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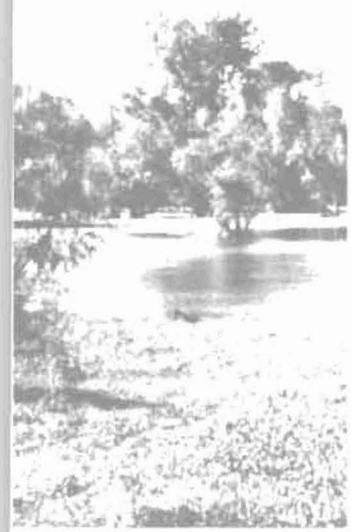

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SIMULATION MODEL OF WATERHYACINTH AND ITS BIOCONTROL AGENTS

Report 1
FIRST-GENERATION MODEL

by

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This report presents the results of initial efforts to develop a microcomputer-based software package that simulates the effectiveness of biological agents in controlling waterhyacinth [*Eichhornia crassipes* Mart. (Solms)]. This first-generation model (INSECT) simulates the development of populations of waterhyacinth and two biocontrol agents [*Neochetina eichhorniae* Warner and *N. bruchi* Hustache (Coleoptera:Curculionidae)] for a 1-year period (i.e., 365 Julian days).

Algorithms included in the model are based on available information concerning the response of these organisms to environmental factors (e.g., temperature and solar radiation). Actual field data have been compared with simulation output with encouraging results. Starting biomass of the plants and numbers of weevils in each life stage can be varied to determine the algorithms' sensitivity to initial conditions. Several iterations of this

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procedure have been performed with realistic responses, shown as graphs of the simulated response compared to corresponding field observations from the same time period. Sample input and output for 1 year of simulation are included as an appendix.

Data and relationships needed to improve the performance of the model are identified, and suggestions for further refinement of the model are included.

PREFACE

This study was conducted as part of the US Army Corps of Engineers Aquatic Plant Control Research Program (APCRP) under Work Units 32356 and 32438, Computer-Aided Evaluation Systems Development. Funds for the effort were provided by the Office, Chief of Engineers, under Department of the Army Appropriation No. 96X3122, Construction General, 902740, through the APCRP at the US Army Engineer Waterways Experiment Station (WES), Vicksburg, Miss.

The investigators for the work were Drs. Kunter S. Akbay, Jean W. Wooten, and Fred G. Howell of the University of Southern Mississippi, under Contract No. DACW39-85-K-0002. Dr. Akbay is presently at Marquette University, Milwaukee, Wis.

This effort was monitored at WES by Mr. Bruce Sabol and Mrs. Katherine Long, Environmental Analysis Group (EAG), Environmental Systems Division (ESD), Environmental Laboratory (EL), WES. Direct supervision throughout this effort was provided by Mr. H. W. West, Chief, EAG. General supervision was provided by Dr. V. E. LaGarde III, Chief, ESD, and Dr. John Harrison, Chief, EL. Mr. J. Lewis Decell was Program Manager of the APCRP. The report was edited by Ms. Jessica S. Ruff of the WES Information Technology Laboratory.

Commander and Director of WES was COL Dwayne G. Lee, CE. Technical Director was Dr. Robert W. Whalin.

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FIRST-GENERATION MODEL

PART I: INTRODUCTION

Background

1. Several methods are now available to control aquatic plants. The choice of methods can be made easier by the use of computer-aided simulation of the various techniques. Two computer models designed by WES for use on personal computers (PCs) can provide such simulations. They are now receiving limited use by waterway and natural resource managers. One model (HARVEST) deals with the mechanical harvesting of submersed aquatic vegetation; the other (WHITE AMUR STOCKING-RATE) deals with the growth of the white amur and its ingestion of hydrilla vegetation.

2. As new biocontrol technologies are developed, simulation models are needed for these techniques. Because one advantage of biocontrol methods is that they can be self-sustaining, a way of determining sufficient populations of prey organisms to effect control is to model these populations and associated environmental parameters. Such a model would potentially save considerable time and effort by conducting model simulations prior to expensive field trials. The models would ideally be designed to allow incorporation of additional relationships revealed when the field trials were actually conducted. A model should reflect, but not be limited to, the responses of a particular aquatic plant and its particular feeder organisms under the assumption that basic forces described as influencing an organism's responses to its environment could be readily modified to reflect those responses under different conditions.

Scope

3. The model presented in this report is a reflection of the interaction and behavior of the waterhyacinth and two species of *Neochetina* weevil. Within the body of this report are suggestions for adaptation of the logical framework of this model to other plant-insect associations. Field data

collected in independent studies are displayed to demonstrate the accuracy of model predictions. Recommendations for improving the performance of this particular model are given.

Immediate Objectives

4. The immediate objectives of this work are as follows:

   a. To identify important factors that influence waterhyacinth growth and to express these factors quantitatively as functions of measurable environmental parameters.

   b. To develop a conceptual model reflecting how waterhyacinth and two species of *Neochetina* weevil interact with each other within a specified environment.

   c. To develop a code for a personal computer that executes in a user-friendly, interactive mode. Such a program should allow a user to specify site-specific conditions of daily light and temperature. If the user has no such file, one may be chosen from the several residing within the code.

Long-Range Objectives

5. The long-range goals of this research project are as follows:

   a. To develop methods, adaptable to any floating aquatic plant species and its proposed biological control agents, for quantitatively describing the results of environmental and target plant/control agent interactions through time.

   b. To develop user-friendly models that enable plant control managers to evaluate the effectiveness of candidate control measures and optimize application techniques.

PART II: THE MODEL

6. The waterhyacinth-*Neochetina* model INSECT is a first-generation computer-based biological simulation model developed for waterhyacinth (*Eichhornia crassipes* (Mart.) Solms) and two species of weevils (*Neochetina bruchi* Hustache and *N. eichhorniae* Warner). In this report, the conceptual model for INSECT, the preliminary results, and general information on operating the model are presented.

7. INSECT is a dynamic model that simulates plant growth, insect development, and plant/insect interactions on a daily basis within an area. Users of INSECT are able to generate simulation results for their particular aquatic area. The simulation period can start on Julian day 1 and end on Julian day 365. However, the user has the option of modifying the simulation period by entering the proper values for the beginning and ending days. (Work is under way to extend the model simulation period to approximately 3 years.)

8. The flowchart of the general conceptual model for INSECT is shown as Figure 1. After the plant and weevil components of the model are initialized on the first day of simulation, an iterative logic simulates the aquatic plant ecosystem. First, on each simulation day, daily weather data are read. Then, the plant module is called to calculate the total plant biomass available to weevils. The weevil module is composed in logic of two submodels that are almost identical. Due to differences in the developmental times and oviposition rates, *N. bruchi* and *N. eichhorniae* (Warner 1970) are modeled separately. After both the plant and weevil modules are called, impact on waterhyacinths by *Neochetina* spp. is calculated, and the daily results are output.

9. In the following sections, the major components of the INSECT model are discussed in the order in which they take place in the model.

10. INSECT is organized into two broad components: the plant module and the weevil module. Each must be initialized with variables of the user's choice to set initial conditions. From that point forward, the simulation proceeds until the prescribed number of simulation days has been accomplished. The user then has the option to select the output he desires.

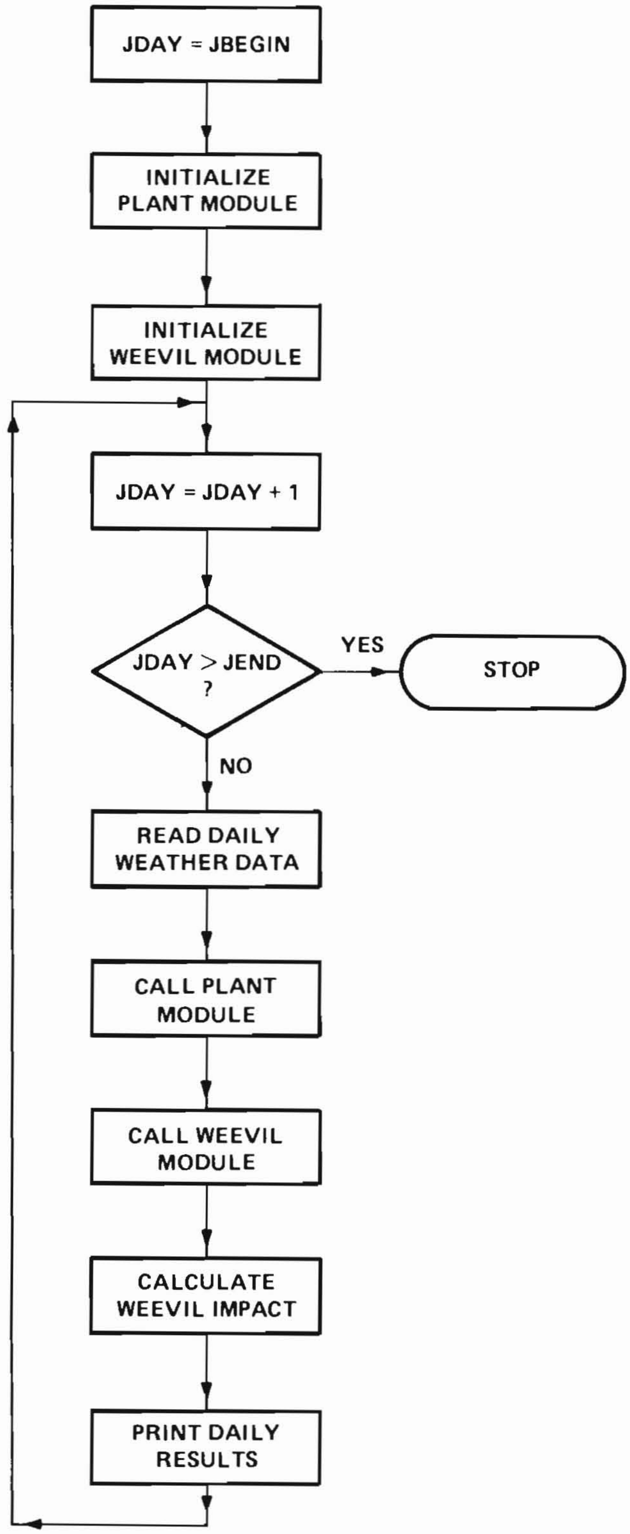

Figure 1. General flowchart of INSECT model

Plant Module

Introduction

11. A flowchart of the plant module is shown as Figure 2. This first-generation model is intended for simulating growth of waterhyacinth and interaction with the weevils in environments where nutrients are not limiting. It is formulated in terms of the dry weight per square meter occupied by plants and ultimately is extrapolated to the area of the body of water covered by plants. (Dry weight for waterhyacinth is conveniently obtained by multiplying wet weight by 0.05.)

12. The plant module was designed after careful study of the techniques of Ewel, Braat, and Stevens (1975); Mitsch (1975, 1976); Vega (1978); Lorber, Mishow, and Reddy (1984); and others. For the study reported here, a nonlinear relationship (with light and temperature as independent variables) derived from the results of the above-named and other studies was used. Thus, the module is a derivation of a deterministic (not stochastic) procedure. Furthermore, because energy balance equations are difficult to handle (partly because required driver data are usually not easily obtained), the procedure chosen to produce simulations of cumulative biomass versus time is reasonable at this development level of the model. Indeed, it is probably the only applicable approach given the present dearth of appropriate data.

13. As environmental data are collected and archived for the limits of geographic range for the waterhyacinth, predictions can be generated for the entire geographic reach of this exotic plant pest. Such a tool as INSECT would be powerful and invaluable to field management programs and could conceivably be extended to encompass entire regions.

Assumptions

14. The assumptions used in the plant module are as follows:

- a. Plant growth is simulated within a 1-sq m area of "a window" arbitrarily located within a population of waterhyacinths. This area is not a confined plot.
- b. Photosynthesis and respiration rates of the plants are functions of the prevailing temperature and light intensity, and past temperature and light experience have no effect on the current photosynthesis and respiration rates other than through effects on the mass of the plant.
- c. Growth takes place by a series of additive daily increments in leaf, rhizome, and root tissue. Each is determined by the

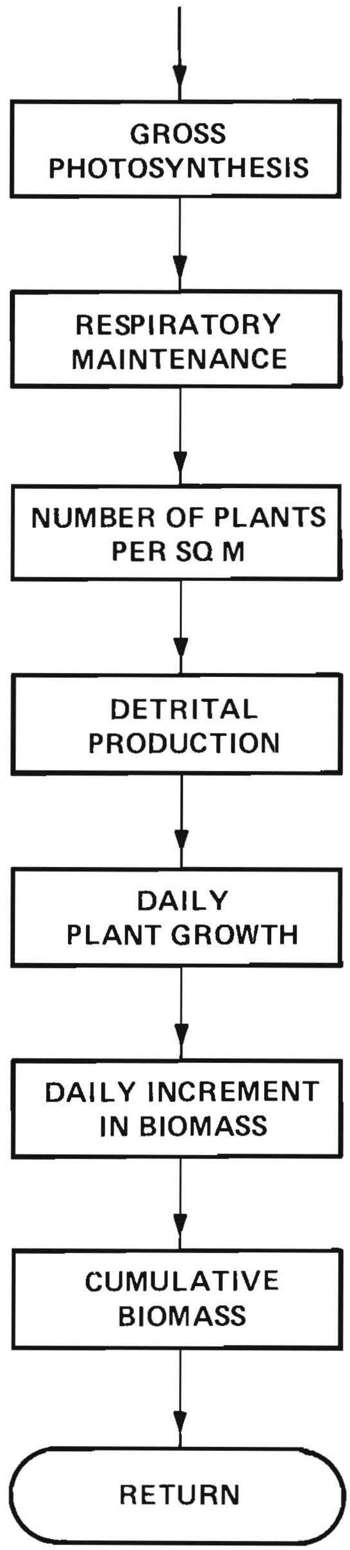

Figure 2. General flow-chart of the plant module

prevailing temperature and light intensity and the biomass density. Thus, any adaptive changes in leaf structure and function that may occur in response to the environment are not accounted for in this model.

d. Day and night respiration rates are equal.

e. Rates of respiration are not dependent on plant age and size.

f. Plant growth occurs under conditions in which nutrients and pH are not limiting.

g. Maintenance respiration cost increases linearly with density of plants.

h. Detritus consists of leaf material only.

i. Waterhyacinth plants are 95 percent water.

j. During the flowering season, efficiency of conversion of carbohydrates to vegetative material is less than when the plants are not flowering.

Initialization of plant module

15. The following variables in the waterhyacinth module must be initialized on the first day of simulation:

a. Initial biomass in kilograms per square meter.

b. Average number of leaves per plant (see Appendix A, Figure A1).

c. Average total leaf weight, in grams, of one plant (see Appendix A, Figure A2).

d. Estimate of dry weight percentage of plant composed of leaves (see Appendix A, Figure A3).

Daily weather data

16. INSECT is dynamic and, therefore, weather dependent. On each simulation day, before the plant and insect modules are called, daily weather data must be read. The following information is needed:

a. Maximum daily temperature in Celsius.

b. Minimum daily temperature in Celsius.

c. Solar radiation in langleys.

17. The logic for the conceptual module for waterhyacinth is demonstrated as a flowchart in Figure 2. In the following sections, the step-by-step procedure is presented.

Gross photosynthesis

18. Daily gross photosynthesis (PG, in grams per square meter) is calculated as follows:

$$PG = PMAX * FT * FN * FP * FDEN$$

where

PMAX = maximum photosynthesis (grams of carbohydrates per square meter)

FT = temperature limiting function

FN = nitrogen limiting function = 1.0

FP = phosphorus limiting function = 1.0

FDEN = density limiting function

19. The relationship for maximum photosynthesis is based on Mitsch (1975) and Lorber, Mishow, and Reddy (1984) and is expressed as follows:

$$PMAX = \begin{cases} 0.32 * SOLR, \text{ if } SOLR \leq 100 \\ 22.318 + 0.102 * SOLR, \text{ otherwise} \end{cases}$$

where SOLR is daily solar radiation in langleys.

20. Temperature limiting function is derived from Knipling, West, and Haller (1970), for temperatures between 15° and 42° C.

$$FT = 1.0 - 0.0037 * (ATEMP - 29)** 2$$

where ATEMP is average daily air temperature in degrees Celsius. If the value of FT becomes negative, the model sets its value equal to 0.028 based on calculation of the slope of the graph of Knipling, West, and Haller (1970).

21. The density limiting function is based on Lorber, Mishow, and Reddy (1984) as follows:

$$FDEN = \begin{cases} DENSTY/1{,}000, \text{ if } DENSTY < 1{,}000 \\ 1.0, \text{ otherwise} \end{cases}$$

where DENSTY is the previous day's total biomass in grams per square meter.

Respiratory maintenance

22. The relationship for daily respiratory maintenance (RM) is established from ranges presented by Penning de Vries (1975a). The RM appears to

vary due to climatic conditions; hence, geographic localities may differ in the number used in the model.

For Florida: RM = 0.019 * DENSTY

For Louisiana: RM = 0.015 * DENSTY

Number of plants per square meter

23. The following expression was derived based on unpublished data from Florida:*

$$ANPLTS = \frac{DENSTY * PRCTLV}{ATLW}$$

where

ANPLTS = number of plants per square meter on current simulation day

PRCTLV = estimated daily percent leaf material

ATLW = average total leaf weight, in grams, of one plant

The reliability of this relationship was established by graphing field-collected* counts of plants per square meter against derived values for the assumed growing season March through October. The correlation coefficient of these compared values was 0.86.

Leaf detrital production

24. The leaf detrital production value was derived by the authors using field data from Florida.* These data indicate that a leaf dies every 10.2 days. Therefore, the following expression was derived:

$$D = \left(\frac{ANPLTS}{10.2}\right)\left(\frac{ATLW}{ANLP}\right)$$

where ANLP is the average number of leaves per plant.

* T. D. Center. 1975-1980. Unpublished data, US Department of Agriculture, Agriculture Research Service, Aquatic Plant Management Lab, Fort Lauderdale, Fla.

Reduction of vegetative
material due to flowering

25. Based on an estimate* of the flowering season (late May to late November), the efficiency of conversion (E) is

For Florida:

$$E = \begin{cases} 0.65 \text{ if } 150 < \text{Julian date} < 330 \\ 0.75, \text{ otherwise} \end{cases}$$

For Louisiana:

$$E = \begin{cases} 0.73 \text{ if } 150 < \text{Julian date} < 330 \\ 0.75, \text{ otherwise} \end{cases}$$

These E values are calibrated from estimates of several genera of plants given by Penning de Vries (1975b).

Daily plant growth

26. Plant growth in dry weight per square meter per day is:

$$\text{DLTBM} = \begin{cases} [(\text{PG} - \text{RM}) * \text{E}] - \text{D}, \text{ if ATEMP} > 0 \\ - \text{D}, \text{ otherwise} \end{cases}$$

where

PG = daily gross photosynthesis, grams of carbohydrates/sq m

RM = respiratory maintenance = 0.019 (based on the range 0.015 to 0.025 of Penning de Vries 1975a)

E = efficiency of conversion

D = daily detrital production, g

Cumulative biomass

27. Cumulative biomass is computed as follows:

$$\text{BIOM(T)} = \text{BIOM(T-1)} + \text{DLTBM}$$

---

* T. D. Center, op. cit.

where

BIOM(T) = cumulative biomass for the current simulation day, g/sq m

BIOM(T-1) = cumulative biomass for the previous simulation day, g/sq m

DLTBM = increase in biomass on current simulation day, T

Nutrient leaching

28. Nitrogen and phosphorus leaching from plant reserves have not been incorporated in the module; therefore, it is assumed that there is no nutrient leaching.

