and Pedigo 1972), in which control measures are economically justifiable when the proportionate reduction in yield due to pest infestation equals or exceeds the control cost expressed as a proportion of the value of the undamaged crop. The difficulty with this approach is that the value of the crop at harvest is not known at the time the decision is made; the simplest solution is to substitute a reasonable estimate. Because the expected yield varies, so does the cost : benefit ratio. Consequently, the economic injury level also varies; rather than give a single estimate, it is preferable to tabulate a range of values based on reasonable combinations of control cost and expected yield.

Numerous groups have established economic injury levels for various potato cultivars in various regions (e.g. Martel et al. 1986; Keiserukhskii and Goncharov 1970; Senanayake and Holliday 1990; Mailloux et al. 1991), but because pest phenology, expected yield, and control costs vary geographically, economic injury levels on a given cultivar do not necessarily apply in regions other than that in which they were derived. Similarly, because susceptibility to damage varies among

cultivars, economic injury levels should not be applied to cultivars other than that on which they were derived.

The objective of this study is to derive economic injury level estimates for Colorado potato beetles on 'Russet Burbank' potato plants in southern Manitoba. In southern Manitoba, 'Russet Burbank' potatoes are planted in late May or early June, and harvested in mid September. Colorado potato beetles in this region are univoltine (Senanayake and Holliday 1988; this thesis, Section IV, Chapter C). Overwintering adults emerge from the soil in mid June, at about the time of crop emergence, and lay the first eggs shortly thereafter. Peak larval population occurs roughly five weeks later, followed by a peak of adult offspring. These adults enter the soil for the winter after the plants are harvested in mid September.

The univoltine nature of the pest, coupled with the general similarity in phenology among years, and the ability of the potato crop to recover from early season damage (Hare 1980), means that pest control measures are most effective around the time of the peak larval population. Local potato producers have adopted this timing (J. Martens, Manager, Almassippi Irrigation farms, Portage la Prairie, MB, pers. comm.), and economic injury level recommendations should take this tendency into account.

MATERIALS AND METHODS

Numbers of Colorado potato beetle adults and larvae of each instar were manipulated on caged plants to achieve a range of infestation intensities. Numbers used were fixed multiples of the mean weekly

population of that life stage, in a naturally infested field. The mean population of an instar in this field is defined as the field density for that instar.

Each week, on each caged plant, the numbers of Colorado potato beetle adults and larvae of each instar were adjusted to one of a range of fixed multiples of field density. Multiples were 4.0, 2.0, 1.0, 0.5, and 0.0 in 1986 and 2.0, 1.0, 0.5, 0.25, and 0.0 in 1987. Two plants with infestation of 0.0 times field density were included per block; one of these was inspected weekly in the same manner as the infested plants, and one was left undisturbed. Details of population estimation in the naturally infested field, and methods used in planting, selecting, and infesting the caged plants, are given in Section IV, Chapter C. These treatments resulted in a range of infestation intensities and tuber yields.

Plants which became completely defoliated were harvested within one week thereafter; the rest were harvested when commercial potato producers began to do so (19 Sep 1986, 11 Sep 1987). Tubers were sorted into marketable ($\geq$ 5.1 cm minimum diameter) and cull grades according to local industry standards (B. Geisel, Manager, Keystone Agri-Food potato project, pers. comm. 1988) Tuber yield was converted to monetary value based on commercial contract criteria (B. Geisel, pers. comm. 1988).

Economic injury level estimates were derived by comparing reduction in the value of the tuber yield to various measures of Colorado potato beetle infestation. To compensate for differences due to growing conditions, tuber yields of infested plants were expressed as a percent of yield of those control plants which were inspected weekly, and yield loss

was expressed as a percent reduction. The percent yield reduction in the cage studies was regressed on various measures of infestation intensity. The robustness of the results obtained by these regressions was assessed by testing for differences among years and by comparing predictions from the cage studies to the validation trial results.

Indices of infestation intensity.

In the first analysis, percent yield reduction was compared to peak beetle populations. Subsequently, relationships were examined between percent yield loss and four indices of Colorado potato beetle infestation in each of weeks 4 and 5 after plant emergence; thus accommodating the practice of Manitoba potato producers to control Colorado potato beetles in this interval. Two indices were based on Colorado potato beetle numbers per plant: (A) total counted number of Colorado potato beetle of instars 3, 4 and adults at the beginning of the given week (i.e. 4 or 5); (B) the sum of all Colorado potato beetle instars on the plant at the beginning of the week. Index (A) accommodates the common producer practice of counting only late Colorado potato beetle instars (B. Geisel, pers. comm.); index (B) was included to test whether ignoring instars 1 and 2 affects the conclusions.

Two further infestation indices were based on estimated defoliation: (C) estimated leaf area removed in the week under consideration; and (D) estimated cumulative leaf consumption (m^2) per plant to the beginning of the week. Larval leaf consumption was estimated from the output of the development and feeding simulations described in Section IV, Chapter C. An estimate of adult feeding was obtained by trapezoidal approximation using adult populations at the beginning and end of each week, and a

feeding rate estimate of 500 $mm^2 \cdot day^{-1} \cdot adult^{-1}$, i.e. approximately the mean rate over temperatures calculated from data given by Ferro et al. (1985). This procedure was detailed in Section IV, Chapter C.

Analysis.

Analysis proceeded in two steps. In the first step, analysis of variance was used to test for year effects on the response of percent yield reduction to each index of infestation. In the second step, data were subjected to linear regression of percent yield reduction on each index. The variance of the percent yield reduction data was homogeneous, so transformation of data was not necessary.

Economic injury level estimates were interpolated from regressions of percent yield reduction on infestation indices. This analysis employed the "gain threshold" (Stone and Pedigo 1972) in which pesticides should be applied when yield value is anticipated to be reduced by a proportion equal to the cost of control divided by the expected yield value of the crop.

If the relationship between percent yield reduction (R) and the measure of infestation intensity (X) is linear, then

$$R = m + nX \tag{16}$$

At the gain threshold, R = control costs divided by yield value of the uninfested crop; an economic injury level is obtained by substituting this value into equation 16 and solving for X. Economic injury level estimates were obtained by calculating R for a series of reasonable expected yields and control costs.

In southern Manitoba, revenues of \$800 to \$1000 ha^{-1} (15 to 20 $T \cdot ha^{-1}$) are typical (B. Geisel, Manager, Keystone Agri-Food potato

project, pers. comm. 1988); 1991 chemical costs per hectare ranged from $8.64 for Decis (deltamethrin) 5EC to $34.09 for Ambush (permethrin) 500EC. Application costs are approximately $10 ha^{-1}, so that the range of realistic costs is $\approx$ $18 to $45 ha^{-1}.

RESULTS AND DISCUSSION

The relationship between multiples of field density on the caged plant, and marketable tuber yield, is shown in Fig. 38. Estimated weekly feeding by larvae and adults, plus final leaf area and tuber yields of the caged plants, are given in Appendix 9.

Mean yield of the control plants which were inspected weekly was less than that of controls which were not inspected. Using the mean yield of the uninspected controls as denominator, the difference was 18.3 and 28.8% in 1986 and 1987, respectively. Therefore, the weekly inspection of plants reduces their yield. This observation complicates the following analysis, because it is not possible to determine whether the effect of inspection on plants is independent of infestation intensity, i.e. whether yield of each is reduced by the same fixed amount. Intuitively, because larger plants must be disturbed more severely during inspection, it seems more likely that yield reduction by inspection is related to plant size. I will assume for the remainder of this analysis that weekly inspection of infested plants reduced all of their yields by the same proportion as yield was reduced in inspected control plants in the same season. Because later analyses consider proportional yield reduction compared to inspected controls, this assumption is equivalent to ignoring the effects of weekly inspection on tuber yield.

Relevant statistics of the analysis of variance and regressions of percent yield reduction on the chosen indices of infestation are summarized in Table 22. Year effect was not significant ($p > 0.05$) for any index. The interaction of infestation index by year was significant for peak population of adults plus instars 3 and 4, and for all indices involving estimated leaf consumption. The significant interaction indicates that these measures do not bear a consistent relationship to yield reduction, and hence do not provide a robust foundation for the development of economic injury level estimates.

Parameters of linear regressions of data pooled over years are also summarized in Table 22. Slopes of regressions were all significant, but the intercept never was. Where the year x infestation index interaction is significant, pooling is invalid and so was not done.

To estimate a widely applicable economic injury level, the index of infestation intensity which is used to quantify the impact of Colorado potato beetle on tuber yield of 'Russet Burbank' potato plants must meet the following criteria. First, yield loss should be significantly related to the index. Second, neither the year effect nor the interaction of year and infestation index can be significant. Only the infestation indices based on insect counts meet these criteria.

Table 23A lists the proportional yield loss which justifies pest control measures, for several combinations of control cost and expected yield. Tables 23B, i - v list economic injury level estimates for each combination listed in 23A, in terms of the three infestation indices which meet the above criteria.

Within the tabulated range of combinations of control, economic

injury level estimates in week 4 after plant range from 5 to 10.3 for large beetles (adults plus instars 3 and 4), and 7.4 to 15.5 for all feeding stages per plant (Table 23 B, i & ii). In week 5, the same ranges are 6.0 to 13.0, and 8.9 to 20.3 per plant for the large beetles and all feeding stages, respectively (Table 23 B, iii & iv). These values are strongly affected by inclusion of the non-significant intercept in equation 16. Fig. 39 illustrates the relationship between yield loss and the total beetle count (adults plus all larvae) in week 4 after plant emergence. Fig 40 provides the same information for total beetle count in week 5. In both figures, panel A illustrates the full range of data; while panel B focuses more closely on the region where the regression line intersects with the gain threshold. The value of the independent variable at which the regression line intersects the broken line corresponds to the economic injury level estimate.

Table 22 also lists slope estimates for regressions forced through the origin, and economic injury level estimates calculated using these no-intercept regressions are given in table 24. All are approximately only 1/3 to 3/4 of the corresponding values calculated using the regressions which include the intercept. For example, the range of economic injury level estimates based on total count of feeding stages in the 5th week after plant emergence, changes from 8.9 - 20.3 (Table 23 B iv), to 3.0 - 15.0 per plant (Table 24 B iv).

The non-significant intercept term appears to have undue influence on the economic injury level estimates. Although the intercept estimate is not significant, it is part of the best available linear statistical description of the observed relationship between yield loss and

infestation. The deviation of this value from 0 is attributable to the apparent tolerance of the plants to low levels of infestation in 1987. For extension purposes, lower economic injury level estimates based on no-intercept regressions may be most acceptable to producers, who are typically risk-averse.

These economic injury level estimates (Tables 23 and 24) are similar to values published for cultivars of similar size and growth habit. Keiserukhskii and Goncharov (1970) estimated that 20 larvae per plant result in 11.5% yield reduction in late-maturing cultivars, of which group 'Russet Burbank' is a member; assuming that 3 to 5% yield loss is economically significant, this translates to an economic injury level of ≈ 5.2 to 8.9 larvae per plant, comparable to the values calculated here using the no-intercept regressions on peak larval populations. Martel et al. (1986) estimated an economic injury level of ≈ 20 larvae per plant on cv. 'Kennebec' and 'Sebago' in Quebec. Plants of these cultivars are approximately the same size as 'Russet Burbank' plants, and mature at about the same time. Mailloux et al. (1991) estimated an economic injury level of 12 larvae per stalk for cv. 'Superior'. They defined a stalk as the primary stem plus all vines; 'Russet Burbank' plants have 2 to 4 vines, so this economic injury level estimate is somewhat higher than those derived in this chapter. Similarity to published values increase confidence in the estimates given here.

Producers in Manitoba use an economic injury level of 10% defoliation (Kolach and McCullough 1992) on 'Russet Burbank' plants. Thus, the present estimate cannot be compared directly.

Table 22. Summary of results of analysis of variance and regressions of percent yield reduction on several measures of infestation intensity. Units of all slopes are %Yield reduction per unit index. <u>Codes</u>: *, $P \leq 0.05$; **, $P \leq 0.01$; ***, $P \leq 0.001$; . , not significant (P > 0.05).
  Where the year or year x index interaction is significant in the ANOVA, pooled regressions are invalid, and are not provided.

INDEX[a]	ANOVA P(EFFECT = 0)			INTERCEPT			SLOPE			MODEL			NO-INT SLOPE	
	INDEX	YEAR	YEAR x INDEX	EST	SE	P(=0)	EST	SE	P(=0)	$F_{1,9}$	r^2	$\sqrt{MSE}$	EST	SE
INDICES BASED ON WEEKLY COUNTS														
BIG(4)	***	.	.	-4.03	4.48	.	1.17	0.12	***	100.9	0.93	10.0	1.11	0.08
ALL(4)	***	.	.	-3.93	3.87	.	0.74	0.06	***	142.0	0.95	8.5	0.69	0.04
BIG(5)	***	.	.	-3.68	3.91	.	0.86	0.07	***	138.3	0.95	8.6	0.81	0.05
ALL(5)	***	.	.	-3.21	4.09	.	0.53	0.05	***	123.7	0.94	9.1	0.50	0.03
INDICES BASED ON FEEDING														
EAT(4)	***	.	**	.	.	.	.	.	.	.	.	.	.	.
TOT(4)	***	.	**	.	.	.	.	.	.	.	.	.	.	.
EAT(5)	***	.	*	.	.	.	.	.	.	.	.	.	.	.
TOT(5)	***	.	*	.	.	.	.	.	.	.	.	.	.	.

[a] <u>INDEX CODES</u>:

BIG(i) = sum of instars 3, 4, and adult per plant at the start of week i = 4, 5.
ALL(i) = sum of adults an all instars per plant at the beginning of week i.
EAT(i) = estimated leaf area (m^2) per plant removed during week i.
TOT(i) = estimated leaf area (m^2) per plant removed to beginning of week i.

Table 23. Economic injury level estimates for Colorado potato beetles on 'Russet Burbank' potato plants in southern Manitoba, using injury/infestation relationships including intercept (Table 22). Values given are mean number per plant.

A) $100 \cdot$ (control cost$\cdot$ha^{-1}/yield value$\cdot$ha^{-1}) for a grid of combinations of control cost and expected yield value. These values correspond to percent yield loss at which pest control is economically justifiable, assuming 100% kill. For kill rate K $(0 < K < 1)$, divide entry by K (Pedigo et al. 1985)

CONTROL COST ($\cdot$ha^{-1})	VALUE OF EXPECTED YIELD ($\cdot$ha^{-1})			
	600	800	1000	1200
18	3.00	2.25	1.80	1.50
27	4.50	3.38	3.70	2.25
36	6.00	4.50	3.60	3.00
45	7.50	6.75	4.50	3.75

B)   Economic injury levels of Colorado potato beetle on 'Russet Burbank' potato plants expressed in terms of population estimates (arithmetic mean/plant).

i)   Number of adults and instars 3 and 4 in week 4 after plant emergence = BIG(4) in table 22.

CONTROL COST ($\cdot$ha^{-1})	VALUE OF EXPECTED YIELD ($\cdot$ha^{-1})			
	600	800	1000	1200
18	6.3	5.6	5.2	5.0
27	7.6	6.6	6.0	5.6
36	9.0	7.6	6.0	5.6
45	10.3	8.7	7.6	7.0

ii)   Number of adults and all larvae in week 4 after plant emergence. = ALL(4) in table 22.

CONTROL COST ($\cdot$ha^{-1})	VALUE OF EXPECTED YIELD ($\cdot$ha^{-1})			
	600	800	1000	1200
18	9.4	8.4	7.8	7.4
27	11.4	9.9	9.0	8.4
36	13.4	11.4	10.2	9.4
45	15.5	12.9	11.4	10.4

Table 23 (Cont'd). Economic injury level estimates for Colorado potato
beetles on 'Russet Burbank' potato plants in Southern Manitoba,
using injury/infestation relationships including intercept
(Table 22). Values given are numbers per plant.

iii)   Number of adults and instars 3 and 4 in week 5 after plant
        emergence = BIG(5) in table 22.

CONTROL COST ($·ha^{-1})	VALUE OF EXPECTED YIELD ($·ha^{-1})			
	600	800	1000	1200
18	7.8	5.9	6.4	6.0
27	9.5	8.2	7.4	6.9
36	11.3	9.5	8.5	7.8
45	13.0	10.8	9.5	8.7

iv)   Number of adults and all larvae in week 5 after plant emergence
       = ALL(5) in table 22

CONTROL COST ($·ha^{-1})	VALUE OF EXPECTED YIELD ($·ha^{-1})			
	600	800	1000	1200
18	11.8	10.4	9.5	8.9
27	14.6	12.5	11.2	10.4
36	17.5	14.6	12.9	11.8
45	20.3	16.8	14.6	13.2

Table 24. Economic injury level estimates for Colorado potato beetles on 'Russet Burbank' potato plants in southern Manitoba, using injury/infestation relationships with no intercept (Table 22). Values given are mean number per plant.

A) 100·(control cost·ha^{-1}/yield value·ha^{-1}) for a grid of combinations of control cost and expected yield value. These values correspond to percent yield loss at which pest control is economically justifiable, assuming 100% kill. For kill rate K (0 < K < 1), divide entry by K (Pedigo et al. 1985)

CONTROL COST ($·ha^{-1})	VALUE OF EXPECTED YIELD ($·ha^{-1})			
	600	800	1000	1200
18	3.00	2.25	1.80	1.50
27	4.50	3.38	3.70	2.25
36	6.00	4.50	3.60	3.00
45	7.50	6.75	4.50	3.75

B) Economic injury levels of Colorado potato beetle on 'Russet Burbank' potato plants expressed in terms of population estimates (arithmetic mean/plant).

i) Number of adults and instars 3 and 4 in week 4 after plant emergence = BIG(4) in table 22.

CONTROL COST ($·ha^{-1})	VALUE OF EXPECTED YIELD ($·ha^{-1})			
	600	800	1000	1200
18	2.7	2.0	1.6	1.4
27	4.1	3.0	2.4	2.0
36	5.4	4.1	3.2	2.7
45	6.8	5.1	4.1	3.4

ii) Number of adults and all larvae in week 4 after plant emergence. = ALL(4) in table 22.