Nutrients recycled from detritus

29. Nitrogen and phosphorus recycling from detritus back to plant nutrient reserves has not been incorporated in the module.

Nutrient levels in the water column

30. Nitrogen and phosphorus levels in the water are not updated in the module.

Weevil Module

Introduction

31. Several accounts of the life histories and ecology of *Neochetina* spp. contain important information on which to construct a simulation model of these insects and their association with waterhyacinths. Initial studies to determine host specificity and the subsequent release of *N. eichhorniae* were performed by Perkins (1973a, 1973b), while DeLoach and Cordo (1976a) and Perkins and Maddox (1976) performed similar studies on *N. bruchi* in Argentina. Stark and Goyer (1983) reported on the life cycle and behavior of *N. eichhorniae* from field sites in Louisiana. El Abjar and Bashir (1984) presented life table data on *N. bruchi* from Sudan. Other studies that were important in development of this model include, Price (1975), Evans (1984), Chiang (1985), and the unpublished Florida field data.* The flowchart of the weevil module is shown in Figure 3.

32. The weevil module contains subroutines for each species of *Neochetina*. This was necessary because the species differ in details of development times and oviposition rates.

* Ibid.

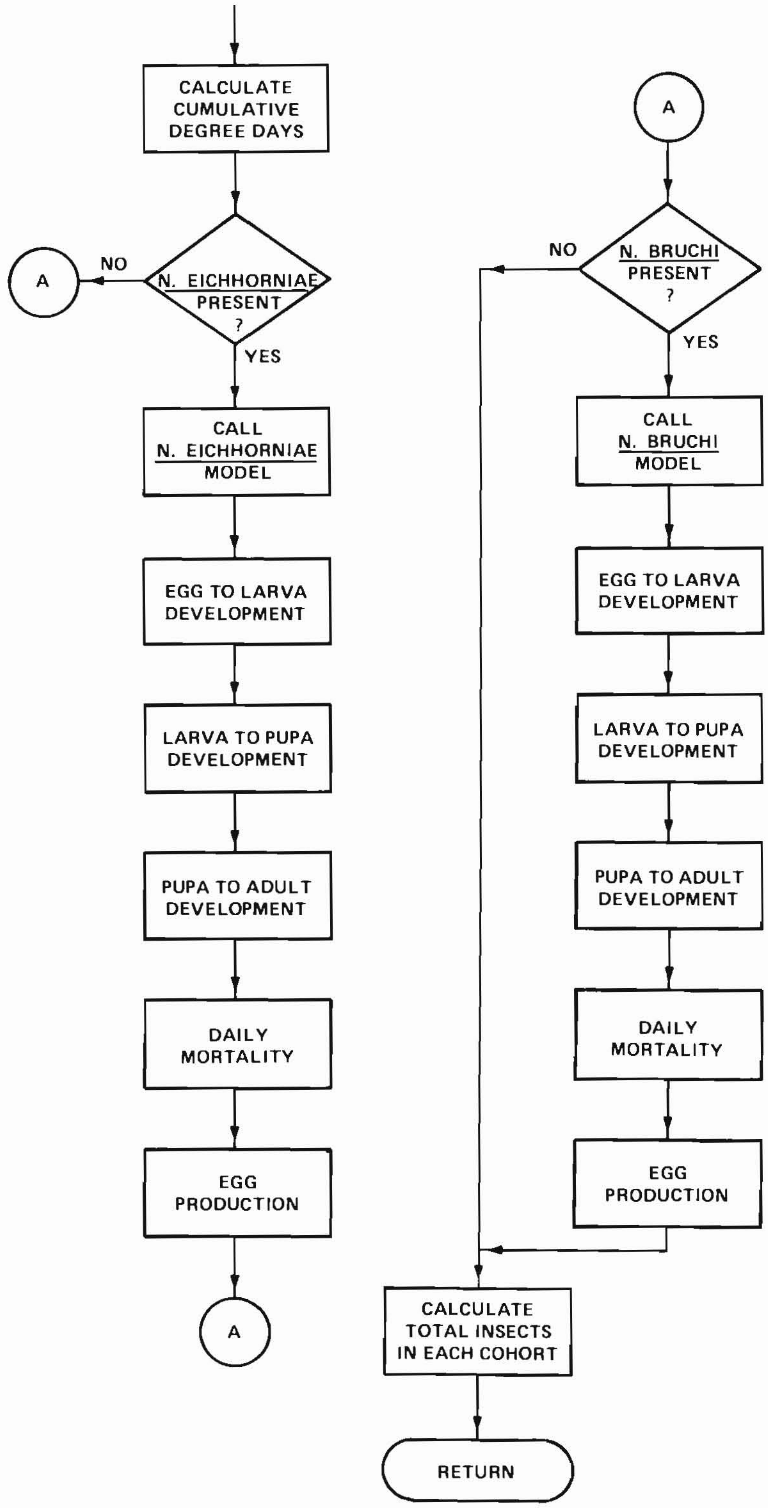

Figure 3. General flowchart of the weevil module

Assumptions

33. The following assumptions were made when developing the weevil module:

a. Temperature is the "governing force" that dictates insect development and, ultimately, the timing of population phenomena.

b. The unpublished data from Florida* for *Neochetina* spp. populations, particularly the 1976 and 1977 data, are accurate reflections of the population dynamics of this weevil under natural conditions in Florida.

c. Values retrieved from the literature regarding population characteristics (fecundity, oviposition rates, mortalities, survivorships) for *Neochetina* spp. are approximate and useful as initial values in model development.

d. No diapause or arrested development occurs during winter or summer months.

e. Distributions of eggs, larvae, and adults are uniform on or in plants and within the 1-sq m area.

f. No immigration occurs to the *Neochetina* populations.

g. Emigration occurs whenever carrying capacity is exceeded.

h. Natural mortalities include predation and other unexplained losses to the weevil populations.

i. Explained mortalities include losses due to subfreezing temperatures, detritus production, and emigration.

j. Other waterhyacinth predators are not present.

k. Larvae that have attained two-thirds of their thermal constant are considered to be third instar larvae.

l. Reduction in plant biomass is a result of bud predation by third instar larvae; daily feeding by adults and first and second instar larvae has no impact on plant biomass.

m. The module, for the most part, incorporates the simplest explanation for an observed population phenomenon. It is possible that more complex logic could be used to improve agreement of simulated data with observed data. However, this first-generation model has been written to maintain as much simplicity as possible. Complexity can and will be added as our understanding of the dynamics of plant/weevil interactions increases.

Initialization of weevil module

34. The weevil module requires the following information concerning the defined 1-sq m area to be input at the beginning of the simulation. The value for each variable should be entered as prompted, along with its appropriate

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* Ibid.

Julian date of collection. If a value is unknown and not entered, the model will assume zero for that value. The required data include:

- a. Total number of eggs and Julian day of collection.
- b. Total number of larvae and Julian day of collection.
- c. Total number of pupae and Julian day of collection.
- d. Total number of adults and Julian day of collection.
- e. Percent ratio of *N. bruchi* and *N. eichhorniae* (also on Julian day of collection).

35. The module was developed to predict numbers of individuals in the existing populations, including numbers of individuals entering or leaving the populations on a given simulation day. Insect cohorts, therefore, are calculated and updated on a daily basis (Brown, McClendon, and Jones 1982).

36. The following variables are used to represent the number of insects in different cohorts:

- a. EGG(I) = number of weevils that entered "egg" stage on day I and remain in the egg stage.
- b. LARVAE(I) = number of weevils that entered "larvae" stage on day I and remain in the larvae stage.
- c. PUPAE(I) = number of weevils that entered "pupae" stage on day I and remain in the pupae stage.
- d. ADULT(I) = number of weevils that entered "adult" stage on day I and remain in the adult stage.

37. The logic for the conceptual module for *Neochetina* spp. is demonstrated as a flowchart in Figure 3. For the sake of simplicity, only one version is presented. (Differences in *N. eichhorniae* and *N. bruchi* are noted.) The logic used in the weevil module is presented in the following sections.

Cumulative day-degrees

38. All stages, including life span of adults, are controlled by use of average temperatures (Chiang 1985). The threshold temperature is 11° C; below this temperature, no development occurs. (This value was empirically derived and was based on model performance under conditions known to exist during the time of field data collection. Brown, McClendon, and Jones (1982) used 13° C as the threshold temperature for cotton bollworms in Mississippi.) Between 11° and 22° C, development is advanced by day-degrees calculated on the difference between 11° C and the average daily temperature up to 22° C. Beyond 22° C, insects gain only 11 day-degrees per calendar day. The module currently uses no upper lethal temperature limit. Thus,

$$PT(I) = \begin{cases} PT(I-1) + \text{maximum of } (0 \text{ or } ATEMP - 11.0), \\ \quad \text{if } ATEMP \le 22 \\ PT(I-1) + 11, \text{ otherwise} \end{cases}$$

where

PT(I) = cumulative day-degrees for days 1 through I

PT(I-1) = previous day's cumulative day-degrees

ATEMP = average daily temperature in degrees Celsius

Based on the definition of cumulative day-degrees, physiological age of each cohort on a given day T is PT(T) - PT(I) given that the cohort entered the particular life stage on day I, where $I < T$.

Egg development

39. DeLoach and Cordo (1976a) reported 7.6 calendar days (at 30° C) for development time for *N. bruchi*; Stark and Goyer (1983) reported 8.0 calendar days (at 30° C) for *N. eichhorniae*. Therefore, the formulas for development of eggs to larvae are calculated by the following algorithms, using the above-stated developmental time:

$$LARVAE(T) = \sum_{I=1}^{T-1} EGG(I) * PE(I,T)$$

where

LARVAE(T) = number of eggs hatching (becoming larvae) on simulation day T

$$PE(I,T) = \begin{cases} 0.0, \text{ if } PT(T) - PT(I) < DDEGG \\ 1.0, \text{ otherwise} \end{cases}$$

DDEGG = required number of day-degrees for egg development

In the module, DDEGG is 88.0 and 83.6 day-degrees for *N. eichhorniae* and *N. bruchi*, respectively.

Larva development

40. Formulas for development of larvae to pupae follow the same logic. Developmental times (at 30° C) for *N. bruchi* are 39.4 calendar days (DeLoach and Cordo 1976a) and 41.0 calendar days for *N. eichhorniae* (Stark and Goyer 1983). Thus,

$$PUPAE(T) = \sum_{I=1}^{T-1} LARVAE(I) * PL(I,T)$$

where

PUPAE(T) = number of larvae becoming pupae on day I

$$PL(I,T) = \begin{cases} 0.0, & \text{if } PT(T) - PT(I) < DDLAR \\ 1.0, & \text{otherwise} \end{cases}$$

DDLAR = required number of day-degrees for larvae development

In the module, DDLAR is 451.0 and 433.4 day-degrees for *N. eichhorniae* and *N. bruchi*, respectively.

Pupa development

41. As above, pupa-to-adult development follows the logic used in other developmental stages. Both species appear to spend 30.0 calendar days (at 30° C) in the pupal stage (DeLoach and Cordo 1976a, Stark and Goyer 1983).

$$ADULT(T) = \sum_{I=1}^{T-1} PUPAE(I) * PP(I,T)$$

where

ADULT(T) = number of pupae becoming adult on day T

$$PP(I,T) = \begin{cases} 0.0, & \text{if } PT(T) - PT(I) < DDPUP \\ 1.0, & \text{otherwise} \end{cases}$$

DDPUP = required number of day-degrees for pupal development

In the module, DDPUP is assumed to be 330.0 day-degrees for both species.

Daily mortality

42. Cohort survival appears to be different than expected in typical holometabolous insects. Price (1975) discusses survivorship among insects and indicates that as much as 80 to 95 percent mortality can be expected as a cohort progresses through the immature stages, depending on whether the insect is a Type A or Type B. Literature accounts of *Neochetina* spp. survival, however, reveal a pattern of survival through these stages that appears to be extreme in comparison. For example, DeLoach and Cordo (1976a) reported these values for cohort survival: eggs - 96.6 percent, larvae - 85.0 percent, and

pupae - 95 percent. They report survival through all immature stages to be 78 to 80 percent.

43. Two classes of natural mortalities are recognized in the weevil module. These were set to respect the differences in seasonal dynamics of predators and other factors that may impact *Neochetina* spp. Winter and spring (through Julian day 180) mortalities are highly reduced (0.1 percent per day for eggs, larvae, and pupae; 0.5 percent for adults). Summer and fall (Julian days 180 through 365) approximate literature values (eggs - 0.90 percent per day, larvae - 0.75 percent per day, pupae - 0.167 percent per day, and adults - 3.4 percent per day). Summer and fall mortalities for larvae and adults are adjusted upward in the module (in comparison to literature values) to assist in matching simulated data to 1976 field data.

Effects of subfreezing temperatures

44. The unpublished Florida field data* for 1976 and 1977, in conjunction with temperature data for the same time intervals and locations, suggest that subfreezing temperatures have serious impacts on standing crops of adults and larvae. Values for adult and larval mortalities, resulting from subfreezing temperatures, are estimated from these data.

45. Information on the impacts to eggs is lacking. However, the impacts are assumed to be severe in that exposure to the environment is the greatest at this stage, since the eggs are embedded on the leaf surface of the host plant. By contrast, pupae are probably the most protected due to their position relative to the host plant and environment, i.e., submersed and entangled within the root hair zone of the host plant.

46. Logically, water temperature will "lag" behind subfreezing air temperatures; internal plant temperature can be expected to be intermediate between water and air temperatures, particularly during nighttime low temperature (Stewart and Howell 1985). Because only minimum and maximum temperature data are available for the years 1976-1978, duration of a subfreezing temperature cannot be used to estimate losses in the insect population. However, logic used in the module "protects" pupae first, larvae second, and adults third (because of their size, exoskeleton, and location on the plants). Eggs are assumed to possess the least amount of protection from adverse conditions.

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* Ibid.

47. Accordingly, the module assumes the following mortalities according to subfreezing temperatures: for light frost to freeze (-0.5 to -1.5° C), 50 percent mortality for eggs, 1 percent for larvae and pupae, and 3 percent for adults. Below -1.5° C, death results to 95 percent of the eggs, 30 percent of the larvae, 1.5 percent of the pupae, and 10 percent of the adults. At this point in model development, these values are speculative.

Threshold plant biomass

48. If plant biomass (dry weight) is below 700 g/sq m, the module will begin to remove insects at a rate equal to the proportion of insects (all stages) (multiplied by the daily mortality factors) over the plant biomass threshold value. (Vega (1978) estimated that 600 g of foliage biomass is required to sustain the insect population.)

Migration and carrying capacity
(ratio of adults to environment)

49. If the total number of adults exceeds 225 per square meter regardless of plant biomass, 15 percent of the first-day adults are removed from the population. This portion of losses is assumed to be migration to other areas via flight and other means. By this logic, flight muscles will be present in emerging adults whenever prevailing adult densities threaten to overwhelm the environment. Evans (1984) cites the work of a French entomologist, L. Bonnemaison, who demonstrated the influence of crowding upon development of flight muscles in vetch aphids. The value of 225 used in the module approximates the highest average densities recorded in the 1976-1978 Florida data.

Immigration

50. No immigration is assumed to occur; therefore, the module does not account for adults coming into the square meter from other areas.

Population losses due
to detrital production

51. Logically, production of detritus impacts oviposition sites and host plant habitat available to incoming eggs and larvae. At this point in development, the module removes the number of larvae occupying the equivalent amount of leaf biomass lost to detritus.

Fecundity

52. Literature accounts differ in reports of numbers of eggs produced per female per day. Stark and Goyer (1983), for example, report that female *N. eichhorniae* collected from Louisiana sites deposit 2.8 (±0.4) eggs per day

(24-hr period) under laboratory conditions (30° C, 70 percent relative humidity, and 14:10 light to dark ratio). DeLoach and Cordo (1976a) report data on oviposition rates and duration of egg stage at various constant temperatures ranging from 10° to 35° C. Their data show that optimum temperature for oviposition lies between 20° and 30° C. In their ecological study of these species, DeLoach and Cordo (1976b) report that the maximum rate for *N. bruchi* was 7.6 eggs per female per day, whereas *N. eichhorniae* produced a maximum 5.0 eggs per female per day. They also note that considerable variation in oviposition rates existed among *N. eichhorniae* females over a 2-year period.

53. Also, age of female is important in the calculation of egg production through time, i.e., fecundity changes with age. DeLoach and Cordo (1976a) report that maximum oviposition for *N. bruchi* females occurs during the first week after eclosion (average of 5.0 eggs per day per female), then declines rapidly to an average of 1.5 eggs per day per female. A given female can be expected to produce 102.3 (±82.0) eggs during her life, making 50 percent of her contribution to the next generation by her 7th day and 95 percent by her 33rd day.

54. Stark and Goyer (1983) reported no significant deviation from a 1:1 male to female ratio among adults collected from three study sites in Louisiana. DeLoach and Cordo (1976a) suggest a 1:1 ratio among adults collected at sites in Argentina, but report that these collections usually had about 20 percent more males than females. Since the collections were made by hand, the authors suspected that because males were more likely than females to occupy exposed sites on plants, males were more likely to be captured.

55. In the module, oviposition rates are based upon the assumption that 50 percent of the adult population is female and that fecundity varies according to age of female and environmental temperature. Variation in fecundity is achieved by recognizing that females up to 7 days are more fecund than older females and produce eggs at the rate of 1.25 eggs per day for their first 7 days. Females 7 days or older but less than or equal to 33 days old produce eggs at the rate of 0.355 egg per day; females older than 33 days do not contribute to the egg population.

56. Temperature affects fecundity by a proportional factor: at 15° C, only 30 percent of the fecundity value is used; at 20° C, 100 percent is used; at 25° C, only 30 percent; and at 30° C, only 8 percent. Beyond 30° C, no

eggs are produced. In the model, this relationship has been shifted toward the cooler side from what has been reported in laboratory studies on the temperature effects on fecundity of *Neochetina* spp. (Figure A4, Appendix A, shows the effect of temperature on the fecundity relationship used in this model.)

57. The weevil portion of the model uses the following relationships to calculate egg production and thus create insect cohorts:

$$\mathrm{EGG(T)} = 0.50 * \sum_{I=1}^{T-1} \mathrm{ADULT(I)} * \mathrm{FMAX(I,T)} * \mathrm{FTEMP(T)}$$

where

EGG(T) = number of eggs laid by female adults on day T

0.50 = percent of females in adult cohort

FMAX(I,T) = maximum daily number of eggs laid by PT(T) - PT(I) day-degrees-old adult female

For *N. eichhorniae*:

$$\mathrm{FMAX(I,T)} = \begin{cases} 1.25, & \text{if } \mathrm{PT(T) - PT(I)} < 77.0 \\ 0.355, & \text{if } 77.0 < \mathrm{PT(T) - PT(I)} < 363.0 \\ 0.0, & \text{if } \mathrm{PT(T) - PT(I)} > 363.0 \end{cases}$$

For *N. bruchi*:

$$\mathrm{FMAX(I,T)} = \begin{cases} 2.5, & \text{if } \mathrm{PT(T) - PT(I)} < 77.0 \\ 0.5, & \text{if } 77.0 < \mathrm{PT(T) - PT(I)} < 363.0 \\ 0.0, & \text{if } \mathrm{PT(T) - PT(I)} > 363.0 \end{cases}$$

FTEMP(T) = temperature effect on fecundity (see Figure B4, Appendix B)

Total insects in each cohort

58. Total numbers of insects in each cohort at the end of each simulation day are computed as follows:

$$\mathrm{TEGGS} = \sum_{I=1}^{T} \mathrm{EGG(I)}$$

$$TLARV = \sum_{I=1}^{T} LARVAE(I)$$

$$TPUPA = \sum_{I=1}^{T} PUPAE(I)$$

$$TADUL = \sum_{I=1}^{T} ADULT(I)$$

where

TEGGS = current total number of eggs

TLARV = current total number of larvae

TPUPA = current total number of pupae

TADUL = current total number of adults

Weevil impact on waterhyacinths

59. Impact on waterhyacinths is produced by large (approximate third instar) larvae consuming plant biomass and, in the process, removing meristematic tissue. The module currently requires 0.50 large larva per plant, feeding over 11 days, to remove the biomass equivalent of one leaf. This logic is based upon unpublished information from Florida;* numbers used in the algorithm were derived empirically. The model does not currently account for removal of biomass by adults, since the amount removed is estimated to be insignificant.

* Ibid.

PART III: ORGANIZATION OF COMPUTER CODE

60. The Waterhyacinth-*Neochetina* model (INSECT) is written in FORTRAN for IBM-AT microcomputers. The software used (IBM Personal Computer Professional FORTRAN by Ryan-McFarland Corporation) requires that an 80287 math coprocessor chip be installed in the computer. This FORTRAN language is designed according to the specifications of the American National Standard Programming Language FORTRAN 77. The model takes approximately 5 min to simulate the interactions between waterhyacinth and the *Neochetina* for 365 days of simulation time.

61. INSECT consists of a main program, BLOCK DATA, and several subroutines. The values for the variables are made available in every portion of the model with the use of labeled COMMON statements. The BLOCK DATA subprogram is used to assign the initial values for the variables included in the COMMON statements. The general scheme of the INSECT model is shown in Figure 4.

Main Program

62. The main program first calls the subroutine INPUT to establish the initial conditions of the simulation run. Once the model is initialized, the main program, on each simulation day, reads the daily weather data and calls the PLANT, WEEVIL, and FEED subroutines to simulate waterhyacinth growth, *Neochetina* development, and the impact of the weevils on the plants. At the end of each simulation day, the main program outputs the daily results.

Subroutine INPUT

63. The subroutine INPUT allows the user to interact with the model to establish the simulation conditions. The user must first determine the length of the simulation run by entering the Julian date for "first" and "last" day of simulation. Then, the model asks the user to select, from the list displayed, the weather data to be used. Next, the user must select the scenario to be implemented for the simulation. Currently, the following alternatives are available:

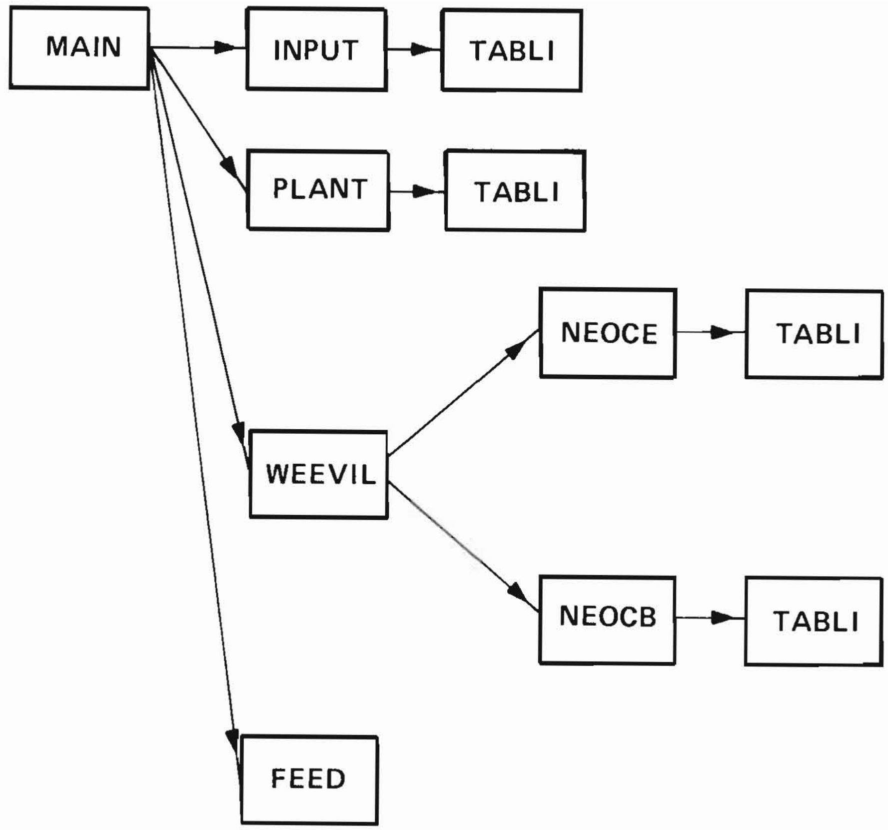

Figure 4. General scheme of the model

a. Simulate plants only.

b. Simulate weevils only.

c. Simulate plants and weevils with interaction.

d. Simulate plants and weevils without interaction.

64. The user must enter the initial plant biomass (dry weight) if any scenario with plants is selected. This value can be obtained by the following procedures:

a. Collect all plants in an area of 1 sq m, discarding dead material.

b. Place these plants atop suspended wire or spread them out on paper until all external dampness has disappeared. (This usually takes about 5 min.)

c. Multiply this number by 0.05 to obtain biomass dry weight in kilograms per square meter.

65. Initially, the model assumes that no weevils are present. If the user wishes to include weevils in a simulation, the initial weevil numbers must be entered into the model. To initialize the weevil module, the user

must input the Julian date for the data point, the life stage of the weevil, and the number per square meter. The following example illustrates this feature. The model will display the following information on the screen:

ENTER JDINS, LSTAGE, AND AMOUNT

JDINS = JULIAN DATE FOR THE INPUT

LSTAGE = WEEVIL LIFE STAGE

1 = EGGS

2 = LARVAE

3 = PUPAE

4 = ADULTS

AMOUNT = NUMBER OF WEEVILS PER SQUARE METER

ENTER: JDINS LSTAGE AMOUNT (TO STOP ENTER 0 0 0)

Assume that the user enters the following input:

JDINS	LSTAGE	AMOUNT
1,	1,	30
1,	2,	20
1,	3,	40
1,	4,	21
181,	3,	100
0,	0,	0

This input can be interpreted as follows: on Julian date 1, there are 30 eggs, 20 larvae, 40 pupae, and 21 adults present. In addition, there are 100 pupae on Julian date 181. If the user makes an error in input, this error can be corrected by entering the data again with the proper values. However, once "0, 0, 0" is entered, there is no more opportunity to correct initial weevil values other than starting over again. Input numbers can be separated by either commas or spaces.

66. The user must also enter the percent ratio of *N. bruchi* and *N. eichhorniae*. The number of weevils initially entered by the user is partitioned according to this ratio to model each species separately.

67. Once the user establishes the scenario for the simulation run, the INPUT subroutine performs other initialization procedures and opens three data files to be accessed during the run. Device number 3 is used for the weather data selected by the user. Device numbers 4 and 5 are assigned for output files for waterhyacinth (PLANT.DTA) and *Neochetina* spp. (INSECT.DTA) related output. These output files can be used to plot the simulation results at the

end of the run. Sample output from an interactive input phase is shown as Figure 5. Also, a sample run complete with input and output is provided as Appendix B.

Subroutine PLANT

68. This module simulates the waterhyacinth growth and computes the amount of plant biomass available for weevil impact. It is called by the main program on a daily basis. Before the control is sent back to the main program, cumulative plant biomass information is stored in an array, and other pertinent plant information is written into the PLANT.DTA file for plotting purposes.

Subroutine WEEVIL

69. This module is called by the main program to simulate the development of *Neochetina* species. Due to differences in the two species, *N. bruchi* (subroutine NEOCB) and *N. eichhorniae* (subroutine NEOCE) are modeled separately. After these two subroutines are called, the module calculates the total number of weevils in each life stage and writes this information into the INSECT.DTA file for plotting purposes.

Subroutines NEOCB and NEOCE

70. Both of these subroutines are called from subroutine WEEVIL and have basically the same structures. In each subroutine the development of insects from one stage to another, fecundity, and mortality activities are simulated. Also, the information regarding the number of weevils in different cohorts as a function of their age distribution is stored in related arrays for further reference.

Subroutine FEED

71. This subroutine simulates the impact of *Neochetina* spp. on waterhyacinths. A portion of total biomass is reduced, if certain conditions are met, due to *Neochetina* feeding on the plants.

```
                         INSECT MODEL

ENTER JULIAN DATE FOR FIRST DAY OF SIMULATION ---> 1

ENTER JULIAN DATE FOR LAST DAY OF SIMULATION ---> 365

ENTER THE CODE FOR WEATHER DATA TO BE USED
EXISTING FILE NAMES:

1 = LAKE CONCORDIA - 1974
2 = NEW ORLEANS - 1979
3 = NEW ORLEANS - 1980
4 = NEW ORLEANS - 1981

5 = FLORIDA - 1975
6 = FLORIDA - 1976
7 = FLORIDA - 1977
8 = FLORIDA - 1978
9 = FLORIDA - 1979 ---> 6

ENTER THE CODE FOR SIMULATION CONDITIONS:
1 = SIMULATE PLANTS ONLY
2 = SIMULATE WEEVILS ONLY
3 = SIMULATE PLANTS & WEEVILS WITH DAMAGE
4 = SIMULATE PLANTS & WEEVILS WITHOUT DAMAGE ---> 3

ENTER INITIAL PLANT BIOMASS (kg per sq m) ---> .769

ENTER PERCENT N. EICHHORNIAE & N. BRUCHI
EXAMPLE:  100 0 ---> 100 0

ENTER INITIAL INSECT POPULATIONS:

       JDINS = JULIAN DATE FOR THE INPUT
      LSTAGE = LIFE STAGE OF THE INSECT
               1 = EGGS
               2 = LARVAE
               3 = PUPAE
               4 = ADULTS
      AMOUNT = NUMBER OF INSECTS per sq m

ENTER:  JDINS LSTAGE AMOUNT (SPACE OR COMMA IS NEEDED BETWEEN NUMBERS)

TO START SIMULATION ENTER 0 0 0 ---> 1,1,30

TO START SIMULATION ENTER 0 0 0 ---> 1,2,20

TO START SIMULATION ENTER 0 0 0 ---> 1,3,40

TO START SIMULATION ENTER 0 0 0 ---> 1,4,31

TO START SIMULATION ENTER 0 0 0 ---> 0,0,0
```

Figure 5. Sample output from the interactive phase

Function TABLI

72. This is a FORTRAN table look-up function used to interpolate linearly between the existing data points (Llewellyn 1965).

Weather Data

73. If the user wishes to use different weather data in a simulation run, records of daily weather data must be stored in a computer file prior to the run. The weather data should include the following information in the order given:

- a. Julian date.
- b. Solar radiation in langleys.
- c. Maximum daily temperature in degrees Fahrenheit.
- d. Minimum daily temperature in degrees Fahrenheit.

There must be a separate line in the file for each day of the weather data. The open format is acceptable. The file containing the weather information is accessed by the main program and subroutine INPUT. Temperatures are in Fahrenheit in the weather data file but are converted to Celsius during model operations.

Computer Programs

74. The following are the names of the files representing the FORTRAN programs necessary to run the model:

MAIN.FOR
INPUT.FOR
PLANT.FOR
WEEVIL.FOR
NEOCB.FOR
NEOCE.FOR
FEED.FOR
TABLI.FOR
BLOCKDTA.FOR

75. These files can be edited using any kind of text editor. The software requires that each FORTRAN file has an extension .FOR. Whenever a change is made in one of these programs using a text editor, the user must recompile that program. The proper statement for compiling a FORTRAN file with an extension .FOR is as follows: PROFORT filename. This statement converts the source code into an object code. When the above statement is executed, the software will generate a new file that has the same name as the source file but with an .OBJ extension.

76. Once all the object files have been created, the user can link all the programs and the necessary FORTRAN library with an executable object module. The following statement will create an executable object module called WHY.EXE: LINK @LINKM.BAT.

77. To run the model, the user must type WHY on the keyboard. The program will then lead the user into the initialization phase executed by subroutine INPUT.

78. The file WHYCOM.INC contains blocks of COMMON statements necessary to transfer information between the subprograms of the model.

79. When a modification is made in this file, all the FORTRAN files must also be recompiled. Entry of the following statement will accomplish this task: COMPILE.

80. As mentioned before, the BLOCK DATA subprogram contains the initial values of the model variables listed in the COMMON statements. Anytime a change is made in COMMON statements, the BLOCKDTA.FOR file must also be updated to reflect the change made.

PART IV: SIMULATION RESULTS

Field Data

Site characterizations

81. Field data describing waterhyacinth populations were obtained from two locations: Lake Alice near Gainesville, Fla.,* and Lake Concordia near Ferriday, La. (Long and Smith 1975). Center* sampled waterhyacinths and weevils in Lake Alice from April 1975 through December 1980, and provided these data for use in development of the model INSECT. Lake Alice, on the University of Florida campus, received discharge from a steam plant, a sewage treatment facility, and from overflow from a small sink hole. The marsh portion of the lake in which Center worked was dominated by waterhyacinth. The waterhyacinths from Lake Alice had weevil damage for at least part of the period of observation.

82. Long and Smith (1975) conducted studies on the effects of the CO_2 laser on waterhyacinth growth in Lake Concordia. Because the lake was surrounded by extensive agriculture, nutrients flowed into it from agricultural fertilizer. Also, household water flowed into the lake. The two sites used in 1973 and 1974 were in the upper (eastern) end of the lake which contained waterhyacinths with no detectable weevil damage.

Treatment of data - plants

83. The Florida plant data* were collected monthly. We used the monthly means of plant biomass and numbers of plants per square meter and calculated 95-percent confidence intervals using critical values of Student's t-distribution.

84. Although about 2 sq m of infected (*N. eichhorniae*) waterhyacinth plants were moved into Lake Alice on 20 February 1974, the insect population was not dispersed throughout the site until spring 1976.* Center's data for the year 1975* were considered preweevil years and used as a "control" to compare with output from simulation of plants alone. The first 3 months of data were estimated by Center using a regression formula relating mean maximum leaf length and the mean number of leaves per plant to plant weight (Center and Spencer 1981). For the 1975 comparison, the number of leaves per plant used

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* Ibid.

is Center's monthly mean* (data variable ANLPT, see Figure A1, Appendix A). For model runs of years after this, the numbers of leaves per plant used are means of monthly means for years 1976 through 1978 (data variable ANLPTA, Figure A1). Weight of all leaves on a plant and percent leaves are monthly means of Center's monthly means* for 1976 through 1978 (data variables ATLWT, PRCLTF, Figures A2 and A3). Weather data (Appendix C) from Gainesville, Fla., were used in the simulations.

85. The control plots of the Long and Smith (1975) studies were used as field data for comparison with simulation results. Wet weight values in kilograms per 3.24 sq m were converted to kilograms per square meter dry weight assuming plants to be 95 percent water. Mean biomass during 1974, including detritus, from plots TS1 (subplots 19, 22, 23), TS2 (subplots 43, 50, 51), and TS3 (subplots 94, 97, 107) were compared using linear correlations. The coefficients of correlations were above 0.87. These data were combined by dates of collection and used to calculate 95-percent confidence intervals using critical values of Student's t-distribution. Weather data (Appendix C) used in the simulation were air temperatures at Jonesville Locks, Louisiana, and daily solar totals from Lake Charles, La.

Treatment of data - weevils

86. The 1976 and 1977 weevil data for Florida were used for comparison with those simulated by the model. These data are for *N. eichhorniae* only and were originally expressed in the form of adults and larvae per plant at approximately weekly (51 data points for 1976) or monthly (12 data points for 1977) intervals. The 1976 data are extremely useful for comparisons because their frequency of sampling illustrates fluctuations of the insect population throughout the year. Monthly data are useful, but such fluctuations may not be evident.

87. Since Center's data* were expressed on a per plant basis, it was necessary to convert his numbers and confidence intervals to square-meter units. This was done by multiplying each mean and standard error by the mean number of plants per square meter for each sampling interval. Confidence intervals were based on Student's t-distribution using a 95-percent level with a sample size of 100.

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* Ibid.

Simulation Conditions

Plants

88. Florida. The 1975 simulation without weevils present was initiated on Julian date 1 (JDAY 1) using 0.769 kg/sq m of biomass. This amount was derived by extrapolation of Center's field data of mean monthly values of 0.867 kg/sq m on JDAY 349 in 1974 and 0.609 kg/sq m on JDAY 24 in 1975. Both of these values were estimated by Center using his regression formula. Subsequent year simulations were initiated on JDAY 1 using the biomass of JDAY 365 of the previous year.

89. Louisiana. The 1974 simulation without weevils present at Lake Concordia was initiated on JDAY 120, the first date of data collection by Long and Smith (1975). Initial plant biomass was the amount calculated from the field data on that date, 0.1039 kg/sq m.

Weevils

90. Starting numbers for the 1976 simulation for weevils (all life stages) were either taken directly (within 95-percent confidence limits) from Center's data or estimated from the first 150 days of the 1976 data. This is justified by considering that, in the early part of the year, increases in the adult population are due to emergence of overwintering immatures. The following starting values were, therefore, based on Center's 9 January 1976 Lake Alice data and used in simulation of the 1976 weevil population:

a. Adults: 21 ± 10.29 (from field data) on JDAY 9.

b. Pupae: 40 (This number was estimated from adult data-number of adults on JDAY 97 minus the number of adults on JDAY 82 = 31; if one allows for daily mortalities, the starting number for pupae on JDAY 9 is approximately 40.)

c. Larvae: 20 (This number was estimated from adult data by assuming the difference between JDAY 147 adults (69) and JDAY 138 adults (49) to be the emergence of overwintering larvae; field data show only 0.65 ± 1.29 on JDAY 9.)

d. Eggs: 30 (empirically derived) on JDAY 9.

Measured Versus Simulation Results - Florida

Plants

91. 1975 - biomass. The model simulation for biomass production (Figure 6) agrees well with observed Florida field data.* The model predicted that biomass production accumulated more slowly early in the growing season and declined less rapidly than field data observations. December biomass values were within observed 95-percent confidence intervals of the mean.

92. 1975 - numbers of plants. The simulation predicts numbers of plants per square meter (Figure 7). Simulation results were higher than field data* collected before spring and early in the growing season. In the latter part of the year, the simulation results for number of plants per square meter were higher than the field data. This is probably due to the algorithm's dependence on monthly values of plant weight, number of leaves per plant, and percentage of a plant that is comprised of leaves.

93. 1976 - biomass and numbers of plants. The simulation with weevils impacting plants was started on JDAY 1 using the ending 1975 biomass of 0.705 kg/sq m. The predicted amount of biomass (Figure 8) was higher than observed field data* early in the growing season and until late July. Simulation results were within the confidence intervals of the observed data on all other sampling dates except for JDAY 354 when the model results showed less plant biomass. Simulated numbers of plants (Figure 9) were higher compared to field data at JDAYs 112 and 140 due to excessive biomass production during these periods.

94. 1977 - biomass. The simulation with weevils impacting plants showed less waterhyacinth biomass (Figure 10) compared to observed field data for 1975 and 1976.* Julian day 1 biomass to initiate this run was 0.382 kg/sq m, the ending biomass for the 1976 simulation.

95. 1977 - numbers of plants. Generally, the simulated number of plants was less than observed. The shape of the simulation curve is similar to that of the observed, indicating that modifications in subroutine FEED might well attain the desired amplitude of the model-generated curve. This, in turn,

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* Ibid.