CONTROL COST ($·ha^{-1})	VALUE OF EXPECTED YIELD ($·ha^{-1})			
	600	800	1000	1200
18	4.3	3.3	2.6	2.2
27	6.5	4.9	3.9	3.3
36	8.7	6.5	5.2	4.3
45	10.9	8.2	6.5	5.4

Table 24 (Cont'd). Economic injury level estimates for Colorado potato beetles on 'Russet Burbank' potato plants in Southern Manitoba using injury/infestation relationships with no intercept (Table 22). Values given are number per plant.

iii) Number of adults and instars 3 and 4 in week 5 after plant emergence = BIG(5) in table 22.

CONTROL COST ($·ha⁻¹)	VALUE OF EXPECTED YIELD ($·ha⁻¹)			
	600	800	1000	1200
18	3.7	2.8	2.2	1.9
27	5.6	4.2	3.3	2.8
36	7.4	5.6	4.4	3.7
45	9.3	6.9	5.6	4.6

iv) Number of adults and all larvae in week 5 after plant emergence = ALL(5) in table 22

CONTROL COST ($·ha⁻¹)	VALUE OF EXPECTED YIELD ($·ha⁻¹)			
	600	800	1000	1200
18	6.0	4.5	3.6	3.0
27	9.0	6.8	5.4	4.5
36	12.0	9.0	7.2	6.0
45	15.0	11.3	9.0	7.5

Figure 38. Yield of caged plants (kg marketable tubers), versus multiple of field density maintained on plant. (A) 1986; (B) 1987.
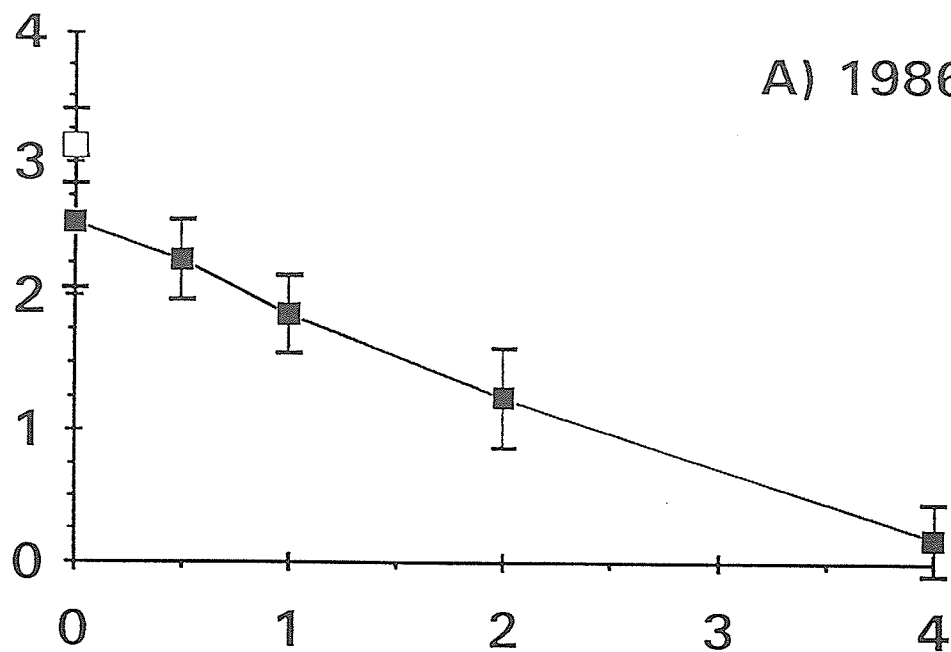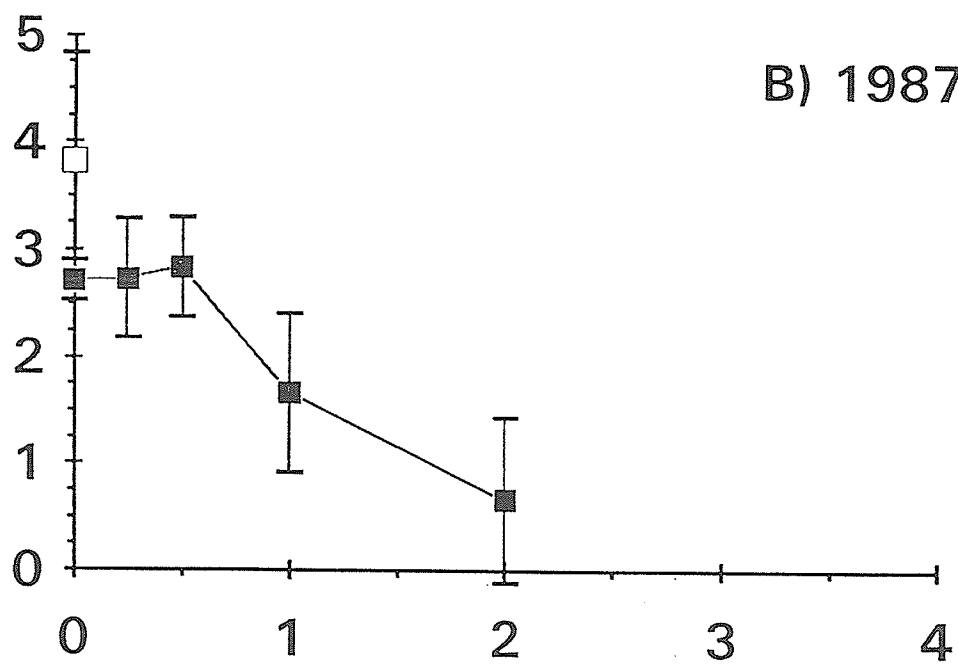
Figure 39.   Percent reduction in marketable tuber yield of caged plants,
versus total number of Colorado potato beetle adults and larvae in
the fourth week after plant emergence.
(A)   full range of data
Open symbols, 1986 data.
Closed symbols, 1987 data
(B)   focus on the region near the intersection of the regression
line and economic percent yield reduction. The horizontal
solid line represents 0 yield loss, and the horizontal broken
line represents 3.5% yield loss, roughly representative of the
range of values at which pest control is justified.

A) FULL VIEW

B) CLOSE-UP

MEAN YIELD REDUCTION (%)

TOTAL COUNT WEEK 4
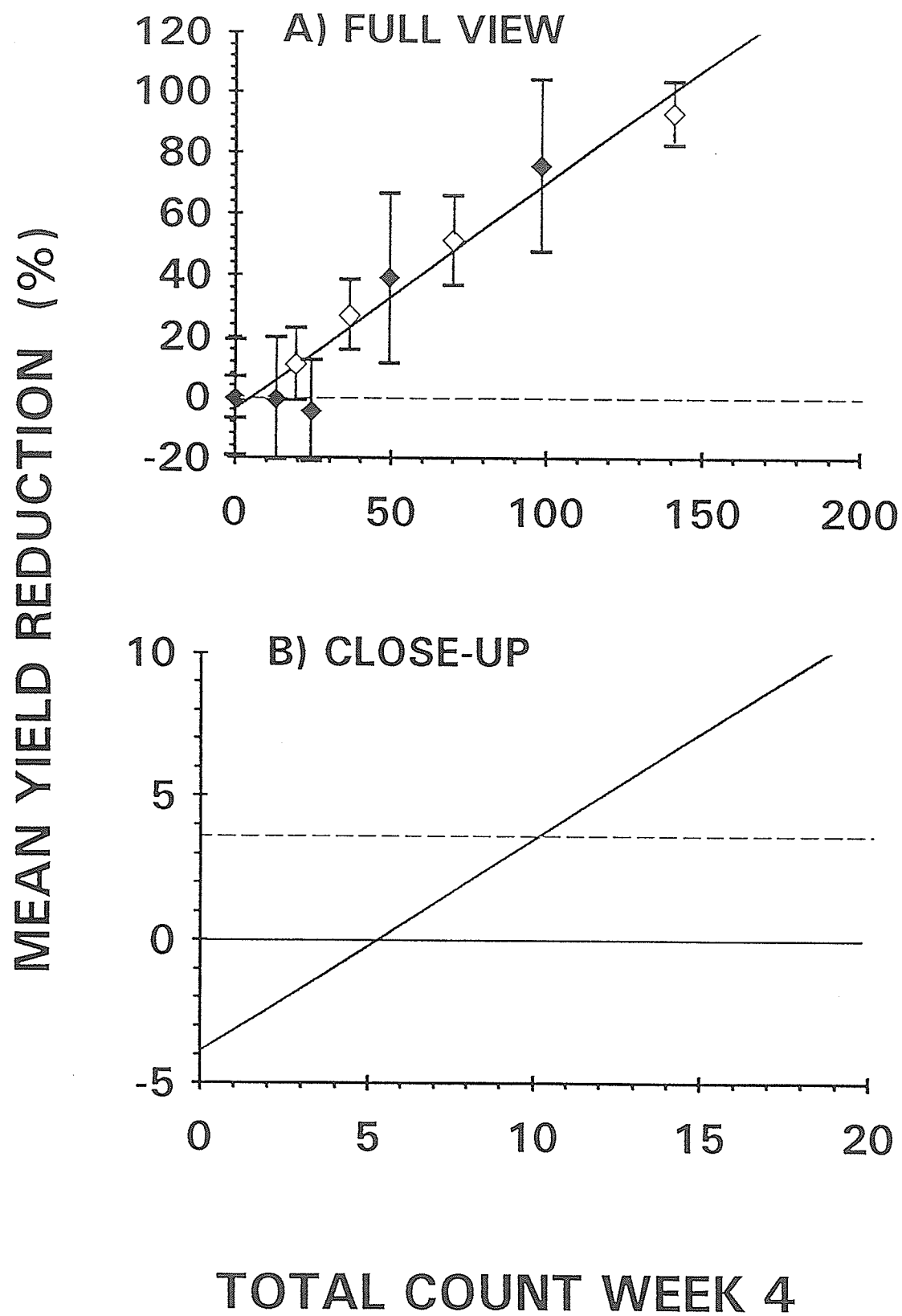
Figure 40.   Percent reduction in marketable tuber yield of caged plants, versus total number of Colorado potato beetle adults and larvae in the fifth week after plant emergence.