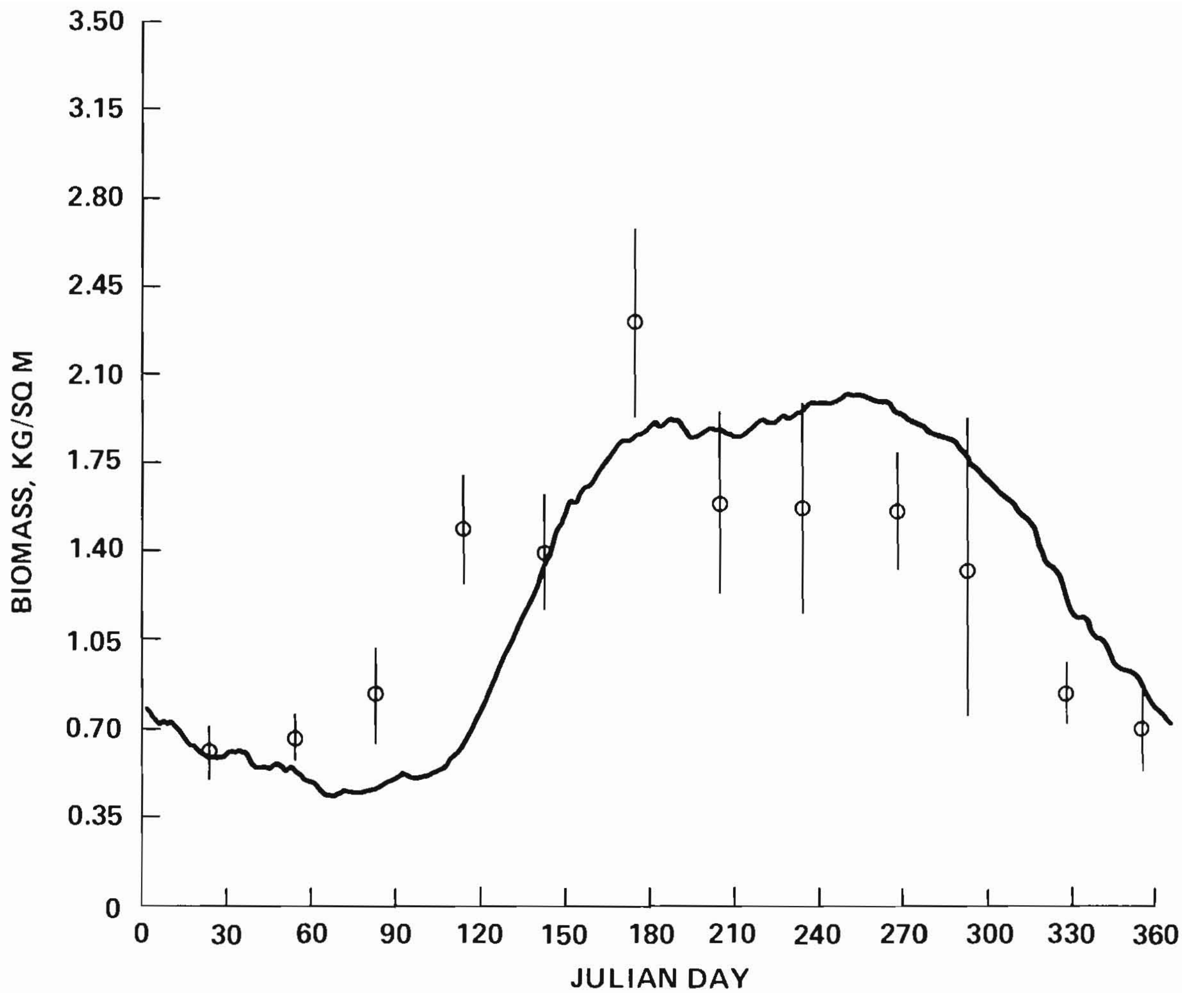

Figure 6. Simulated (plant biomass) values for 1975, Florida, without insects. Solid line = simulation results; circles = monthly means of field data collected at Lake Alice, Florida; vertical lines = 95-percent confidence intervals of monthly means

would cause numbers of plants per square meter (Figure 11) to reflect observed data more closely.

Weevils

96. 1976 - numbers of adults. Simulation results, using the starting numbers of weevils given in paragraph 90, are shown in Figures 12 and 13. Figure 12 illustrates the numbers of adults generated by the model for JDAYs 9 through 365. Of the 51 field data observations, simulated values for 34 fell within the 95-percent confidence intervals. Largest differences occurred between JDAYs 170 and 210 where the model showed higher values for the adult population. Also, field data indicate that first-generation adults (adults

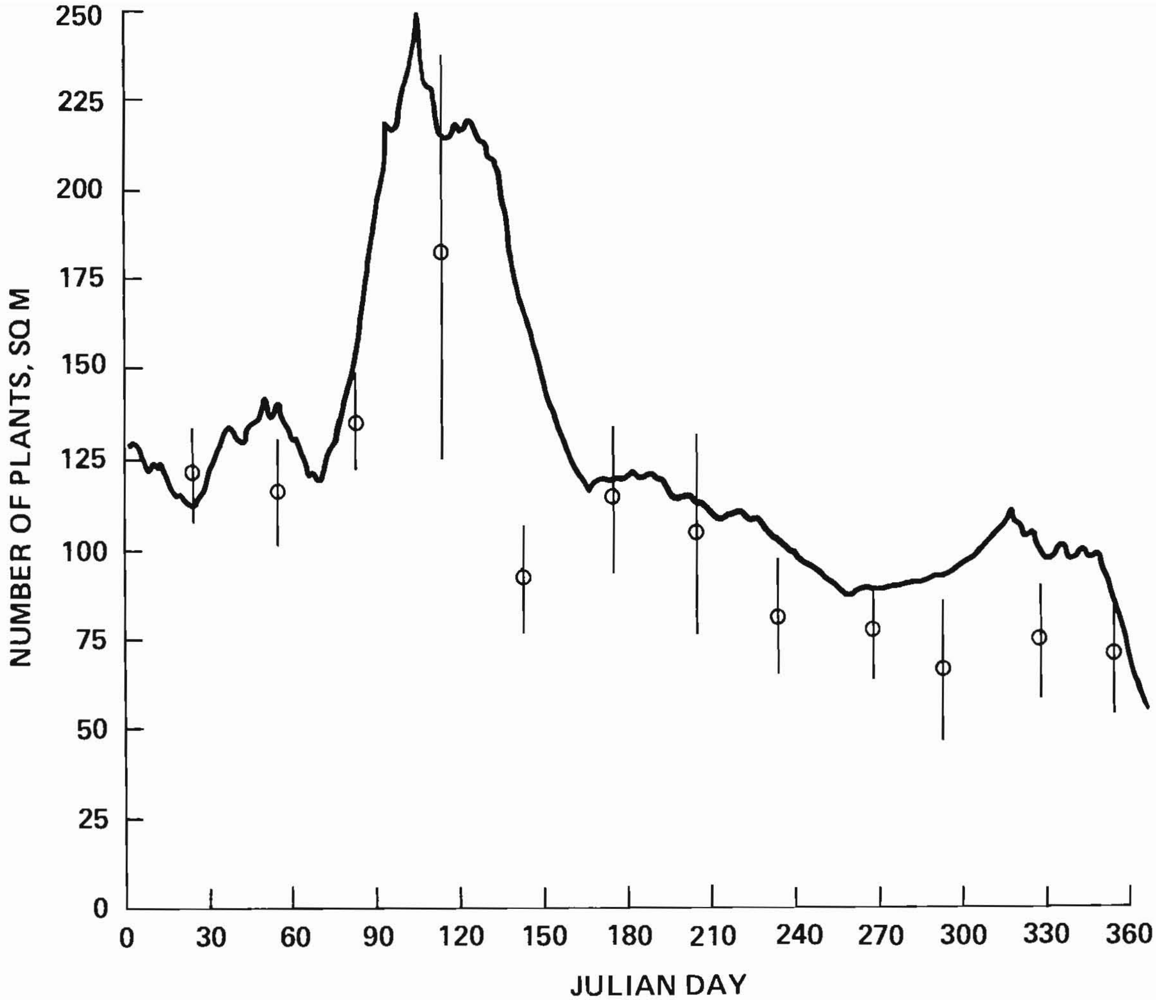

Figure 7. Simulated (numbers of plants) values for 1975, Florida, without insects. Solid line = simulation results; circles = monthly means of field data collected at Lake Alice, Florida; vertical lines = 95-percent confidence intervals of monthly means

originating from overwintering pupae) first appear just after JDAY 90, whereas the model showed this to happen on about JDAY 70. However, the model illustrated the general trend of the field data in the timing of adult population fluctuations.

97. 1976 - numbers of larvae. Figure 13 illustrates the model's estimate of third instar larvae. Since it assumes that damage to plants is caused by older larvae, this graph reflects the presence of potential bud predators in the insect population through a year's cycle. Simulation results showed good agreement with field data during the early part of the year as plants were beginning their growth (for JDAYs 90 through 170). The model results

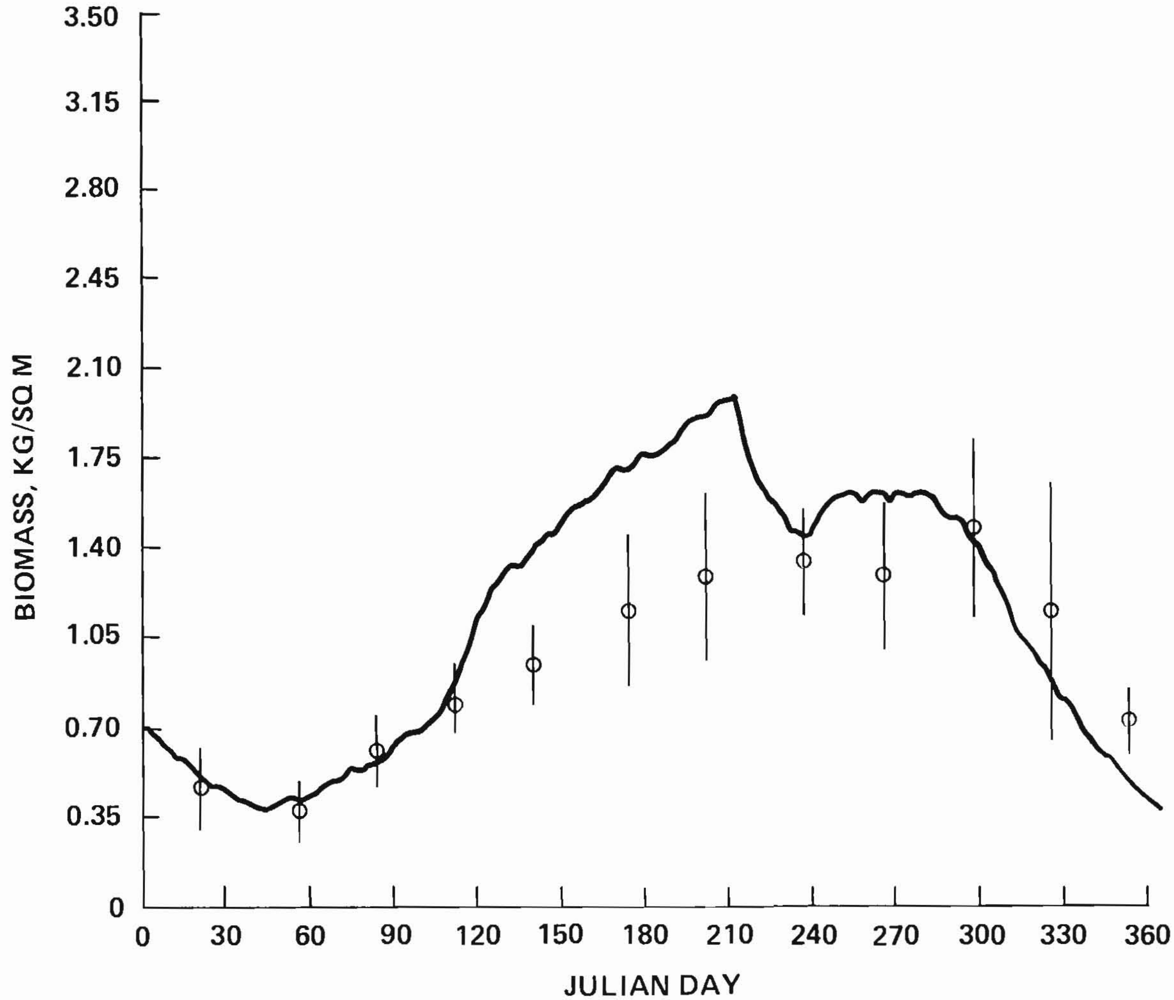

Figure 8. Simulated (plant biomass) values for 1976, Florida, with insects. Solid line = simulation results; circles = monthly means of field data collected at Lake Alice, Florida; vertical lines = 95-percent confidence intervals of monthly means

depart from field data by showing higher numbers for the July through August third instar population. Plus, the model showed higher values for this portion of the insect population during November when compared to the field data.

98. 1977 - numbers of adults. For this simulation, JDAY 1 starting numbers were the ending numbers for 1976, i.e., 4 eggs, 62 larvae, 87 pupae, 27 adults, and 0.382 kg of waterhyacinth. Results of this simulation are shown in Figures 14 and 15. Simulations for the adult population (Figure 14) generally agreed with the trends found in the field data but were of less magnitude than those of the 1976 simulation. The major differences occurred in

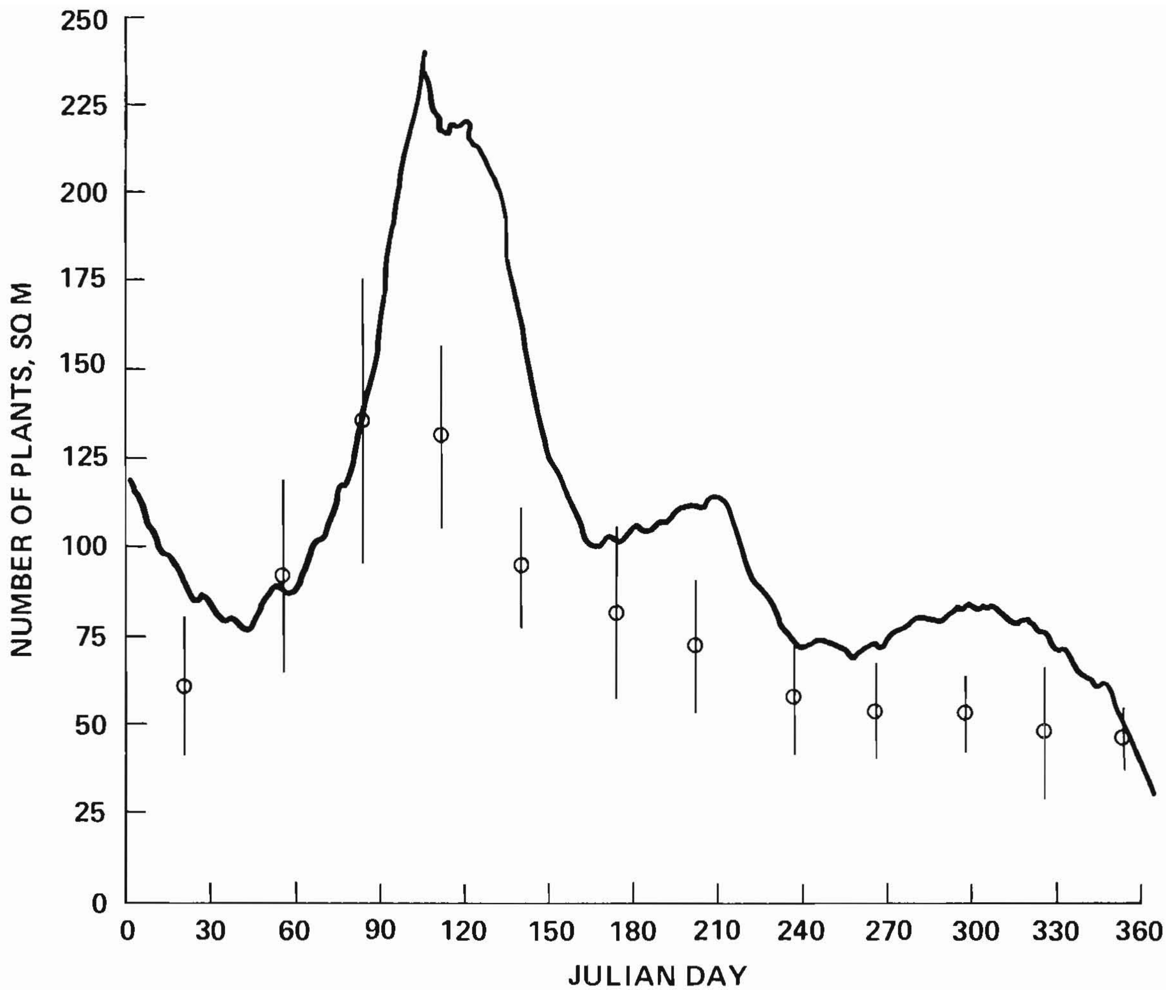

Figure 9. Simulated (numbers of plants) values for 1976, Florida, with insects. Solid line = simulation results; circles = monthly means of field data collected at Lake Alice, Florida; vertical lines = 95-percent confidence intervals of monthly means

mid-growing season where the simulated values showed fewer adult insects. While this trend is indicated in the field data, the numbers were much higher than the simulation results. However, both data sets indicate an increase in adults between approximately JDAYs 250 and 300. The field data show a slight increase in adults at the end of the year, whereas the simulation results show a constant decrease during the last month of the year.