(A)   full range of data
      Open symbols, 1986 data.
      Closed symbols, 1987 data

(B)   focus on the region near the intersection of the regression line and economic percent yield reduction. The horizontal solid line represents 0 yield loss, and the horizontal broken line represents 3.5% yield loss, roughly representative of the range of values at which pest control is justified.
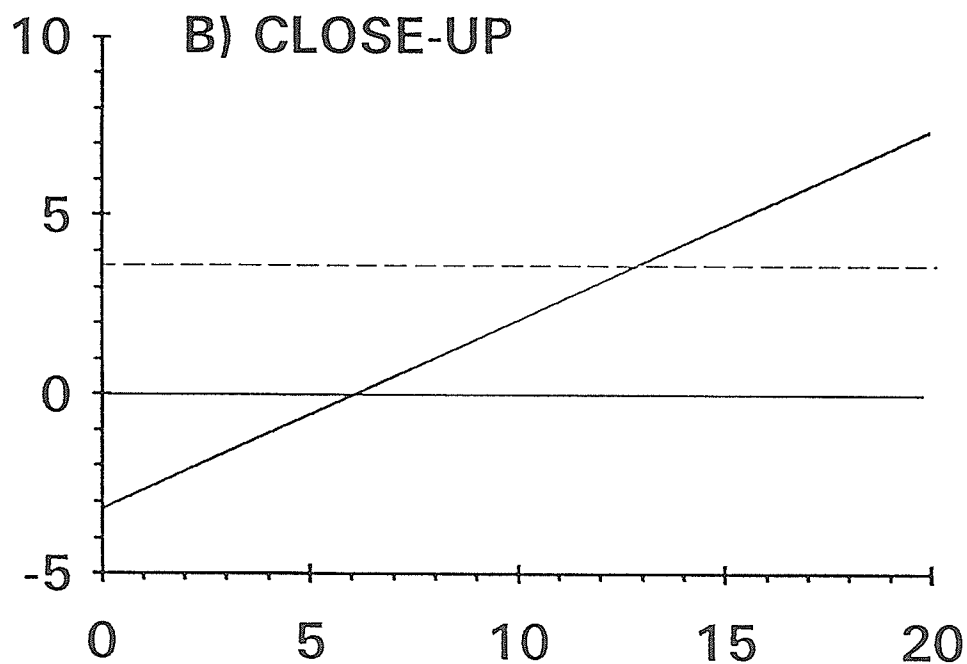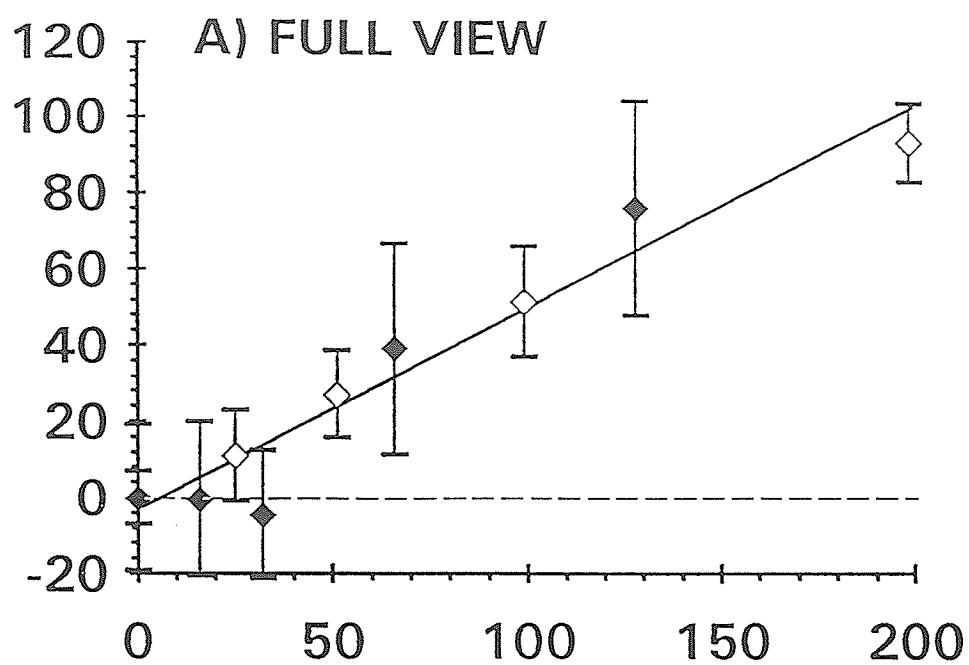
SECTION V. GENERAL DISCUSSION AND CONCLUSIONS

1) GENERAL DISCUSSION

1) GENERAL DISCUSSION

Salient points were discussed in the chapters in which they arose. This general discussion addresses some of the broader implications of the complete document.

1.1 THE PHYSICAL INTERPRETATION OF T^*

In Section III, Chapter B, the response of Colorado potato beetle larvae to combinations of temperature and insolation was quantified; this allowed combination of these two variables into a single quantity, T^*, which could be used to predict the larval behavioral response. Because of the importance of T^* in the subsequent models, the physical meaning of this quantity is of interest.

In several insect species, direct measurement has demonstrated a correlation between body core temperature and thermoregulatory behavior. This has been observed in ectotherms (Sullivan and Wellington 1953; Dreisig 1990) and endotherms (Heinrich 1971; Heinrich and Kammer 1973). Some grasshoppers respond to high temperature so quickly that peripheral receptors are probably involved (Uvarov 1977). Some dragonflies and cicadas retreat from a heat source at lower body temperatures when heated quickly, than when heated slowly; this suggests a response to peripheral receptors, or to the rate of change of body temperature (May 1979).

These results indicate that insect thermoregulatory behavior is a reaction either to body temperature, or to perceived potential body temperature. If this premise is valid, then the conclusion follows directly that T^* may be actual or potential body core temperature under specified conditions of insolation and ambient temperature. No direct evidence was provided for this interpretation in Section III, Chapter B;

but the superior performance of the versions of models of feeding and development which use T* as the measure of body temperature, over versions which use ambient temperature as the measure of body temperature, supports the hypothesis.

Hence the quantity $z/y = 0.0838°C/(W·m^{-2})$ in equation (9) seems to be an estimate of the potential effect of measured insolation on body temperature. The Licor LI-210S photometer used in the behavior trial is calibrated to approximate the sensitivity of the 'average' human eye (CIE 1979), and detects only approximately 40% of total solar energy (Dan Morgan, Li-Cor Inc, Lincoln Nebraska, pers. comm. 1992). Thus, $0.0838°C/(W·m^{-2}$ measured insolation) is equivalent to $\approx 0.03°C/(W·m^{-2}$ full spectrum radiation). This value will be termed the "insolative heating coefficient".

Comparison of this inferentially-obtained insolative heating coefficient with directly measured values is of interest. May's (1982) estimate was only $0.00213°C$ per $W·m^{-2}$, but this is an estimate of the mean body elevation of a population; this value is a mean body temperature in full sun and in shade, weighted by the proportion of larvae in each microhabitat. This value will certainly be lower than the body temperature of a larva in full sun, the quantity estimated by this trial.

The present inferential estimate of the impact of insolative heating on individual body temperature is also slightly greater than values obtained by direct measurement. In several studies, insect body temperatures were typically elevated by ≈ 0.01 to $0.02°C/(W·m^{-2})$ (Table 25). The insolative heating coefficient obtained in the present trial

($\approx 0.03^{\circ}C/(W \cdot m^{-2}$ full spectrum radiation)) is slightly greater than this range.

In contrast, $0.03^{\circ}C/(W \cdot m^{-2})$ agrees more closely with the temperature elevation of the <u>leaf</u> <u>surface</u> (0.027 to 0.039 $^{\circ}C/(W \cdot m^{-2})$) as reported by Henson (1958) (Table 25). Significantly, although Colorado potato beetle larval body temperature generally exceeds air temperature, it is only slightly greater than leaf surface temperature (May 1981, 1982). In ectotherms with mass $\leq \approx 1$ g, heat conduction from the substrate has an impact on body temperature which approaches that of insolation, especially if the area of contact between insect and surface is large (Stevenson 1985); larval Colorado potato beetles meet both criteria. Possibly, "thermoregulatory" behavior of Colorado potato beetle larvae consists of locating surfaces with preferred temperatures.