99. <u>1977 - numbers of larvae.</u> The third instar larvae (Figure 15), in general, showed better agreement with field data than did those of 1976. Again, occurrence of larvae capable of impacting plants peaked between JDAYs 120 and 180. These are the larvae that produced the reduction in the

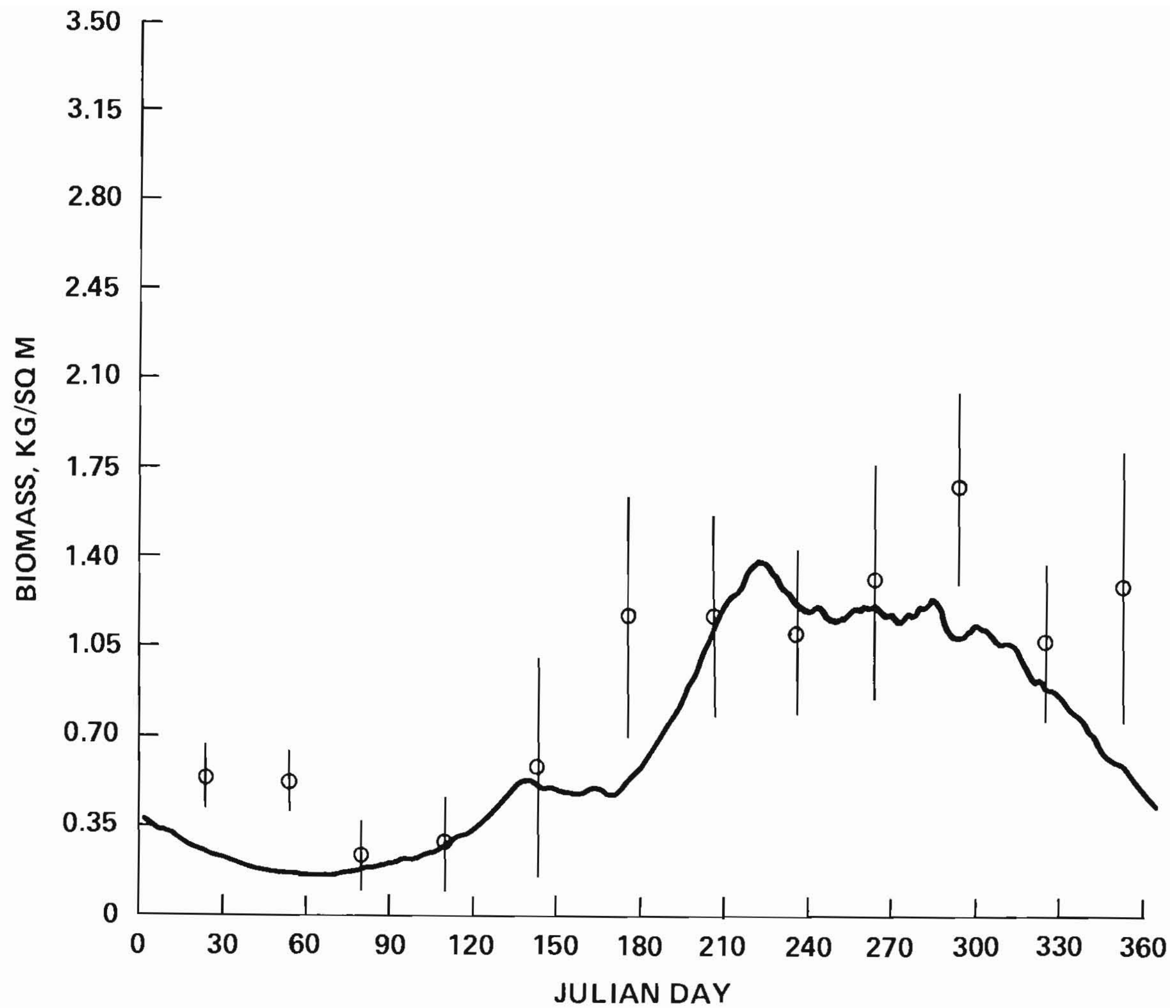

Figure 10. Simulated (plant biomass) values for 1977, Florida, with insects. Solid line = simulation results; circles = monthly means of field data collected at Lake Alice, Florida; vertical lines = 95-percent confidence intervals of monthly means

simulated plant biomass for 1977. The predicted second generation of larvae was less than the first and third, a pattern which matched field data.

Measured Versus Simulation Results - Louisiana

Plants

100. Since Long and Smith (1975) included detritus in their waterhyacinth biomass measurements, input data for this run were adjusted so that the calculated daily amount of detritus was not subtracted from the plant growth of each day. The simulation results (Figure 16) are very close to the

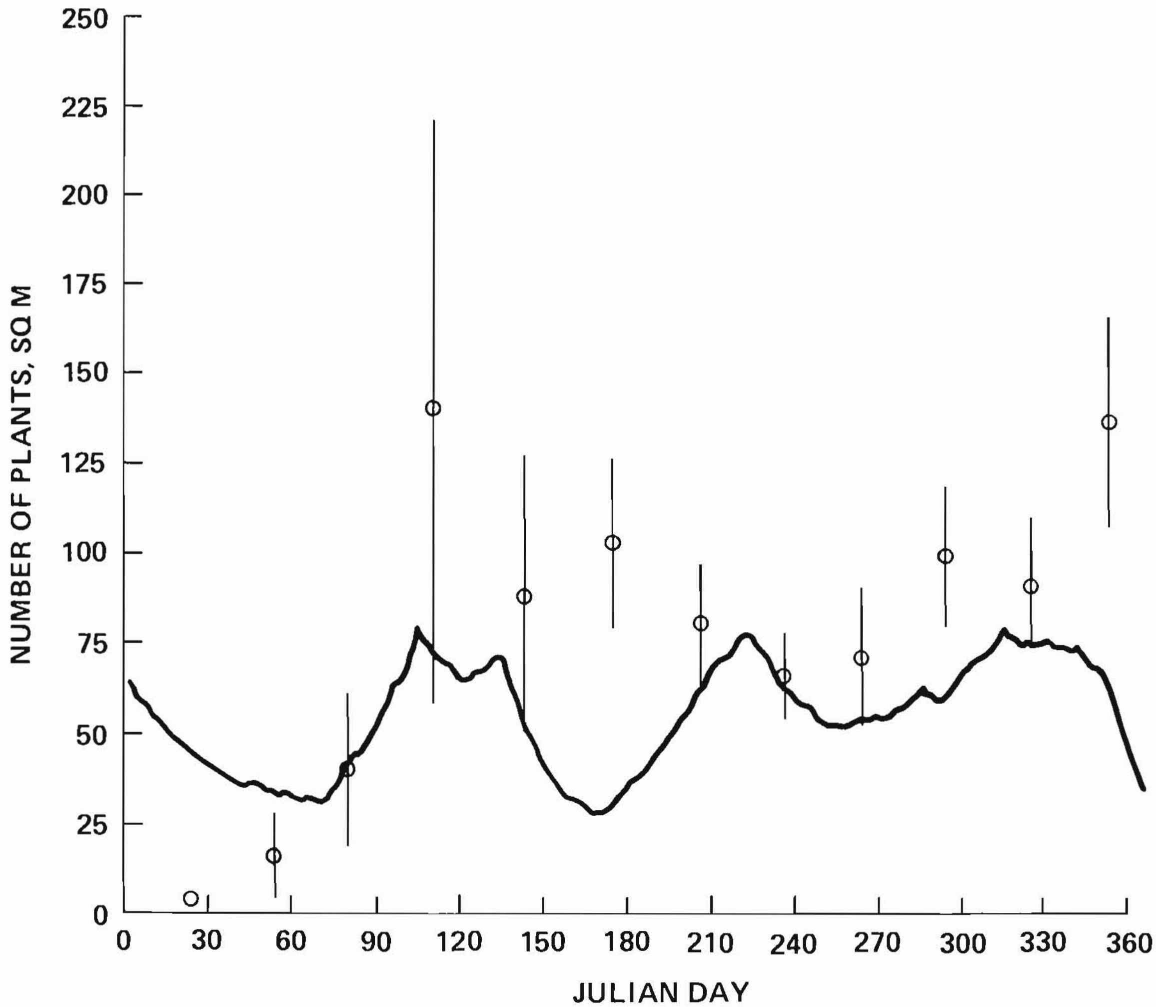

Figure 11. Simulated (numbers of plants) values for 1977, Florida, with insects. Solid line = simulation results; circles = monthly means of field data collected at Lake Alice, Florida; vertical lines = 95-percent confidence intervals of monthly means

11 means and 95-percent confidence intervals of the field-measured biomass converted to dry weight per square meter. The plant module of the model generated lower estimates for biomass early in the growing season than actually occurred in Lake Concordia. By JDAY 210 the simulation results, in general, compared to field results.

Weevils

101. Weevils were not present in the waterhyacinth population sampled by Long and Smith (1975). Therefore, simulations for weevils using these data were not appropriate.

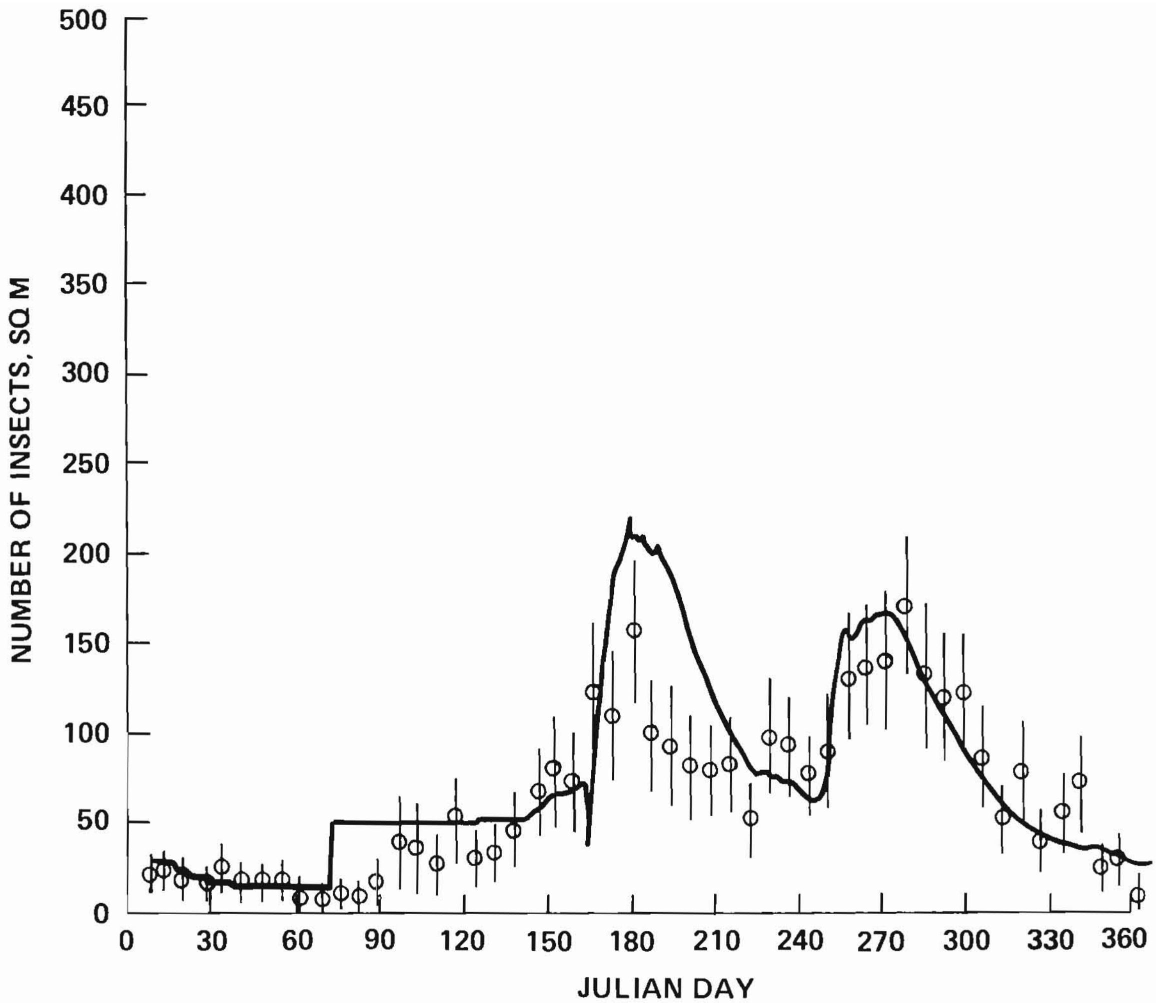

Figure 12. Simulated (numbers of adult *N. eichhorniae*) values for 1976, Florida. Solid line = simulation results; circles = weekly means of field data collected at Lake Alice, Florida; vertical lines = 95-percent confidence intervals of weekly means

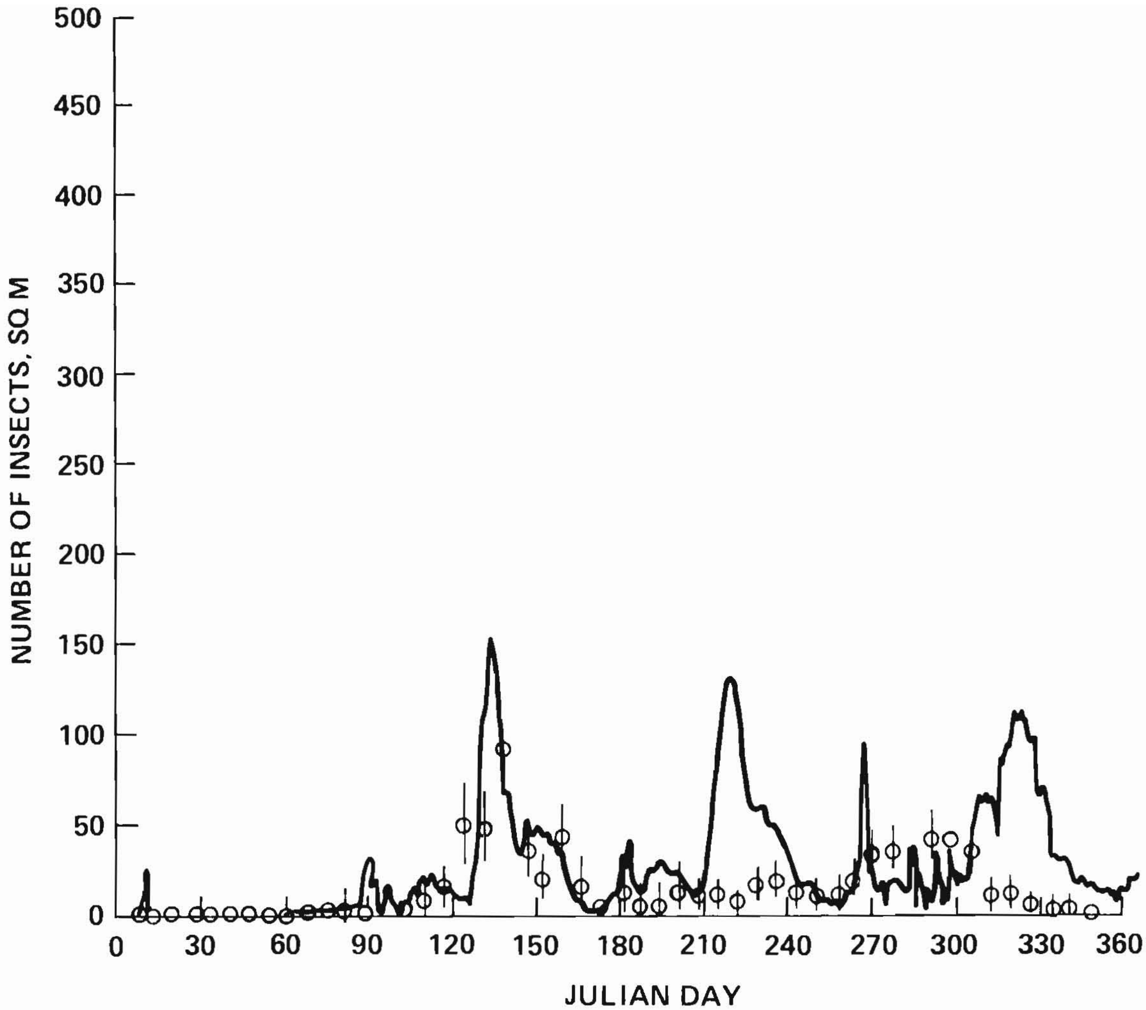

Figure 13. Simulated (numbers of third instar *N. eichhorniae*) values for 1976, Florida. Solid line = simulation results; circles = weekly means of field data collected at Lake Alice, Florida; vertical lines = 95-percent confidence intervals of weekly means

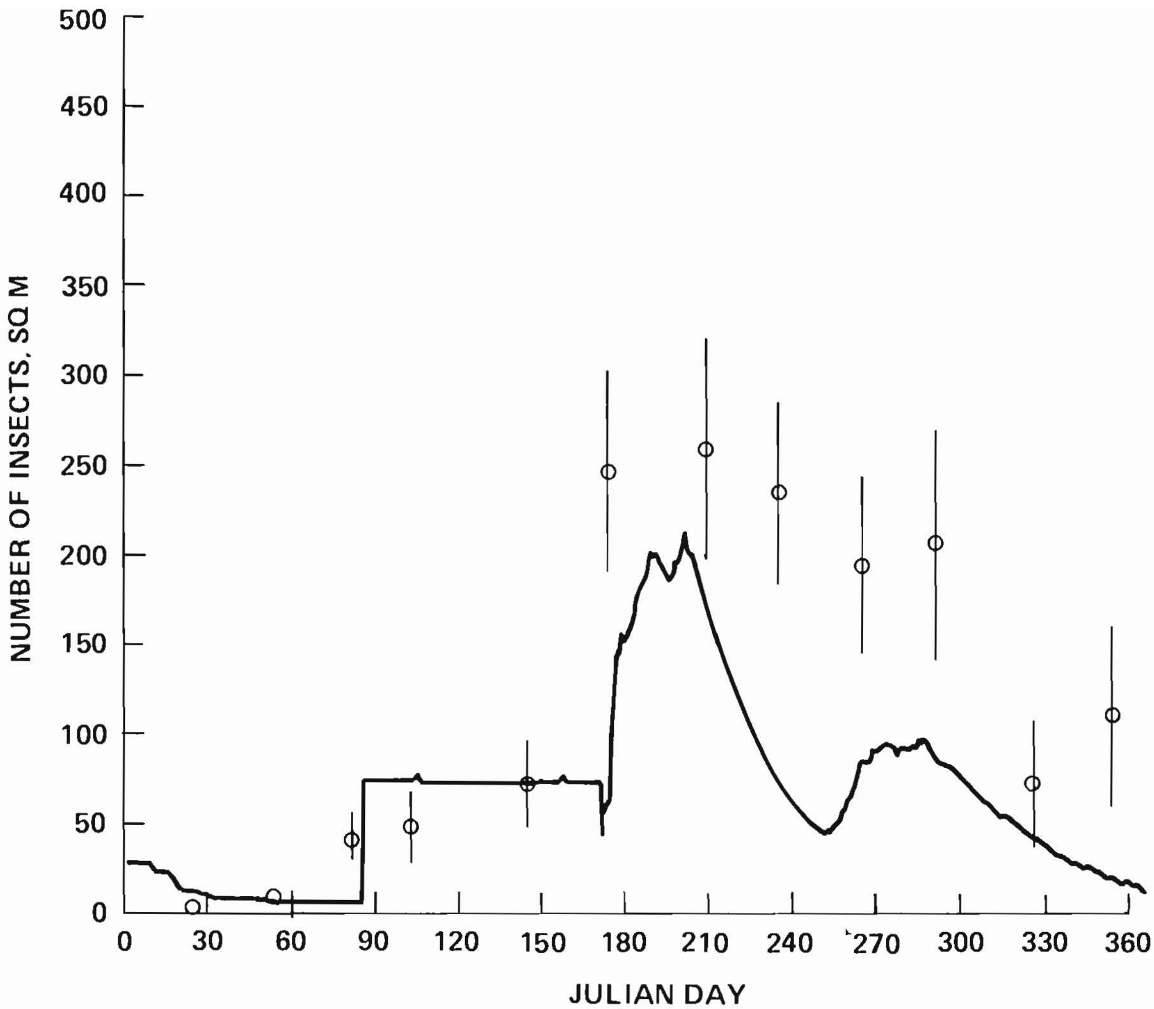

Figure 14. Simulated (numbers of adult *N. eichhorniae*) values for 1977, Florida. Solid line = simulation results; circles = monthly means of field data collected at Lake Alice, Florida; vertical lines = 95-percent confidence intervals of monthly means

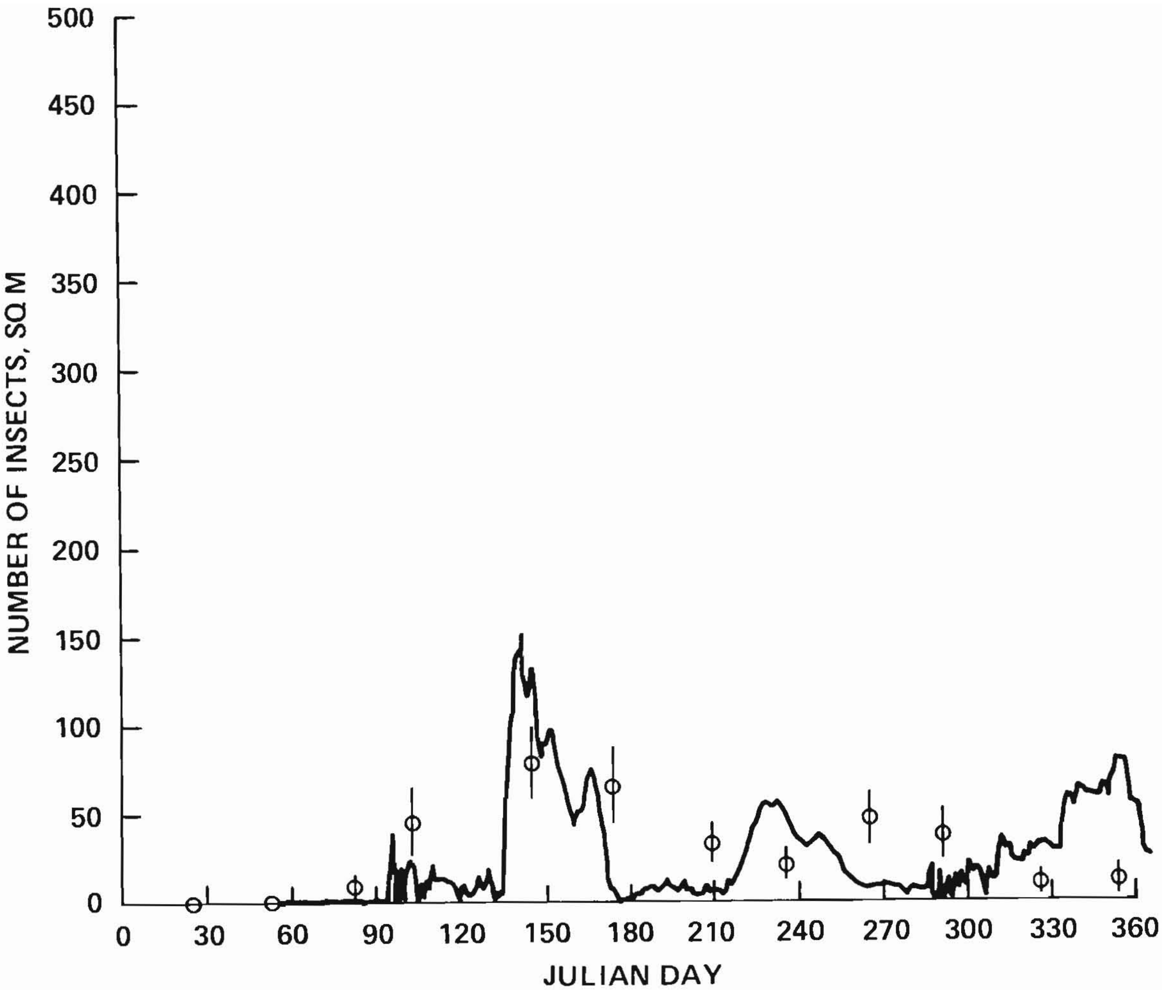

Figure 15. Simulated (numbers of third instar *N. eichhorniae*) values for 1977, Florida. Solid line = simulation results; circles = monthly means of field data collected at Lake Alice, Florida; vertical lines = 95-percent confidence intervals of monthly means

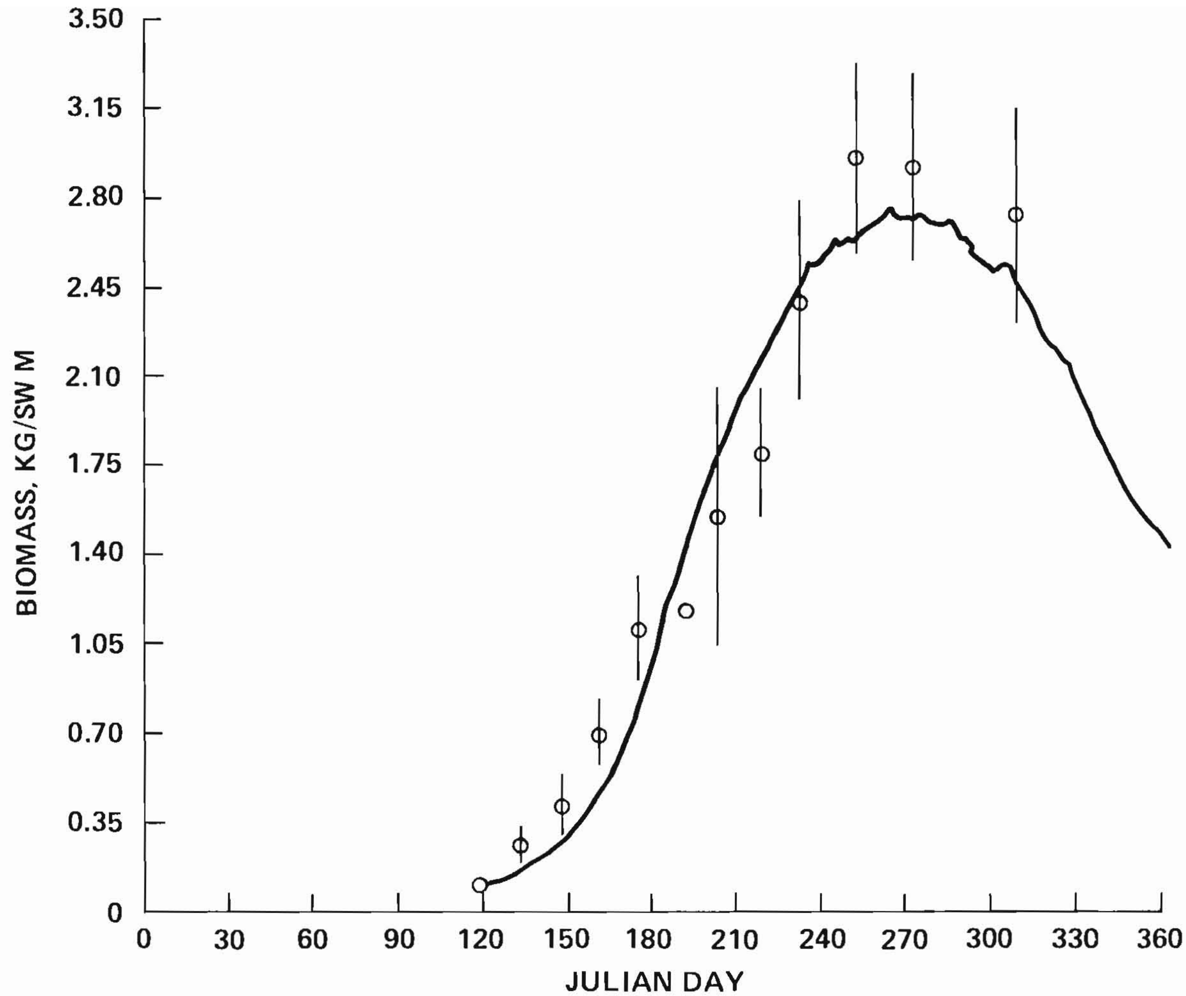

Figure 16. Simulated (plant biomass) values for 1974, Louisiana, without insects. Solid line = simulation results; circles = monthly means of field data collected at Lake Concordia, Louisiana; vertical lines = 95-percent confidence intervals of monthly means

PART V: DISCUSSION

General Comments

102. A first-generation simulation model of waterhyacinth and its biological control agents has been developed. The model (INSECT) is based on currently understood biological and environmental relationships that determine the population dynamics of waterhyacinth and *Neochetina*, and on factors that result from interactions within this host plant/herbivore system. Model-generated simulations have been compared to population estimates derived from field data for Florida and Louisiana, with results showing encouraging agreement.

103. Because the model was developed as a decision tool to help aquatic plant managers and operations personnel, user-friendliness was a primary consideration in developing model structure. Initialization requirements have been limited to easily obtainable information, and output is formatted to allow rapid visual interpretation of simulation results.

104. The model has been structured to easily accommodate the addition of new or improved relationships that may result from future research. At this stage of development, some relationships used in the model are based on generalized knowledge of similar biological systems. The following section provides further elaborations on various facets of waterhyacinth/*Neochetina* interactions that should be understood or considered prior to implementing modifications to the model.

Special Considerations

Plants

105. Number of plants. One of the major connections between the plant and weevil modules is the calculation of number of plants per square meter. This calculation depends on table look-up functions for the percent of plant weight that is leaves, number of leaves per plant, and weight of all the leaves on one plant. More data on these parameters could increase the accuracy of this calculation.

106. Detritus. Detritus both lessens biomass and removes larvae in dead leaves. No field data exist for evaluation of the detrital algorithm.

107. Temperature data. Ultsch (1973) established that the temperature at the surface of a waterhyacinth mat was higher in winter than that of an open-water surface. Conversely, the waterhyacinth mat shades the water surface from direct sunlight, and surface temperatures are cooler in summer than those of open water; variations during a 24-hr period in July were small (Ultsch 1973). Dale and Gillespie (1977) have shown that floating macrophytes may influence diurnal temperature fluctuation at, and close to, the air/water interface. These authors found that "at noon on clear days, the temperature at the water surface with floating mats of Lemnaceae were 4 to 11 degrees C above those without." Waterhyacinth populations may well be expected to have great effect on water temperatures and, hence, to affect both plant growth and weevil life cycle and the weevil impact on the plants. The model might be improved by using water temperatures from the root zone of plants instead of air values.

108. Recolonization by waterhyacinths following control operations. Center and Durden (1986) observed recolonization of an area by waterhyacinths after control operations in Palm Beach, Fla. They found the sequence of events to be first, recolonization, followed by increase in plant size; then, colonization by insects, reduced plant size, and finally decreased plant coverage. This cycle required approximately 3 years in the middle section of Canal-M (plants were removed by 2,4-D about 34 months before their study). This cycle required 2 years in the upstream section (plants were removed by mechanical means about 16 months before their study). These authors reported "the decline phase only required approximately 18 months" in both sections. This information may be useful in later attempts to evaluate the accuracy of model predictions over an extended time period.

109. Time required for effective control of waterhyacinths by *Neochetina* spp. The report of Center and Durden (1986) reviewed the literature concerning the time required for effective control of waterhyacinths by *N. eichhorniae* and *N. bruchi* and concluded that effective biocontrol "can take place rapidly and persist for long periods." It is evident that the simulations produced by the model must extend beyond a 1-year period.

Weevils

110. Several problems currently exist that limit the utility of the weevil module. While some can be solved with more complex logic, others may require additional information on the biology and ecology of the plant/insect interaction.

111. Starting numbers. In working with the 1976 and 1977 Florida field data,* attempts to use the January numbers of weevils (adults and larvae) as starting numbers in simulations tended to underestimate the standing crop of insects during the remainder of the year. Two potential solutions exist for this problem: one, use the first 150 days to estimate the numbers of weevils by stage which, logically, had to be present to produce the spring adult population (regardless of the field data). It is reasonable to assume that field estimates of adults are more accurate than those for larvae. Adults are more visible and of the same relative size, whereas larvae can range in size from a newly hatched individual to a pupating third instar and are "hidden" in plant tissue. Therefore, more confidence can be placed upon adult numbers collected from field samples than on the numbers of larvae dissected from plant tissue. The other possibility is to assume that some individuals, particularly pupae, overwinter in detritus and are not revealed by field sampling. A third possibility, of course, is to assume that the insect population is being augmented by other, unknown sources.

112. "Stair steps." The "stair-step" phenomenon in spring populations of the simulated data is a result of beginning the simulation by assigning values to each of the four life stages of weevils. This artificially creates cohorts of the same physiological age with each cohort then progressing through development at its particular rate. The result is that all individuals of that cohort have the same physiological age in the simulated data and all switch to the next life stage at the same time. In nature, one could expect that these changes to the succeeding life stage would be spread out more smoothly, due to slight differences in physiological ages of the overwintering individuals. From that standpoint, the model either needs to "run" for more than 1 year, so that "winter" individuals will accumulate physiological age based upon their development rates, or an algorithm needs to be written to assign starting individuals to varying physiological ages.

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* Ibid.

113. Population peaks. The 1976 Florida field data* show two distinct adult population peaks whereas the 1977 data do not. Simulated data, however, show population peaks in both 1976 and 1977. While it may be true that the 1977 Florida data cannot be expected to detail fluctuations in population numbers (due to fewer observations), the JDAY 240 point (Figure 14) may still be an accurate reflection of the adult population under those conditions. There are at least two explanations for this difference among the results for the 2 years.

114. Certain algorithms in the weevil module are "set" to favor population increases during the spring growing season (reduced mortalities; fecundity shifted toward cooler average temperatures) and to depress population growth during the warmest months of the growing season (mortalities are higher; fecundity is reduced). On this logic, the module creates two distinctive adult populations during the growing season. (This is an outcome of our efforts to synchronize simulated data with the 1976 field data* by keeping the numbers of adults and larvae and the amount of plant damage as close as possible to the observed data.) However, in making these adjustments, the 1977 simulated data tend to follow the 1976 pattern. Scrutiny of the 1977 field* and simulated data reveals that the simulated data track the field data, except for the single point around JDAY 240. Perhaps adjustments in the module via starting numbers and/or adjustments in the environmental carrying capacity could remedy the problem.

115. A more intriguing explanation, however, is that because of the unusually "hard" winter of 1976, surviving adults came into the new growing season more fecund than were those of 1976. Chiang (1985) reports this phenomenon for flour beetles and milkweed bugs. Given greater fecundity during the first part of the growing season, followed by elevated fecundity slowly returning to "normal" as Chiang reports, the adult population could be expected to remain high through the middle portion of the growing season.

116. Weevil damage to waterhyacinths. There is no direct evidence that would permit the construction of an algorithm for weevil impact on host plants. As stated earlier, the algorithm in this module uses the philosophy of Center* (see paragraph 59) concerning bud predation. It is, therefore,

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* Ibid.

based not on actual data, but on the ideas of others who have worked closely with these populations for several years.

117. Adjustments in the weevil impact algorithm as it exists in the current version of the model can be made in two places. Either age or numbers of larvae can be adjusted, but care must be taken to avoid inconsistencies in logic. For example, the algorithm assumes that for every 0.5 "large" larvae present, 0.0909 of the biomass equivalent of a leaf is removed per day. Age of the larva and its duration inside the plant prior to pupating must be consistent, i.e., 30-day-old larvae during mid-growing season have 11 days more to develop before exiting the larval stage and the host plant. The 0.0909 is the amount removed per day, and if the larvae survive, 0.5 larvae will have removed the equivalent of one leaf from the host plant. The other adjustment point is the number of larvae required to remove the biomass equivalent of a leaf.

118. Effect of temperature on fecundity. One of the major problems encountered in the initial attempts to adjust the weevil module was the generation of extremely large numbers for all life stages. The problem was eventually brought under control by making adjustments in fecundity according to average air temperature.

119. Average air temperature is the "driving force" that determines fecundity in the weevil module. If literature values for percent fecundity are used, numbers of individuals in all life stages "explode." The solution was to "slide" the fecundity temperature function toward the cooler end of the scale, as shown in Figure A4 (Appendix A). It can be reasoned that since literature data are based upon laboratory studies where temperature, relative humidity, and light cycle are controlled, it is possible that field conditions, with all the accompanying environmental vicissitudes, could be different from or at least not accurately predicted by average air temperatures. As discussed earlier, temperatures vary considerably according to location within the vegetation mat. The relationship between average air temperature and published information on temperature effects on fecundity is unknown.

120. Effects of subfreezing temperatures on survival of life stages. Information is needed on the ability of each *Neochetina* spp. life stage to survive subfreezing temperatures. Values used in the module have been derived empirically.

121. Thermal constants and threshold temperatures. It should be noted that the weevil module presently is not only "driven" by average air temperatures but is highly dependent upon assumptions made for thermal constants and threshold temperatures. Precisely defined studies to elucidate the effects of temperatures on the development of *Neochetina* spp. are certainly in order. Such information, in connection with improved daily temperature data sets, would markedly improve the model's ability to predict weevil numbers.

Relationship to Future Biocontrol Modeling Work

122. One of the major outcomes of the production of this first-generation model is the potential for inclusion of other biocontrol agents in this model. The model has been written so that components such as the plant and weevil modules are virtually independent of each other. Other components or modules can be incorporated without major disruption of the basic parts. Therefore, modules of *Sameodes* or *Cercospora* could be added to the overall model as they become available. Too, based upon the outcome of this project, it appears feasible to model the interactions of other nuisance aquatic plants and their biocontrol agents, such as waterlettuce and *Neohydronomus*.

PART VI: CONCLUSIONS AND RECOMMENDATIONS

Conclusions

123. This report documents work conducted to develop a first-generation simulation model of waterhyacinth and *Neochetina*. Conclusions drawn from this work are as follows:

- a. Site-specific temperature and solar radiation measurements can be used to represent functions that satisfactorily express growth and development of waterhyacinth and *Neochetina*.
- b. The conceptual framework developed to address interactions between waterhyacinth and *Neochetina* provides a satisfactory account of actual interactions within this system.
- c. The computer program INSECT, which is a PC-compatible version of this simulation model, is sufficiently user-friendly to allow interactive execution of the model by an "operator" with limited computer experience.
- d. Because INSECT has been developed as a package of independent modules that separately address different biological processes, updating the model when new information becomes available will not be difficult.
- e. INSECT can be used as a generalized plan for development of simulation models for other biological control techniques of aquatic plants.

Recommendations

124. Some secondary data needs exist which should be supplemented before more accurate, predictive algorithms can be formulated. For example, more frequent field observations coupled with other sets of daily weather data need to be collected and used in the model. To be included in subsequent field efforts is the collection of data regarding weight distribution of the specific plant parts, detritus production, and associated impacts to the weevil population. Investigations of temperature damping by the presence of the water and the plants upon it are needed; only air temperature drives current algorithms. Direct measurements could be made of actual weevil damage on waterhyacinths to strengthen algorithms presently based only on inferential evidence. Survival of weevils by life stage can be observed concurrently. Flight muscle data should be collected to aid development of emigration and

immigration algorithms for inclusion in future model development. In anticipated logical development of this effort, insects other than *Neochetina* spp. that are found on the plants could be noted as well.

125. Finally, simulation of biocontrol techniques should be extended to encompass a greater span of time than the 1 year to which it is now limited. This increase is deemed necessary when attempting to establish a self-sustaining population for a stable, acceptable level of control.