Thus, evidence currently available suggests that T^* may be actual or potential body temperature of Colorado potato beetle larvae under specified conditions of temperature and insolation. Because the measurement is indirect and the conclusion is *a posteriori*, this hypothesis should be tested directly by measuring body temperature and the thermoregulatory response simultaneously. Due to the intrusive nature of direct measurement with thermistors (Stone and Willmer 1989), some method of remote sensing should be used.

1.2 THE MODELS

1.2.1 EVALUATIONS

This project has examined the feasibility of applying feeding and developmental rates from constant-temperature laboratory conditions, to the variable conditions in the field. Because the models were assembled

from a series of simple, well-defined functions, each function can be examined directly for its possible contributions to model performance.

For example, in the initial evaluation of the feeding and developmental rate models (Section III, Chapters C and D), the feeding rate model estimates agreed well with observations, but the developmental rate estimates showed consistent bias. These two models share all functions except those describing temperature-dependent feeding and developmental rates; this implicates the developmental rate function as the most likely source of error in the latter model.

In laboratory experiments, Colorado potato beetle larvae continue to feed under brief exposures to temperatures which are lethal on chronic exposure (Section II, Chapter A). The developmental response to similar brief exposures to lethal temperatures was not examined, but a literature review (Hagstrum and Milliken 1991) revealed that developmental times under varying temperatures cannot be calculated directly from constant-temperature times. By analogy with the feeding rate response, this imperfect transference may occur because the constant-temperature development relationship does not pertain where temperatures briefly exceed the constant-temperature optimum. Colorado potato beetle eggs develop at a greater rate than expected, when briefly exposed to nominally lethal temperatures Logan et al. (1985); if larvae respond similarly, this effect could be the source of the 9% disagreement between the development times predicted by the model, and those observed under field conditions in 1991. A trial in which larvae are transferred among controlled temperature regimes for various intervals, is necessary to test this possibility. Although simple in concept, such a study would be extremely

demanding logistically. If done well, it would characterise the response surface (developmental rate = f(temperature, exposure time)) and provide a sound foundation for better understanding of the response under natural conditions. This is an important deficiency in the current understanding of the thermal biology of this species.

The impact of larval thermoregulation on body temperature may be the most important source of model error. The insolative heating coefficient ($°C/(W \cdot m^{-2})$) which was estimated in Section III, Chapter B was a constant, but this might be due to the narrow interval over which behavioral data were collected. Seasonal variations in solar elevation affect the amount of atmosphere through which light must pass, and hence the spectral composition of the transmitted light. Hence, the insolative heating coefficient might be expected to change seasonally, with impact on the performance of the models. This possibility should be assessed by repeating the trial described in Section III, Chapter B, several times during one or more growing seasons. Some direct measurement of body temperature should be included.

1.2.2 IMPLICATIONS OF THE MODELS.

Despite the long series of empiricisms and approximations, the models seem to perform relatively well. I believe that the performance of the models indicates that they have successfully abstracted the essence of the mechanisms by which temperature and insolation affect larval feeding and development. If this assessment is correct, then the performance of the models may provide insight into these mechanisms.

In discussing the implications of the model output, I wish to make an explicit distinction between a model and reality; the following

discussion focuses only on insights gained from comparison of model outputs. To save space, the ensuing remarks will be presented as simple declarative statements, but they are all postulates which are dependent on the validity of the models.

In addition to examination of the model output, the following arguments incorporate two premises. First, in many insect species, the physiological response to temperature seems to be relatively static in an evolutionary sense (e.g. Ushakov 1964; Huey and Kingsolver 1989; van Damme et al. 1990). The Colorado potato beetle conforms to this observation: there is no measurable difference in physiological response to temperature among populations of this species (Tauber et al. 1988; this thesis, Section II, Chapter D). The second premise is that behavioral responses, particularly orientation to the sun, are more effective than physiological responses in modifying the body temperature of terrestrial ectotherms (Stevenson 1985).

If the models assembled in this thesis have adequately abstracted the essence of the response by which the larvae respond to temperature and insolation, then certain implications follow. The first is that the effects of behavioral thermoregulation must be considered explicitly when examining the population processes of Colorado potato beetles, and probably those of any species in which individuals may select from a range of microclimates at relatively little cost. Behavioral thermoregulation buffers the impact of meteorological variation on physiological functions. Thus, feeding rate (and to a lesser extent, also developmental rate), can be maintained relatively constant as long as microhabitats are available in which these rates are near optimal.

The second implication is that limits to the geographic distribution of a species may be established in large part by the capacity of the behavioral response to maintain body temperatures within a range which allows the local population to maintain a non-negative intrinsic rate of increase. (I disregard the special case where peripheral populations are maintained by immigration. I also acknowledge other limits to species distribution, such as the range of acceptable hosts, the length of growing season, and the severity of winter, but this discussion focuses on the implications of the present study only.) The results of this study suggest that in Colorado potato beetles, the northern (cold) geographic limit may coincide with the limit of conditions in which thermoregulatory strategy ALL TOP (Section III, Parts C and D) is necessary to maintain body temperature within this range. In colder regions, no amount of behavioral thermoregulation would suffice. The southern (hot) limit has a similar relationship with thermoregulatory strategy ALL UNDER (Section III, Parts C and D). In both cases, physiological adaptation in the local population would be required for the extension of the range, but this would be impeded by gene flow from populations in more favorable areas (Wright 1932; Ushakov 1964).

Within the geographic range defined by these limits, behavioral thermoregulation would buffer the effects of climatic change on population dynamics. Except in populations near the limits of the distribution, climatic change would have little effect. The only consequence might be a change in the limits of the distribution. The potential ecological and agricultural effects of such distributional changes are a subject for further study.

2) CONCLUSIONS

2.1 CONTRIBUTIONS TO KNOWLEDGE

Most Chapters in sections II to IV report novel information, including:

1)   The discovery that Colorado potato beetle larvae continue to feed at measurable rates under brief exposure to temperatures which are lethal on long-term exposure (Section II, Chapter A); this observation has application to estimation of feeding rates under natural conditions.

2)   The quantification of the behavioral response of individual Colorado potato beetle larvae to combinations of temperature and insolation under natural conditions (Section III, Chapter B). This information led to the hypothesis that a behavioral bioassay response might allow non-lethal estimation of the effect of insolative heating on body temperature.

3)   The assembly of models of development and feeding by Colorado potato beetle larvae under conditions of naturally varying temperature and insolation (Section III, Chapters C and D), which describe measured response well (the feeding model), or demonstrated consistent bias (the developmental rate model). The bias in the developmental rate model suggests that developmental rates obtained under constant temperatures may not apply directly to variable conditions.

4)   Development and validation of a rapid method for estimation of fresh
        leaflet mass of potato plants (Section IV, Chapter A), and the
        demonstration that the area:mass ratio of leaflets is neither
        constant, linear, or unaffected by insect damage (Section IV,
        Chapter B). These discoveries may simplify verification of submodels
        describing leaf area change and the effects of insect damage in
        potato growth models.

5)   This thesis also includes the first economic-injury level estimates
        for Colorado potato beetles in on 'Russet Burbank' potato plants in
        Southern Manitoba (Section IV, Chapter D)

2.2 SUGGESTIONS FOR FURTHER STUDY

        After examination of model output and the functions used in their
assembly, the following studies are suggested.

1)   A direct test of the hypothesis that T^* is body temperature, by
        measuring the latter directly under specified combinations of
        temperature and insolation.

2)   Quantification of the developmental response of Colorado potato
        beetle larvae to brief exposure to temperatures which are lethal
        under constant exposure.

3)   An attempt to assemble a phenology model of Colorado potato beetles.
        The development and feeding models assembled here could constitute
        portions of such a model.   Before this is possible, further

information is required. This includes quantification of the determinants and time-course of adult emergence from the soil in spring and summer; adult feeding, mortality and oviposition rates as affected by age and temperature; rates of egg development under naturally varying conditions; and the time course in mortality rates of all instars under field conditions.

4)   If such a phenology model is assembled, it could be linked with a potato growth model to provide a basis for damage prediction and a guide for pest management decision making.

5)   Furthermore, it may be useful to examine the possibility that plant spacing affects the economic injury level, for example by distributing an insect infestation among more plants, or by reducing the leaf area of the plants such that they are less able to tolerate limited injury, or both.

Table 25. Insolation-dependent body temperature elevation (Insolative heating coefficient H, in $°C/[W \cdot m^{-2}]$) obtained from published reports.