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APPENDIX A: RELATIONSHIPS USED IN THE MODEL

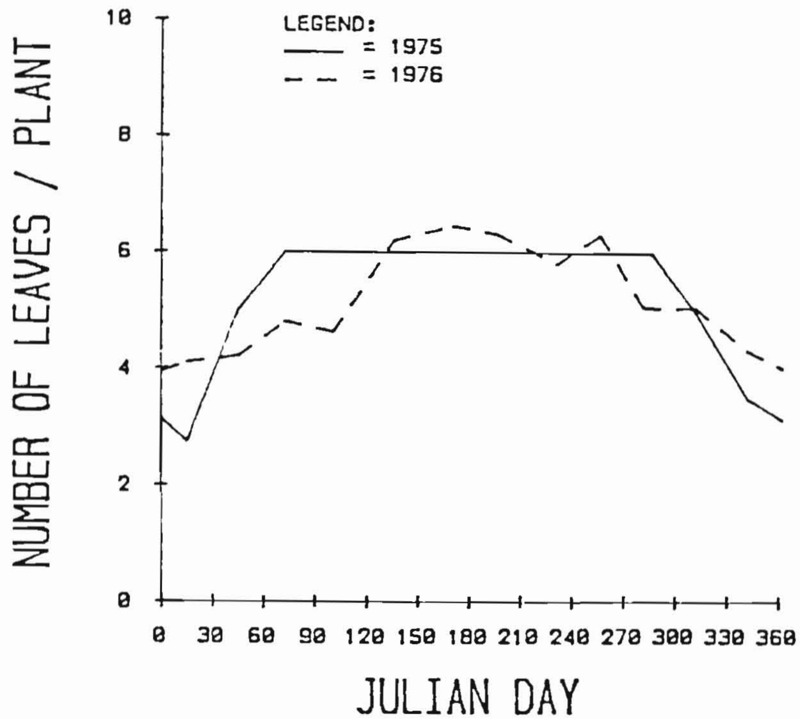

Figure A1. Number of leaves per plant used in the model

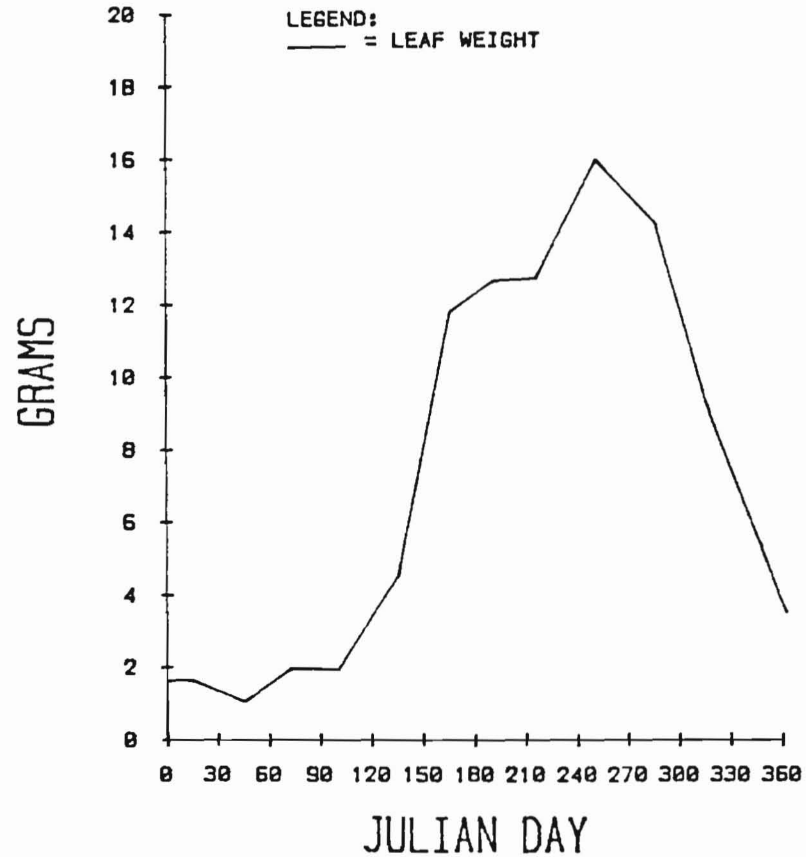

Figure A2. Weight, in grams, of all the leaves on a waterhyacinth plant used in the model

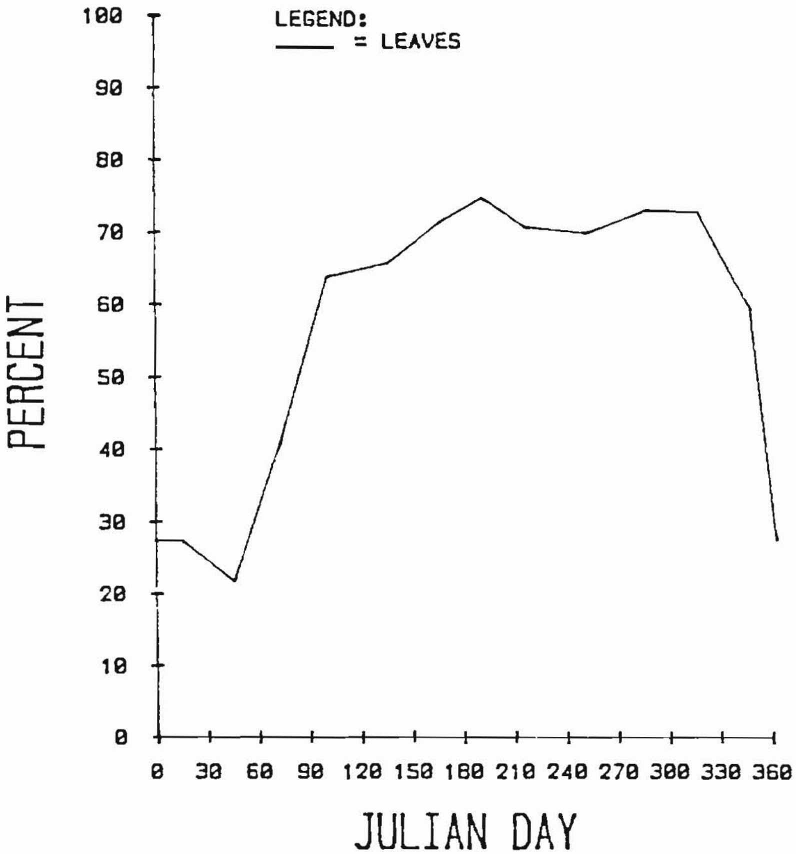

Figure A3. Percent leaf composition of a plant used in the model

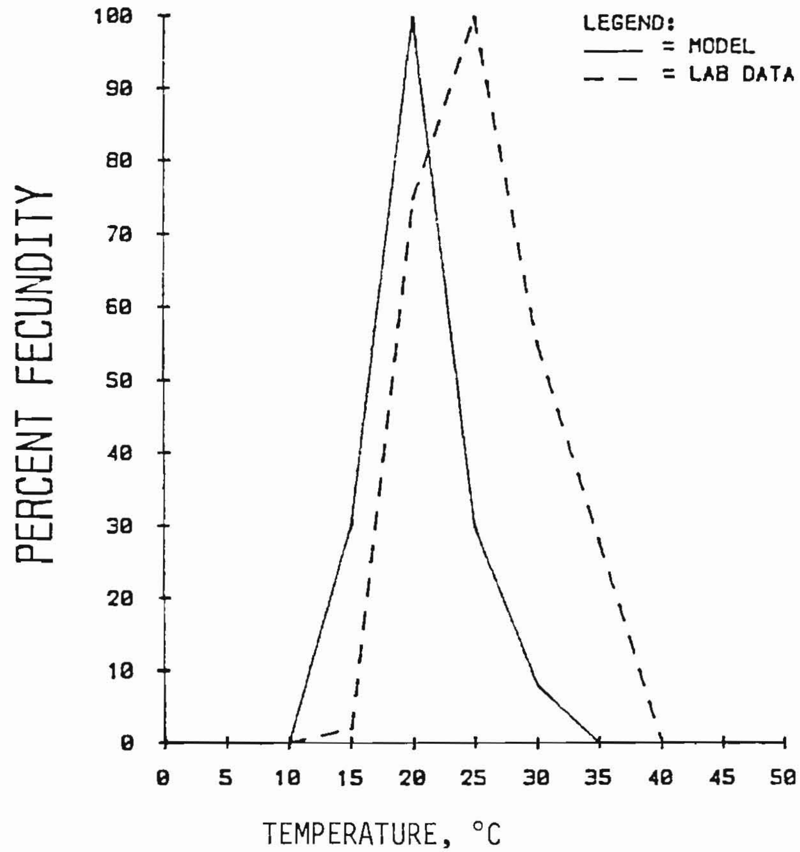

Figure A4. Temperature effect on fecundity relationship used in the model

APPENDIX B: INPUT AND OUTPUT FROM SIMULATION FOR 1 YEAR

```
                 ********************************
                           INSECT MODEL
                 ********************************

ENTER JULIAN DATE FOR FIRST DAY OF SIMULATION---> 1

ENTER JULIAN DATE FOR LAST DAY OF SIMULATION ---> 365

ENTER THE CODE FOR  WEATHER DATA TO BE USED
EXISTING FILE NAMES:

 1 = LAKE CONCORDIA - 1974
 2 = NEW ORLEANS - 1979
 3 = NEW ORLEANS - 1980
 4 = NEW ORLEANS - 1981

 5 = FLORIDA - 1975
 6 = FLORIDA - 1976
 7 = FLORIDA - 1977
 8 = FLORIDA - 1978
 9 = FLORIDA - 1979  ---> 6

ENTER THE CODE FOR SIMULATION CONDITIONS :
1 = SIMULATE PLANTS ONLY
2 = SIMULATE WEEVILS ONLY
3 = SIMULATE PLANTS & WEEVILS WITH DAMAGE
4 = SIMULATE PLANTS & WEEVILS WITHOUT DAMAGE ---> 3

ENTER INITIAL PLANT BIOMASS (Kg per sq m) ---> .705

ENTER PERCENT N. EICHHORNIAE & N. BRUCHI
EXAMPLE: 100 0 ---> 100,0

ENTER INITIAL INSECT POPULATIONS:

   JDINS  = JULIAN DATE FOR THE INPUT
   LSTAGE = LIFE STAGE OF THE INSECT
            1 = EGGS
            2 = LARVAE
            3 = PUPAE
            4 = ADULTS
   AMOUNT = NUMBER OF INSECTS per sq m

ENTER:  JDINS  LSTAGE  AMOUNT (SPACE OR COMMA IS NEEDED BETWEEN NUMBERS)
TO START SIMULATION ENTER 0 0 0 ---> 9,1,30

TO START SIMULATION ENTER 0 0 0 ---> 9,2,20

TO START SIMULATION ENTER 0 0 0 ---> 9,3,40

TO START SIMULATION ENTER 0 0 0 ---> 9,4,31

TO START SIMULATION ENTER 0 0 0 ---> 0,0,0
```

JULIAN DATE	BIOMASS Kg/sq m	# OF PLANTS	LARGE LARVAE	FEEDING g/sq m	TOTAL EGGS	TOTAL LARVAE	TOTAL PUPAE	TOTAL ADULTS
2	0.690	118.	0.	0.	0.	0.	0.	0.
3	0.688	116.	0.	0.	0.	0.	0.	0.
4	0.678	115.	0.	0.	0.	0.	0.	0.
5	0.663	114.	0.	0.	0.	0.	0.	0.
6	0.648	111.	0.	0.	0.	0.	0.	0.
7	0.644	109.	0.	0.	0.	0.	0.	0.
8	0.632	108.	0.	0.	0.	0.	0.	0.
9	0.618	106.	20.	0.	30.	20.	40.	31.
10	0.604	104.	0.	0.	1.	14.	39.	28.
11	0.592	101.	0.	0.	5.	14.	39.	28.
12	0.587	99.	0.	0.	12.	14.	39.	28.
13	0.586	98.	0.	0.	24.	14.	39.	28.
14	0.584	98.	0.	0.	38.	14.	39.	28.
15	0.577	98.	0.	0.	43.	14.	39.	28.
16	0.567	97.	0.	0.	47.	14.	39.	28.
17	0.554	96.	0.	0.	49.	14.	39.	28.
18	0.542	94.	0.	0.	2.	10.	39.	25.
19	0.530	93.	0.	0.	0.	7.	38.	23.
20	0.519	91.	0.	0.	1.	7.	38.	23.
21	0.508	90.	0.	0.	1.	7.	38.	23.
22	0.498	88.	0.	0.	1.	7.	38.	23.
23	0.487	87.	0.	0.	0.	5.	38.	20.
24	0.478	86.	0.	0.	1.	5.	38.	20.
25	0.476	84.	0.	0.	8.	5.	38.	20.
26	0.480	85.	0.	0.	20.	5.	38.	20.
27	0.479	86.	0.	0.	29.	5.	38.	20.
28	0.470	86.	0.	0.	15.	5.	37.	20.
29	0.461	85.	0.	0.	1.	3.	37.	18.
30	0.452	84.	0.	0.	0.	3.	36.	17.
31	0.443	83.	0.	0.	2.	3.	36.	17.
32	0.438	82.	0.	0.	6.	3.	36.	17.
33	0.430	82.	0.	0.	6.	3.	36.	17.
34	0.422	81.	0.	0.	7.	3.	36.	17.
35	0.417	80.	0.	0.	10.	3.	36.	17.
36	0.416	79.	0.	0.	16.	3.	36.	17.
37	0.414	80.	0.	0.	18.	3.	36.	17.
38	0.409	80.	0.	0.	19.	3.	36.	17.
39	0.402	80.	0.	0.	1.	2.	36.	15.
40	0.395	79.	0.	0.	1.	2.	36.	15.
41	0.388	78.	0.	0.	1.	2.	35.	15.
42	0.382	78.	0.	0.	1.	2.	35.	15.
43	0.380	77.	0.	0.	3.	2.	35.	15.
44	0.384	77.	0.	0.	5.	2.	35.	15.
45	0.387	79.	0.	0.	6.	2.	35.	15.
46	0.392	80.	0.	0.	8.	2.	35.	15.
47	0.398	81.	0.	0.	11.	2.	35.	15.
48	0.406	83.	0.	0.	13.	2.	35.	15.
49	0.412	84.	0.	0.	15.	2.	35.	15.

JULIAN DATE	BIOMASS Kg/sq m	# OF PLANTS	LARGE LARVAE	FEEDING g/sq m	TOTAL EGGS	TOTAL LARVAE	TOTAL PUPAE	TOTAL ADULTS
50	0.418	85.	0.	0.	17.	2.	35.	15.
51	0.426	87.	0.	0.	20.	2.	35.	15.
52	0.426	88.	0.	0.	22.	3.	35.	15.
53	0.433	88.	2.	0.	21.	5.	35.	15.
54	0.425	90.	0.	0.	21.	5.	35.	15.
55	0.417	88.	0.	0.	21.	5.	35.	15.
56	0.418	86.	2.	0.	21.	7.	35.	15.
57	0.419	87.	2.	0.	21.	8.	35.	15.
58	0.423	87.	0.	0.	23.	8.	35.	15.
59	0.425	87.	2.	0.	22.	10.	35.	15.
60	0.432	88.	2.	0.	22.	13.	35.	15.
61	0.444	89.	3.	0.	21.	15.	35.	15.
62	0.446	92.	2.	0.	20.	17.	35.	15.
63	0.460	92.	2.	0.	19.	19.	35.	15.
64	0.472	95.	3.	0.	18.	22.	35.	15.
65	0.480	98.	2.	0.	18.	24.	35.	15.
66	0.485	99.	4.	0.	16.	27.	35.	15.
67	0.489	100.	2.	0.	16.	29.	35.	15.
68	0.495	101.	3.	0.	15.	32.	35.	15.
69	0.499	102.	0.	0.	17.	31.	35.	15.
70	0.499	103.	2.	0.	16.	33.	35.	15.
71	0.510	103.	2.	0.	17.	35.	35.	15.
72	0.521	105.	1.	0.	18.	36.	35.	15.
73	0.530	108.	1.	0.	18.	37.	0.	50.
74	0.543	109.	1.	0.	38.	38.	0.	50.
75	0.547	114.	2.	0.	53.	40.	0.	50.
76	0.536	117.	0.	0.	58.	40.	0.	50.
77	0.526	117.	0.	0.	60.	39.	0.	50.
78	0.525	117.	2.	0.	72.	39.	0.	50.
79	0.532	118.	4.	0.	85.	41.	0.	50.
80	0.549	122.	4.	0.	99.	43.	0.	50.
81	0.557	128.	6.	0.	117.	46.	0.	50.
82	0.556	132.	3.	0.	128.	47.	0.	50.
83	0.559	134.	2.	0.	144.	47.	0.	50.
84	0.565	137.	4.	0.	157.	49.	0.	50.
85	0.574	141.	4.	0.	161.	51.	0.	50.
86	0.578	145.	4.	0.	165.	53.	0.	50.
87	0.582	148.	23.	0.	149.	73.	0.	50.
88	0.597	152.	25.	0.	130.	96.	0.	50.
89	0.614	158.	27.	0.	106.	121.	2.	50.
90	0.632	165.	16.	0.	93.	136.	2.	50.
91	0.649	172.	21.	0.	78.	157.	2.	50.
92	0.654	179.	12.	0.	69.	168.	2.	50.
93	0.658	183.	0.	0.	73.	167.	2.	50.
94	0.669	187.	16.	0.	61.	182.	2.	50.
95	0.681	193.	16.	0.	51.	197.	2.	50.
96	0.683	199.	12.	0.	43.	207.	2.	50.
97	0.686	202.	0.	0.	49.	206.	2.	50.
98	0.684	206.	6.	0.	48.	210.	2.	50.
99	0.691	208.	4.	0.	48.	213.	2.	50.

JULIAN DATE	BIOMASS Kg/sq m	# OF PLANTS	LARGE LARVAE	FEEDING g/sq m	TOTAL EGGS	TOTAL LARVAE	TOTAL PUPAE	TOTAL ADULTS
100	0.692	213.	2.	0.	50.	212.	2.	50.
101	0.696	216.	6.	0.	50.	214.	2.	50.
102	0.709	220.	7.	0.	53.	216.	2.	50.
103	0.727	227.	11.	0.	52.	220.	2.	50.
104	0.730	235.	9.	0.	55.	222.	2.	50.
105	0.751	239.	16.	0.	52.	229.	2.	50.
106	0.764	235.	15.	0.	53.	233.	2.	50.
107	0.775	230.	10.	0.	58.	231.	2.	50.
108	0.799	225.	21.	0.	54.	239.	2.	50.
109	0.827	223.	17.	0.	54.	242.	2.	50.
110	0.839	223.	19.	0.	53.	245.	3.	50.
111	0.867	218.	22.	0.	46.	252.	5.	50.
112	0.894	218.	18.	0.	44.	255.	6.	50.
113	0.924	217.	18.	0.	42.	257.	7.	50.
114	0.960	218.	17.	0.	38.	260.	9.	50.
115	0.987	220.	15.	0.	37.	263.	10.	50.
116	1.015	219.	15.	0.	31.	266.	10.	50.
117	1.040	219.	13.	0.	26.	269.	12.	50.
118	1.073	218.	11.	0.	21.	271.	13.	50.
119	1.103	219.	10.	0.	16.	272.	15.	50.
120	1.134	220.	8.	0.	13.	273.	15.	50.
121	1.153	220.	9.	0.	10.	273.	17.	50.
122	1.157	219.	8.	0.	6.	274.	18.	50.
123	1.183	214.	8.	0.	4.	274.	18.	50.
124	1.210	214.	10.	0.	0.	277.	18.	50.
125	1.233	214.	7.	0.	0.	275.	16.	52.
126	1.240	213.	26.	0.	1.	274.	16.	52.
127	1.262	210.	47.	0.	1.	272.	17.	52.
128	1.272	209.	73.	0.	2.	271.	17.	52.
129	1.281	206.	86.	0.	2.	268.	18.	52.
130	1.289	203.	114.	14.	3.	265.	20.	52.
131	1.297	201.	114.	15.	3.	264.	20.	52.
132	1.312	198.	142.	18.	4.	262.	21.	52.
133	1.313	197.	152.	20.	4.	260.	21.	52.
134	1.309	193.	132.	18.	3.	240.	41.	52.
135	1.294	189.	117.	16.	3.	218.	63.	52.
136	1.315	178.	94.	14.	2.	192.	89.	52.
137	1.342	173.	81.	0.	2.	177.	103.	52.
138	1.369	169.	66.	0.	2.	158.	123.	52.
139	1.383	166.	57.	0.	2.	147.	133.	52.
140	1.411	161.	50.	0.	2.	132.	147.	52.
141	1.424	158.	39.	0.	2.	117.	162.	52.
142	1.423	154.	37.	0.	2.	107.	170.	52.
143	1.419	149.	37.	0.	2.	103.	173.	54.
144	1.440	144.	39.	0.	3.	100.	175.	55.
145	1.441	141.	46.	0.	5.	97.	176.	57.
146	1.461	137.	48.	0.	7.	95.	176.	58.
147	1.457	135.	48.	0.	10.	90.	180.	59.
148	1.452	131.	44.	0.	13.	82.	186.	61.
149	1.472	127.	44.	0.	16.	77.	190.	62.