TAXON	H	CITATION	COMMENTS
Onymacris rugatipennis (Coleoptera: Tenebrionidae)	0.018	Edney 1971	Subelytral temperature of horizontally restrained adults
Melanoplus spp. (Orthopera: Acrididae)	0.0084 to 0.012	Pepper and Hastings 1952	
Apis mellifera L. (Hymenoptera: Apidae)	0.0086	Cena and Clark 1972	Abdominal temperature of worker honeybees
Six species	0.004 to 0.01	Digby 1955	H increases with body mass
Schistocerca gregaria (Forskål) (Orthoptera: Acrididae)	0.0029 to 0.011	Stower and Griffiths 1966	Thoracic temperatures of first and fifth instars, respectively.
Several poplar-feeding species	0.008 to 0.023	Henson 1958	Habitat temperatures under artificial illumination
Poplar leaf surface	0.027 to 0.039	Henson 1958	Nonlinear relationship; values are at 420 and 140 $W \cdot m^{-2}$, respectively

Section VI. REFERENCE MATERIAL

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2) APPENDICES

Appendix 1. Developmental rate (stadia·day^{-1}) of pre-imaginal Colorado potato beetles at constant temperatures, by year and isolate, as measured in the present studies. (MB, Manitoba isolate; BC, British Columbia isolate; N, initial sample size; S, number surviving).

EGGS

	1990 MB				1991 BC				1991 MB				ALL DATA POOLED	
°C	MEAN	S.E.	N	S	MEAN	S.E.	N	S	MEAN	S.E.	N	S	MEAN	S.E.
17	0.069	0.012	111	13	0.077	0.005	107	64	0.073	0.006	119	64	0.073	0.003
21	0.137	0.021	68	14	0.141	0.005	141	34	0.136	0.016	106	67	0.137	0.004
24	.	.	.	.	0.203	0.017	156	53	0.210	0.016	112	51	0.207	0.011
25	0.191	0.071	54	10	.	.	.	.	.	.	.	.	0.191	0.071
27	.	.	.	.	0.238	0.016	195	45	0.217	0.016	68	21	0.231	0.013
29	0.252	0.047	83	20	.	.	9	0	0.289	0.054	194	47	0.266	0.017
31	.	.	.	.	0.257	0.009	143	27	0.271	0.025	114	13	0.262	0.012

FIRST INSTAR

	1990 MB				1991 BC				1991 MB				ALL DATA POOLED	
°C	MEAN	S.E.	N	S	MEAN	S.E.	N	S	MEAN	S.E.	N	S	MEAN	S.E.
17	.	.	.	.	0.137	0.012	118	29	0.108	0.004	51	12	0.128	0.009
21	.	.	.	.	0.240	0.022	49	35	0.271	0.021	67	49	0.258	0.015
24	.	.	.	.	0.390	0.065	87	45	0.390	0.022	63	40	0.390	0.032
25	.	.	.	.	.	.	.	.	.	.	.	.	.	.
27	.	.	.	.	0.451	0.031	81	51	0.450	0.069	34	15	0.451	0.029
29	.	.	.	.	.	.	.	.	0.486	0.037	51	27	0.486	0.037
31	.	.	.	.	0.547	0.054	110	68	0.470	0.026	33	7	0.540	0.045

SECOND INSTAR

	1990 MB				1991 BC				1991 MB				ALL DATA POOLED	
°C	MEAN	S.E.	N	S	MEAN	S.E.	N	S	MEAN	S.E.	N	S	MEAN	S.E.
17	0.173	0.176	42	10	0.134	0.006	39	16	0.114	.	11	1	0.164	0.037
21	0.300	0.079	18	12	0.317	0.028	37	27	0.274	0.023	48	31	0.296	0.015
24	.	.	.	.	0.424	0.023	39	25	0.384	0.022	38	26	0.403	0.017
25	0.410	0.134	19	11	.	.	.	.	.	.	.	.	0.410	0.134
27	.	.	.	.	0.439	0.029	58	39	0.458	0.043	22	11	0.443	0.025
29	0.614	0.177	26	9	.	.	.	.	0.473	0.064	28	15	0.562	0.049
31	.	.	.	.	0.580	0.074	64	27	0.551	0.050	18	9	0.573	0.052

Appendix 1. (Cont'd). Developmental rate (stadia·day^{-1}) of pre-imaginal Colorado potato beetles at constant temperatures, by year and isolate, as measured in the present studies. (MB, Manitoba isolate; BC, British Columbia isolate; N, number surviving).

| | 1990 | | | | 1991 | | | | | | | | ALL DATA | |
| | MB | | | | BC | | | | MB | | | | POOLED | |

THIRD INSTAR

'C	MEAN	S.E.	N	S	MEAN	S.E.	N	S	MEAN	S.E.	N	S	MEAN	S.E.
17	0.160	0.035	23	12	0.112	0.005	15	9	.	.	.	.	0.145	0.010
21	0.272	0.061	19	15	0.239	0.165	26	20	0.254	0.013	31	30	0.258	0.009
24	.	.	.	.	0.362	0.021	26	22	0.353	0.017	26	24	0.358	0.014
25	0.349	0.069	17	12	.	.	.	.	.	.	.	.	0.349	0.069
27	.	.	.	.	0.448	0.028	39	30	0.380	0.022	13	9	0.432	0.024
29	0.575	0.354	23	14	.	.	.	.	0.538	0.046	15	12	0.565	0.062
31	.	.	.	.	0.450	0.032	39	21	0.438	0.058	6	3	0.447	0.028

FOURTH INSTAR

'C	MEAN	S.E.	N	S	MEAN	S.E.	N	S	MEAN	S.E.	N	S	MEAN	S.E.
17	0.123	0.070	23	13	0.089	0.005	12	8	.	.	.	.	0.110	0.014
21	0.198	0.032	26	22	0.172	0.008	22	18	0.196	0.017	30	28	0.191	0.006
24	.	.	.	.	0.226	0.018	21	17	0.238	0.018	23	21	0.233	0.010
25	0.225	0.050	28	23	.	.	.	.	.	.	.	.	0.225	0.050
27	.	.	.	.	0.295	0.016	32	23	0.295	0.023	9	9	0.294	0.013
29	0.320	0.174	39	27	.	.	.	.	0.340	0.000	14	2	0.321	0.032
31	.	.	.	.	0.329	0.038	9	5	.	.	1	0	0.329	0.038

Appendix 2.   Comparative effect of insolation and temperature in
      behavioral response of Colorado potato beetle larvae.

$$\ln[U/(1-U)] \equiv \text{logit}(U) = x + yT + zP \qquad\qquad \text{al.1}$$

Temperature effect on logit(U) $\equiv \partial(\text{logit}(U))/\partial T = y$

Insolation effect on logit(U) $\equiv \partial(\text{logit}(U))/\partial P = z$

For an arbitrarily small constant value of logit(U),

$$\frac{\partial(\text{logit}(U))/\partial P}{\partial(\text{logit}(U))/\partial T} = \frac{z}{y} = \frac{\partial T}{\partial P} = 0.0838$$

This solution is independent of both T and P.

The units of z are $\text{logits}/(W \cdot m^{-2})$.

The units of y are $\text{logits}/(°C)$.

Therefore the units of (z/y) are $°C/(W \cdot m^{-2})$ and the units of $z/y \cdot P$ are
°C. Consequently, the units of T^* are also $°C.y$

Appendix 3. Comparison of measured insolation (W·m⁻²) above canopy, with insolation above and below caged and uncaged leaflets, Glenmore, B.C. 1991.

| | | ABOVE | CAGE TYPE | | | | | |
| | | | NONE[a] | | CLEAR | | OPAQUE | |
DATE	TIME	CANOPY	ABOVE	BELOW	ABOVE	BELOW	ABOVE	BELOW
09 Jul	11:30	290.7	279.9	66.0	169.3	36.0	8.0	4.0
09 Jul	17:00	240.0	269.3	40.7	140.0	18.8	8.3	5.1
23 Jul	12:00	314.7	329.1	65.0	170.7	60.7	16.0	7.1
23 Jul	14:00	382.7	405.1	72.7	224.0	80.0	6.9	4.9
27 Jul	15:00	162.7	145.3	48.0	93.3	7.6	11.3	1.4
01 Aug	8:00	86.7	84.6	13.6	46.7	20.0	5.7	1.5
01 Aug	9:00	153.3	135.7	32.1	73.3	6.7	8.5	0.4
21 Aug	9:30	166.7	156.2	35.8	60.0	33.3	7.6	2.9
21 Aug	15:30	261.3	273.2	51.1	120.0	56.0	6.7	2.7

[a] measurement taken within canopy near leaflet without cage

Appendix 4. Behavioral thermoregulation trial. Temperature (T, °C); photometer reading (P, $W \cdot m^{-2}$); and proportion of larvae moving under the leaf (U), by instar and shade treatment (0, 1, 2 and 4 refer to numbers of layers of shade; C means shade = opaque card). n = 5/cell except repetition 1 (n=3) and cells marked *, where n = 4 through misadventure.

Repetition (RUN) dates and times were as follows. RUN 1: 28 Jul 0930 - 1030h; RUN 2 30 Jul 1400 - 1600h; RUN 3 31 Jul 1600 - 1800h; RUN 4 01 Aug 0800 - 0900h; RUN 5 01 Aug 1500 - 1600h.

RUN	INSTAR	SHADE TREATMENT														
		0			1			2			4			C		
		T	P	U	T	P	U	T	P	U	T	P	U	T	P	U
1	1	27.6	300	0.33	.	.	.	.	.	.	.	.	.	.	.	.
	2	27.3	293	1.0	.	.	.	.	.	.	.	.	.	.	.	.
	3	27.5	300	1.0	.	.	.	.	.	.	.	.	.	.	.	.
	4	27.2	293	0.67	.	.	.	.	.	.	.	.	.	.	.	.
2	1	34.3	320	1.0	33.1	203	1.0	32.0	125	0.6	32.3	73	0.4	32.6	46	0.4
	2	34.4	331	1.0	33.0	207	1.0	32.3	124	0.8	32.0	76	0.4	32.4	47	0.0
	3	35.2	331	1.0	34.5	200	1.0	34.1	125	1.0	34.5	73	0.75*	34.2	45	0.6
	4	36.2	335	1.0	35.8	205	1.0	35.0	123	1.0	35.2	72	0.8	34.7	44	0.8
3	1	27.7	300	1.0	27.4	184	1.0	27.1	113	0.5*	27.4	70	0.6	27.1	43	0.0
	2	27.7	293	1.0	26.8	152	1.0	27.2	125	0.4	27.1	72	0.4	27.8	47	0.0
	3	26.4	300	1.0	25.1	207	1.0	24.8	147	0.6	24.8	91	0.6	24.5	56	0.4
	4	25.4	293	1.0	24.5	160	0.2	25.4	136	0.0	24.9	104	0.2	25.0	83	0.0
4	1	17.8	288	1.0	17.4	179	0.2	17.5	110	0.0	.	.	.	.	.	.
	2	19.0	295	1.0	19.0	181	0.0	19.2	114	0.0	.	.	.	.	.	.
	3	20.7	302	0.8	20.2	191	0.6	19.8	119	0.2	.	.	.	.	.	.
	4	18.8	293	0.8	18.7	175	0.8	18.4	110	0.0	.	.	.	.	.	.
5	1	.	.	.	30.7	200	1.0	30.4	125	1.0	30.4	73	0.6	31.0	46	0.2
	2	.	.	.	30.7	192	1.0	30.4	120	1.0	30.4	69	0.6	30.7	40	0.0
	3	.	.	.	31.0	188	1.0	29.7	109	0.4	30.1	71	0.4	29.4	43	0.0
	4	.	.	.	30.4	189	1.0	30.0	111	0.2	29.4	68	0.0	29.1	40	0.0

Appendix 5. Comparison of larval stadia (days) as observed (REAL) and
as estimated by developmental rate model versions. Cohorts 1 to 6
pinned to plants 12 Jun 91; Cohorts 7 to 10 pinned to plants
03 Jul 91; Cohorts 11 to 16 pinned to plants 28 Jul 91. Dashes
indicate cohort extinction.

FIRST INSTAR

STADIUM

			MODEL VERSION PREDICTIONS			
COHORT	OBSERVED	n[a]	1.1	1.2	2.1	2.2
1	-	-	-	-	-	-
2	-	-	-	-	-	-
3	4.00	8	6.00	6.00	5.25	4.25
4	4.50	3	6.00	6.00	5.25	4.25
5	4.25	17	6.25	6.25	5.50	5.00
6	-	-	-	-	-	-
7	5.25	11	4.00	4.00	7.00	5.50
8	5.25	18	4.25	4.25	7.25	5.50
9	5.25	16	4.00	4.00	7.50	6.00
10	5.25	22	4.75	4.75	7.25	5.75
11	5.50	15	4.50	4.50	6.75	5.75
12	6.25	24	4.00	4.00	7.25	6.50
13	5.25	26	4.50	4.50	6.75	5.75
14	5.25	7	4.25	4.25	6.50	5.75
15	5.25	22	4.25	4.25	6.00	5.25
16	5.00	15	4.25	4.25	6.00	5.25

[a] maximum number observed during instar

SECOND INSTAR

| | | | STADIUM MODEL VERSION PREDICTIONS | | | |
COHORT	OBSERVED	n	1.1	1.2	2.1	2.2
1	-	-	-	-	-	-
2	-	-	-	-	-	-
3	3.50	4	4.75	4.75	4.25	4.00
4	3.25	3	4.00	4.00	4.50	3.75
5	-	-	-	-	-	-
6	-	-	-	-	-	-
7	-	-	-	-	-	-
8	3.00	8	3.00	3.00	4.50	3.50
9	3.25	11	3.25	3.25	4.75	3.75
10	3.25	17	2.75	2.75	4.50	3.50
11	3.00	10	3.00	3.00	4.00	3.25
12	2.75	16	3.00	3.00	4.00	3.25
13	2.75	8	3.00	3.00	4.00	3.25
14	3.00	2	3.00	3.00	4.00	3.25
15	-	-	-	-		
16	2.75	8	2.75	2.75	4.00	3.25

THIRD INSTAR

| | | | STADIUM MODEL VERSION PREDICTIONS | | | |
COHORT	OBSERVED	n	1.1	1.2	2.1	2.2
1	-	-	-	-	-	-
2	-	-	-	-	-	-
3	3.75	3	4.25	4.25	5.50	4.50
4	4.50	1	4.25	4.25	6.25	4.75
5	-	-	-	-	-	-
6	-	-	-	-	-	-
7	-	-	-	-	-	-
8	4.50	6	3.75	3.75	5.50	5.00
9	4.50	11	3.75	3.75	5.75	5.25
10	-	-	-	-	-	-
11	5.00	5	5.25	5.00	5.25	5.00
12	5.00	15	5.00	5.00	5.50	5.25
13	-	-	-	-	-	-
14	4.50	2	5.00	5.00	5.00	4.75
15	-	-	-	-	-	-
16	4.25	7	5.00	5.00	5.25	4.75

FOURTH INSTAR STADIUM

			MODEL VERSION PREDICTIONS			
COHORT	OBSERVED	n	1.1	1.2	2.1	2.2
1	-	-	-	-	-	-
2	-	-	-	-	-	-
3	5.25	3	5.75	6.00	7.00	5.75
4	5.25	1	5.50	5.75	7.75	6.00
5	-	-	-	-	-	-
6	-	-	-	-	-	-
7	-	-	-	-	-	-
8	4.75	5	6.50	6.50	6.25	5.25
9	5.50	3	6.25	6.25	6.25	5.25
10	-	-	-	-	-	-
11	-	-	-	-	-	-
12	4.75	10	5.25	5.50	8.25	5.50
13	-	-	-	-	-	-
14	4.75	1	5.25	5.25	7.50	5.75
15	-	-	-	-	-	-
16	5.00	3	5.25	5.25	7.50	5.75

TOTAL LARVAL STAGE. SUM OF PRECEDING MODEL ESTIMATES[a]

		MODEL VERSION PREDICTIONS			
COHORT	OBSERVED	1.1	1.2	2.1	2.2
1	-		-	-	--
2	-	-	-	-	-
3	16.50	20.75	21.00	22.00	18.50
4	17.50	19.75	20.00	23.75	18.75
5	-	-	-	-	-
6	-	-	-	-	-
7	-	-	-	-	-
8	17.50	17.50	17.50	23.50	19.25
9	18.50	17.25	17.25	24.25	20.25
10	-	-	-	-	-
11	-	-	-	-	-
12	18.75	17.25	17.50	25.00	20.50
13	-	-	-	-	-
14	14.50	14.50	14.50	19.00	16.25
15	-	-	-	-	-
16	17.00	17.25	17.25	22.75	19.00

[a] As opposed to the value obtained by running the model without intervention from hatch to prepupation. Method adopted minimizes errors resulting from mismatch between instar and thermal regime, owing to model and observed phenology getting progressively further out of phase.

Appendix 6. Mean temperatures (°C), with standard deviations (SD) during cohort ontogeny from date eggs pinned to plants to final observed prepupation, as estimated by model versions.

	OBSERVED[a]		MODEL VERSION							
			1.1		1.2		2.1		2.2	
COHORTS	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD
1 - 6	16.9	6.09	18.5	7.01	18.5	6.98	23.0	10.6	21.9	8.65
7 -10	19.5	6.52	21.2	7.40	21.2	7.37	26.2	11.2	24.2	8.75
11 -16	21.2	6.95	22.9	7.88	22.8	7.84	27.7	11.5	25.4	9.11

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[a]   Macroclimate temperature in Stevenson screen at Kelowna Municipal Airport, ≈ 5 km S of experimental site

Appendix 7. Equivalence of ratio and extrapolation methods of estimating fresh leaflet mass of potato plants.

By the ratio method:

$$\hat{F}_L = F_H \cdot \frac{r_h - r_s}{r_l - r_s} \tag{1a}$$

By the extrapolation method:

$$\hat{F}_L = F_H \cdot \frac{f_l}{f_h} \tag{2a}$$

Therefore, (a1) and (a2) are equivalent if:

$$\frac{f_l}{f_h} = \frac{r_h - r_s}{r_L - r_s} \tag{3a}$$

Right hand side (RHS) of (3a), top:

$$r_h - r_s = \frac{D_h}{F_h} - \frac{D_s}{F_s} = \frac{D_h F_s - D_s F_h}{F_h F_s}$$

Similarly, 3a, RHS of 3a, bottom:

$$r_L - r_s = \frac{D_L}{F_L} - \frac{D_s}{F_s} = \frac{D_L F_s - D_s F_L}{F_L F_s}$$

Reconstituting equation (3a):

$$\frac{r_h - r_s}{r_L - r_s} = \frac{\dfrac{D_h F_s - D_s F_h}{F_h F_s}}{\dfrac{D_L F_s - D_s F_L}{F_L F_s}}$$

$$= \frac{F_L}{F_h} \cdot \frac{D_h F_s - D_s F_h}{D_L F_s - D_s F_L}$$

Assuming that f_L/f_h is an unbiased estimator of F_L/F_h, and that estimates of the dry/fresh mass ratio are unbiased, equation 3a is true if:

$$\frac{D_h F_s - D_s F_h}{D_L F_s - D_s F_L} = 1$$

Appendix 7 (Cont'd). Equivalence of ratio and extrapolation methods of
    estimating fresh leaflet mass of potato plants.
i.e. if

$$D_h F_s - D_s F_h = D_L F_s - D_s F_L \qquad (4a)$$

Left hand side of 4a:

$$
\begin{aligned}
D_h F_s - D_s F_h &= (D_L + D_s) F_s - D_s (F_L + F_s) \\
&= D_L F_s + D_s F_s - D_s F_L - D_s F_s \\
&= D_L F_s - D_s F_L
\end{aligned}
$$

= right hand side of 4a; therefore, 4a is true, therefore 3a is
true: the two methods are equivalent. (Q.E.D.)

Appendix 8. Macroclimate air temperature at Winnipeg International Airport, and temperature and insolation in microclimates within large cages used in study validating models of Colorado potato beetle larval feeding and development rates under fluctuating conditions. Dates are 1992.
OUTSIDE, outside cage; INSIDE, inside cage; ABOVE, above leaflet; BELOW, below leaflet.

DATE	TIME	MICROCLIMATE						AIRPORT
		TEMPERATURE (°C)			INSOLATION ($W \cdot m^{-2}$)			TEMP (°C)
		OUTSIDE	INSIDE		OUTSIDE	INSIDE		
			BELOW	ABOVE		BELOW	ABOVE	
01 Aug	06:15	13.7	13.7	13.7	8.0	6.7	3.0	12.4
01 Aug	07:00	15.7	15.7	15.8	36.7	25.3	3.0	13.5
01 Aug	07:30	20.2	20.3	20.3	60.0	44.0	9.8	14.6
01 Aug	08:00	20.9	20.7	20.7	90.0	72.0	12.6	15.7
01 Aug	09:00	24.9	24.9	24.8	176.0	105.2	25.8	18.5
01 Aug	09:30	24.7	25.5	24.5	206.7	126.7	28.6	19.2
01 Aug	10:00	27.3	26.8	26.9	253.3	156.0	37.8	19.8
01 Aug	10:30	28.3	27.8	27.9	306.7	173.3	43.4	20.6
01 Aug	11:00	26.9	27.2	27.4	326.7	184.0	48.4	21.5
01 Aug	12:00	27.3	27.8	27.6	360.0	202.7	54.2	21.9
01 Aug	13:00	28.4	28.8	28.9	373.3	220.0	56.0	22.3
01 Aug	14:00	30.4	29.9	30.1	366.7	214.7	52.0	22.8
01 Aug	15:00	29.9	29.3	29.4	365.3	180.0	54.6	22.8
01 Aug	16:00	29.7	29.4	29.3	346.7	174.7	50.4	22.8
20 Aug	09:30	25.4	25.4	25.5	186.7	100.0	26.0	19.9
20 Aug	10:00	26.6	26.4	26.5	173.3	80.0	24.2	21.0
20 Aug	11:00	28.4	28.4	28.4	297.3	166.7	44.6	23.1
20 Aug	11:50	27.9	28.2	28.2	84.8	58.0	12.0	23.2
20 Aug	12:00	29.1	29.1	29.0	369.3	220.0	55.2	23.2
20 Aug	13:00	30.5	30.5	30.6	380.0	240.0	58.8	22.9
20 Aug	14:10	28.1	28.0	27.9	86.0	68.0	13.0	24.2
20 Aug	14:20	28.9	28.8	28.7	393.3	229.3	61.0	22.5
20 Aug	15:00	29.4	29.1	29.2	356.0	193.3	52.0	21.7
20 Aug	16:00	27.3	27.8	27.8	309.3	180.0	27.4	20.7
20 Aug	17:00	25.3	25.1	25.1	216.0	153.3	32.0	17.6
20 Aug	17:30	20.8	20.7	20.8	52.8	33.1	6.2	17.6
29 Aug	07:20	15.4	15.3	15.3	2.4	1.1	0.2	13.8
29 Aug	07:50	14.4	14.4	14.4	4.0	2.5	0.6	13.7
29 Aug	08:50	15.0	15.3	15.1	58.8	34.7	9.6	13.8
29 Aug	09:45	19.2	19.0	19.0	240.0	140.0	32.6	13.0
29 Aug	10:30	19.8	19.8	19.6	266.7	153.3	35.6	13.6
29 Aug	11:20	19.1	19.1	19.0	294.7	180.0	42.6	13.2

Appendix 9. Estimated leaf area removed (cm²) by adults and larvae (weekly and seasonal total), final harvested leaf areas (m²) and tuber yield, by year and multiple of field density maintained on plant.

1986

MULTIPLE OF FIELD DENSITY

WEEK	0 ADULT	0 LARVAE	0.5 ADULTS	0.5 LARVAE	1 ADULTS	1 LARVAE	2 ADULTS	2 LARVAE	4 ADULTS	4 LARVAE
1	0	0	0	0	0	0	0	0	0	0
2	0	0	0	12	32	12	32	35	42	7
3	0	0	0	146	18	198	25	436	60	846
4	0	0	0	661	7	1316	21	2595	28	5247
5	0	0	0	788	0	1627	4	3184	4	6387
6	0	0	0	571	0	1265	7	2416	25	4821
7	4	0	67	217	126	468	249	945	571	1851
8	0	0	224	124	455	233	938	506	1759	1012
9	5	0	298	95	742	238	1386	412	1943	411
10	11	0	389	58	833	132	1663	307	2170	556
11	4	0	249	0	543	35	1117	68	1969	68
12	0	0	105	5	186	19	396	38	831	45
13	0	0	70	0	119	1	245	5	490	2
SUM[a] (cm²)	53	0	1400	2677	3059	5545	6080	10946	9889	21316
FLA[b] (m²)	5.04 ± 2.25		4.55 ± 1.08		3.68 ± 0.35		2.60 ± 0.91		0.55 ± 0.59	
TOT1[c] (m²)	5.05		4.83		4.23		3.69		2.68	
TOT2[d] (m²)	5.05		4.96		4.54		4.30		3.67	
YIELD[e] (kg)	2.55 ± 0.49		2.27 ± 0.30		1.86 ± 0.29		1.24 ± 0.37		0.18	0.27
	(3.12 ± 0.28)[f]									

[a] Column total

[b] Final leaf area per plant ± standard error (n = 5)

[c] Final leaf area + estimated larval feeding

[d] Final leaf area plus estimated larval feeding plus estimated adult feeding

[e] marketable tubers only

[f] mean marketable yield of undisturbed control plants

Appendix 9 (Cont'd). Estimated feeding rates (cm^2) by adults and larvae (weekly and seasonal total), final harvested leaf areas (m^2) and tuber yield, by year and multiple of field density maintained on plant.

1987

MULTIPLE OF FIELD DENSITY

WEEK	0 ADULT	0 LARVAE	0.25 ADULTS	0.25 LARVAE	0.5 ADULTS	0.5 LARVAE	1 ADULTS	1 LARVAE	2 ADULTS	2 LARVAE
1	0	0	0	0	0	9	0	18	0	35
2	0	0	0	345	0	728	25	1490	32	2944
3	0	0	0	370	0	763	18	1593	21	3090
4	0	0	0	401	4	707	14	1462	28	2880
5	0	0	7	430	7	900	46	1840	60	3587
6	0	0	109	129	161	257	308	506	620	1026
7	4	0	140	17	294	47	504	95	1113	82
8	18	0	221	12	410	14	858	34	1225	32
9	7	0	231	0	389	74	809	176	1654	352
10	28	0	119	0	203	0	410	81	866	182
11	21	0	49	1	102	0	179	0	420	0
12	0	0	18	0	25	0	56	0	96	0
13	0	0	14	14	7	3	25	6	26	0
SUM (cm²)	77	0	907	1720	1600	3502	3248	7301	6160	14209
FLA (m²)	5.81 ± 2.41		5.65 ± 1.13		.	.	3.42 ± 2.53		0.85 ± 1.11	
TOT1 (m²)	5.82		5.82		.	.	4.15		2.27	
TOT2 (m²)	5.82		5.91		.	.	4.47		2.89	
YIELD (kg)	2.72 ± 0.19		2.73 ± 0.55		2.84 ± 0.29		1.66 ± 0.37		0.66 ± 0.77	
	(3.82 ± 1.01)									