JULIAN DATE	BIOMASS Kg/sq m	# OF PLANTS	LARGE LARVAE	FEEDING g/sq m	TOTAL EGGS	TOTAL LARVAE	TOTAL PUPAE	TOTAL ADULTS
150	1.502	125.	49.	0.	20.	77.	187.	65.
151	1.522	124.	45.	0.	22.	69.	195.	65.
152	1.536	123.	46.	0.	24.	66.	197.	67.
153	1.548	121.	45.	0.	25.	61.	202.	67.
154	1.564	119.	40.	0.	25.	54.	210.	68.
155	1.568	117.	42.	0.	21.	56.	214.	68.
156	1.559	115.	37.	0.	22.	54.	218.	68.
157	1.565	112.	34.	0.	22.	53.	223.	68.
158	1.574	110.	34.	0.	21.	52.	228.	68.
159	1.587	108.	23.	0.	20.	45.	237.	68.
160	1.583	107.	18.	0.	19.	43.	240.	69.
161	1.587	105.	14.	0.	18.	41.	242.	71.
162	1.605	103.	12.	0.	18.	41.	244.	71.
163	1.613	102.	9.	0.	17.	40.	246.	72.
164	1.636	101.	8.	0.	15.	41.	248.	38.
165	1.651	101.	7.	0.	13.	43.	229.	58.
166	1.662	100.	3.	0.	14.	42.	211.	79.
167	1.677	100.	2.	0.	18.	44.	185.	105.
168	1.691	101.	2.	0.	26.	45.	171.	119.
169	1.710	102.	2.	0.	36.	46.	151.	139.
170	1.718	103.	2.	0.	46.	47.	141.	149.
171	1.719	103.	2.	0.	69.	49.	126.	164.
172	1.703	103.	3.	0.	99.	50.	112.	178.
173	1.702	102.	3.	0.	122.	51.	102.	188.
174	1.696	102.	6.	0.	157.	55.	97.	193.
175	1.711	102.	7.	0.	171.	61.	95.	195.
176	1.725	103.	10.	0.	178.	69.	93.	197.
177	1.744	103.	12.	0.	180.	80.	87.	204.
178	1.763	104.	12.	0.	182.	91.	78.	212.
179	1.776	105.	25.	0.	167.	115.	74.	217.
180	1.778	106.	31.	0.	146.	145.	74.	210.
181	1.763	106.	24.	0.	134.	167.	66.	211.
182	1.754	105.	39.	0.	110.	203.	62.	208.
183	1.755	104.	20.	0.	99.	221.	57.	207.
184	1.758	105.	16.	0.	93.	234.	48.	209.
185	1.768	105.	13.	0.	91.	244.	44.	206.
186	1.783	105.	13.	0.	88.	254.	40.	204.
187	1.789	106.	12.	0.	87.	261.	35.	202.
188	1.797	106.	19.	0.	87.	269.	30.	201.
189	1.815	107.	22.	0.	83.	278.	21.	204.
190	1.810	108.	26.	0.	76.	289.	17.	201.
191	1.826	107.	24.	0.	78.	295.	13.	199.
192	1.838	108.	27.	0.	75.	302.	11.	195.
193	1.854	109.	29.	0.	73.	309.	8.	191.
194	1.864	110.	28.	0.	70.	314.	6.	188.
195	1.873	110.	28.	0.	65.	318.	6.	183.
196	1.885	111.	25.	0.	57.	320.	8.	181.
197	1.894	111.	23.	0.	52.	323.	10.	175.
198	1.900	111.	23.	0.	46.	325.	12.	169.
199	1.911	111.	24.	0.	41.	329.	15.	164.

JULIAN DATE	BIOMASS Kg/sq m	# OF PLANTS	LARGE LARVAE	FEEDING g/sq m	TOTAL EGGS	TOTAL LARVAE	TOTAL PUPAE	TOTAL ADULTS
200	1.918	112.	20.	0.	37.	331.	17.	159.
201	1.917	112.	20.	0.	32.	334.	18.	154.
202	1.925	112.	17.	0.	29.	336.	19.	149.
203	1.922	112.	15.	0.	27.	335.	20.	145.
204	1.941	112.	12.	0.	26.	334.	21.	140.
205	1.954	112.	10.	0.	25.	331.	24.	136.
206	1.968	113.	8.	0.	23.	328.	26.	132.
207	1.975	114.	11.	0.	19.	328.	27.	128.
208	1.982	114.	13.	0.	16.	327.	28.	124.
209	1.983	114.	18.	0.	14.	326.	28.	121.
210	1.982	114.	26.	0.	13.	326.	28.	117.
211	1.983	113.	32.	0.	12.	324.	28.	114.
212	1.984	113.	50.	0.	10.	323.	28.	110.
213	1.959	113.	73.	28.	9.	321.	29.	107.
214	1.924	111.	89.	34.	9.	319.	29.	104.
215	1.870	109.	115.	44.	9.	314.	31.	101.
216	1.815	106.	125.	48.	9.	308.	35.	98.
217	1.769	103.	129.	50.	8.	299.	41.	95.
218	1.731	100.	130.	50.	8.	290.	48.	93.
219	1.691	98.	130.	50.	6.	281.	56.	90.
220	1.657	95.	118.	45.	6.	262.	73.	87.
221	1.628	93.	102.	39.	5.	238.	95.	85.
222	1.604	91.	93.	36.	5.	220.	112.	82.
223	1.595	90.	76.	29.	4.	191.	139.	80.
224	1.586	89.	68.	26.	3.	176.	152.	78.
225	1.561	88.	63.	24.	3.	164.	162.	77.
226	1.556	87.	61.	24.	3.	155.	165.	79.
227	1.548	86.	59.	23.	3.	146.	171.	79.
228	1.532	85.	59.	23.	4.	138.	175.	78.
229	1.518	83.	59.	23.	4.	130.	179.	78.
230	1.498	82.	56.	22.	7.	121.	185.	78.
231	1.490	80.	51.	20.	9.	110.	193.	77.
232	1.458	79.	52.	21.	12.	104.	198.	76.
233	1.456	77.	50.	20.	14.	96.	203.	74.
234	1.454	76.	49.	20.	15.	89.	209.	73.
235	1.446	75.	48.	20.	15.	83.	212.	74.
236	1.438	74.	44.	18.	15.	77.	216.	74.
237	1.433	73.	38.	16.	15.	70.	221.	73.
238	1.432	73.	36.	15.	14.	67.	225.	72.
239	1.450	72.	32.	0.	12.	63.	230.	70.
240	1.470	72.	29.	0.	11.	58.	236.	68.
241	1.491	73.	26.	0.	10.	55.	240.	67.
242	1.509	73.	22.	0.	9.	51.	245.	65.
243	1.521	73.	19.	0.	9.	47.	248.	64.
244	1.541	74.	17.	0.	9.	45.	251.	62.
245	1.559	74.	17.	0.	8.	44.	250.	61.
246	1.568	74.	16.	0.	8.	42.	247.	61.
247	1.572	74.	16.	0.	8.	42.	243.	63.
248	1.582	74.	13.	0.	9.	40.	238.	67.
249	1.584	74.	11.	0.	11.	38.	233.	71.

JULIAN DATE	BIOMASS Kg/sq m	# OF PLANTS	LARGE LARVAE	FEEDING g/sq m	TOTAL EGGS	TOTAL LARVAE	TOTAL PUPAE	TOTAL ADULTS
250	1.594	73.	9.	0.	13.	37.	218.	85.
251	1.605	73.	8.	0.	18.	35.	198.	102.
252	1.612	73.	7.	0.	24.	34.	184.	114.
253	1.610	73.	6.	0.	35.	33.	158.	136.
254	1.620	72.	6.	0.	61.	33.	146.	145.
255	1.619	72.	6.	0.	83.	33.	136.	150.
256	1.608	72.	7.	0.	107.	34.	128.	154.
257	1.589	71.	8.	0.	143.	37.	121.	156.
258	1.581	69.	5.	0.	202.	36.	121.	152.
259	1.591	69.	8.	0.	223.	38.	115.	152.
260	1.598	70.	9.	0.	246.	43.	109.	154.
261	1.611	71.	10.	0.	253.	48.	102.	157.
262	1.620	72.	14.	0.	251.	58.	93.	161.
263	1.624	73.	28.	0.	235.	82.	88.	162.
264	1.619	73.	25.	0.	225.	103.	81.	163.
265	1.625	73.	27.	0.	210.	127.	75.	164.
266	1.580	74.	94.	44.	125.	219.	70.	164.
267	1.582	72.	25.	0.	110.	240.	64.	164.
268	1.591	73.	29.	0.	92.	265.	58.	166.
269	1.604	74.	17.	0.	86.	277.	53.	165.
270	1.612	75.	13.	0.	83.	285.	48.	165.
271	1.620	75.	14.	0.	79.	293.	41.	166.
272	1.614	76.	18.	0.	73.	303.	36.	166.
273	1.615	76.	18.	0.	70.	311.	31.	165.
274	1.611	77.	7.	0.	107.	308.	27.	164.
275	1.607	77.	17.	0.	135.	314.	24.	161.
276	1.608	77.	18.	0.	156.	320.	23.	158.
277	1.611	78.	19.	0.	169.	326.	22.	155.
278	1.614	78.	18.	0.	173.	332.	20.	151.
279	1.620	79.	16.	0.	173.	336.	18.	150.
280	1.616	79.	14.	0.	172.	338.	17.	148.
281	1.612	80.	13.	0.	170.	340.	17.	145.
282	1.608	80.	14.	0.	178.	343.	17.	142.
283	1.590	80.	41.	0.	156.	375.	17.	138.
284	1.578	80.	39.	0.	137.	405.	16.	135.
285	1.569	80.	4.	0.	153.	400.	16.	132.
286	1.558	79.	32.	0.	140.	425.	16.	128.
287	1.543	79.	25.	0.	129.	443.	15.	125.
288	1.537	79.	3.	0.	147.	438.	15.	122.
289	1.525	90.	16.	0.	145.	447.	14.	119.
290	1.526	80.	10.	0.	139.	451.	14.	116.
291	1.519	81.	8.	0.	140.	453.	15.	112.
292	1.514	82.	8.	0.	143.	454.	15.	109.
293	1.521	82.	33.	0.	116.	479.	14.	107.
294	1.499	84.	3.	0.	119.	474.	14.	104.
295	1.464	93.	19.	0.	104.	485.	14.	101.
296	1.447	83.	3.	0.	108.	481.	14.	99.
297	1.435	83.	36.	0.	84.	507.	13.	96.
298	1.425	83.	19.	0.	78.	513.	12.	94.
299	1.414	83.	29.	0.	69.	526.	12.	91.

JULIAN DATE	BIOMASS Kg/sq m	# OF PLANTS	LARGE LARVAE	FEEDING g/sq m	TOTAL EGGS	TOTAL LARVAE	TOTAL PUPAE	TOTAL ADULTS
300	1.392	84.	12.	0.	72.	521.	12.	89.
301	1.361	84.	23.	0.	62.	527.	12.	87.
302	1.336	83.	18.	0.	63.	522.	12.	84.
303	1.322	83.	22.	0.	64.	520.	12.	82.
304	1.320	83.	43.	0.	62.	522.	11.	80.
305	1.289	84.	35.	0.	63.	517.	11.	78.
306	1.268	83.	50.	0.	64.	512.	11.	76.
307	1.253	83.	58.	0.	59.	516.	11.	74.
308	1.229	83.	65.	0.	59.	511.	11.	72.
309	1.202	83.	63.	0.	60.	504.	12.	70.
310	1.172	82.	62.	0.	30.	498.	12.	69.
311	1.144	81.	63.	0.	29.	495.	12.	67.
312	1.120	81.	61.	0.	30.	490.	12.	65.
313	1.092	80.	43.	0.	1.	342.	12.	60.
314	1.065	80.	42.	0.	2.	339.	12.	59.
315	1.050	79.	86.	0.	3.	335.	12.	57.
316	1.041	79.	85.	0.	5.	332.	12.	56.
317	1.026	80.	95.	0.	7.	328.	12.	54.
318	1.003	80.	94.	0.	8.	325.	12.	53.
319	0.994	80.	105.	0.	10.	320.	14.	52.
320	0.975	79.	110.	0.	12.	317.	14.	51.
321	0.951	79.	107.	0.	12.	312.	16.	49.
322	0.946	77.	110.	0.	13.	309.	16.	48.
323	0.934	77.	105.	0.	14.	302.	20.	47.
324	0.917	77.	108.	0.	15.	299.	20.	46.
325	0.905	76.	97.	0.	16.	286.	30.	45.
326	0.882	76.	97.	0.	16.	285.	30.	45.
327	0.859	75.	97.	0.	16.	284.	30.	45.
328	0.836	73.	68.	0.	1.	198.	30.	42.
329	0.815	72.	68.	0.	1.	198.	30.	42.
330	0.806	71.	71.	0.	2.	196.	30.	41.
331	0.795	71.	67.	0.	3.	188.	36.	40.
332	0.793	71.	59.	0.	3.	179.	42.	40.
333	0.781	71.	33.	0.	4.	149.	70.	39.
334	0.759	71.	33.	0.	4.	149.	70.	39.
335	0.737	70.	33.	0.	4.	149.	70.	39.
336	0.716	68.	33.	0.	4.	148.	70.	39.
337	0.695	67.	33.	0.	4.	148.	70.	39.
338	0.678	66.	32.	0.	4.	147.	70.	38.
339	0.660	65.	32.	0.	5.	145.	70.	37.
340	0.650	64.	27.	0.	5.	137.	76.	36.
341	0.635	64.	19.	0.	6.	128.	84.	36.
342	0.617	63.	19.	0.	6.	127.	84.	35.
343	0.599	62.	19.	0.	3.	125.	83.	34.
344	0.589	61.	21.	0.	3.	124.	81.	35.
345	0.587	61.	19.	0.	5.	119.	84.	35.
346	0.585	62.	18.	0.	6.	115.	84.	36.
347	0.578	62.	17.	0.	9.	111.	86.	35.
348	0.561	62.	17.	0.	10.	110.	85.	35.
349	0.551	62.	16.	0.	12.	106.	88.	35.

JULIAN DATE	BIOMASS Kg/sq m	# OF PLANTS	LARGE LARVAE	FEEDING g/sq m	TOTAL EGGS	TOTAL LARVAE	TOTAL PUPAE	TOTAL ADULTS
350	0.538	60.	15.	0.	13.	105.	87.	34.
351	0.523	58.	15.	0.	13.	104.	87.	34.
352	0.510	55.	15.	0.	13.	103.	87.	33.
353	0.499	53.	12.	0.	14.	99.	89.	32.
354	0.488	51.	14.	0.	15.	98.	89.	31.
355	0.475	49.	14.	0.	15.	98.	89.	31.
356	0.462	47.	9.	0.	1.	68.	87.	30.
357	0.450	45.	9.	0.	1.	68.	87.	30.
358	0.439	43.	9.	0.	1.	68.	87.	30.
359	0.429	41.	16.	0.	1.	67.	87.	29.
360	0.422	39.	16.	0.	2.	66.	87.	28.
361	0.412	37.	16.	0.	2.	66.	87.	28.
362	0.403	36.	22.	0.	3.	65.	86.	28.
363	0.395	34.	21.	0.	3.	63.	87.	27.
364	0.386	32.	21.	0.	3.	63.	87.	27.
365	0.382	30.	21.	0.	4.	62.	87.	27.

Execution terminated : 0

APPENDIX C: WEATHER DATA USED IN SIMULATIONS

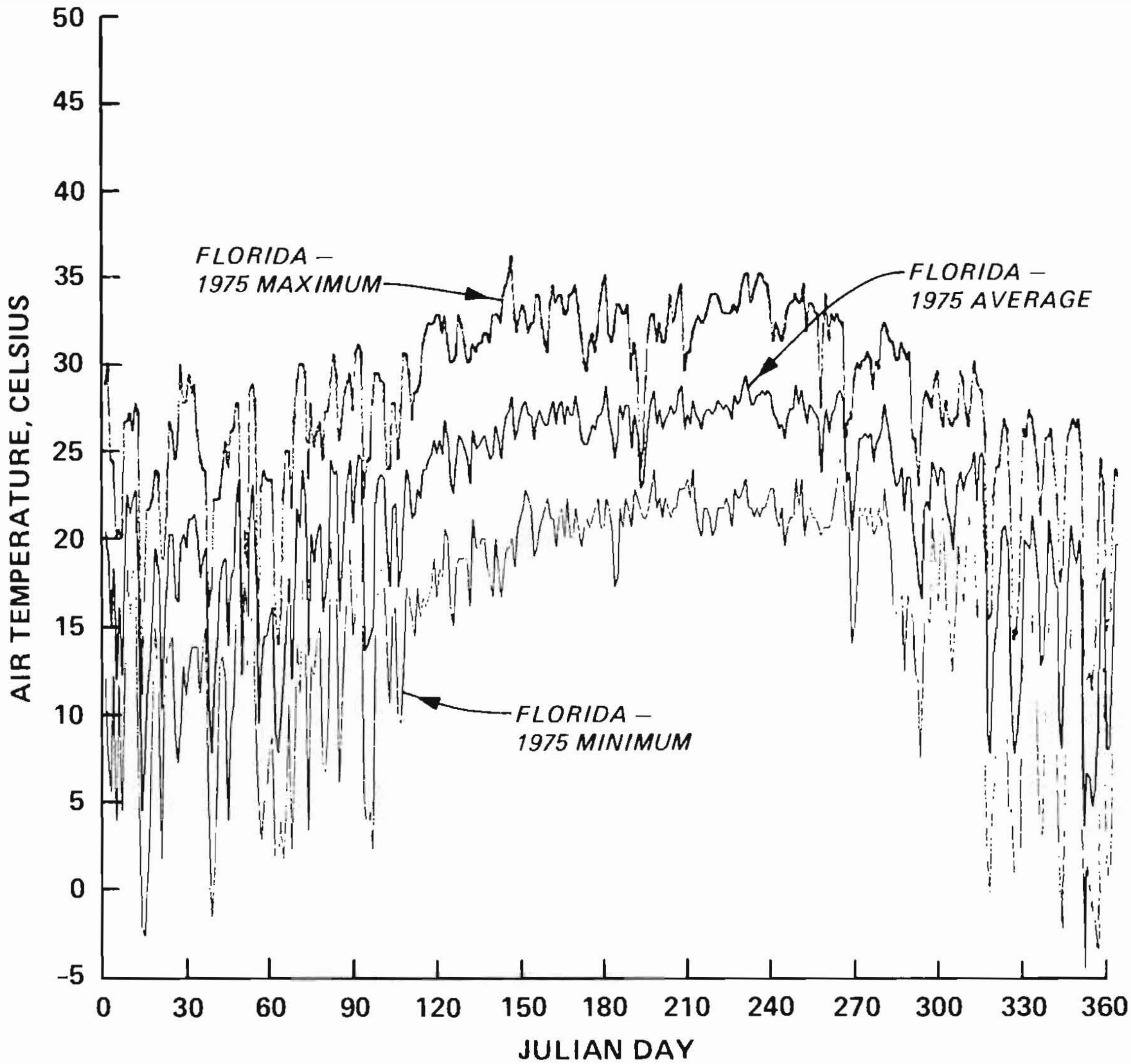

Figure C1. 1975 daily air temperatures, Gainesville, Fla.

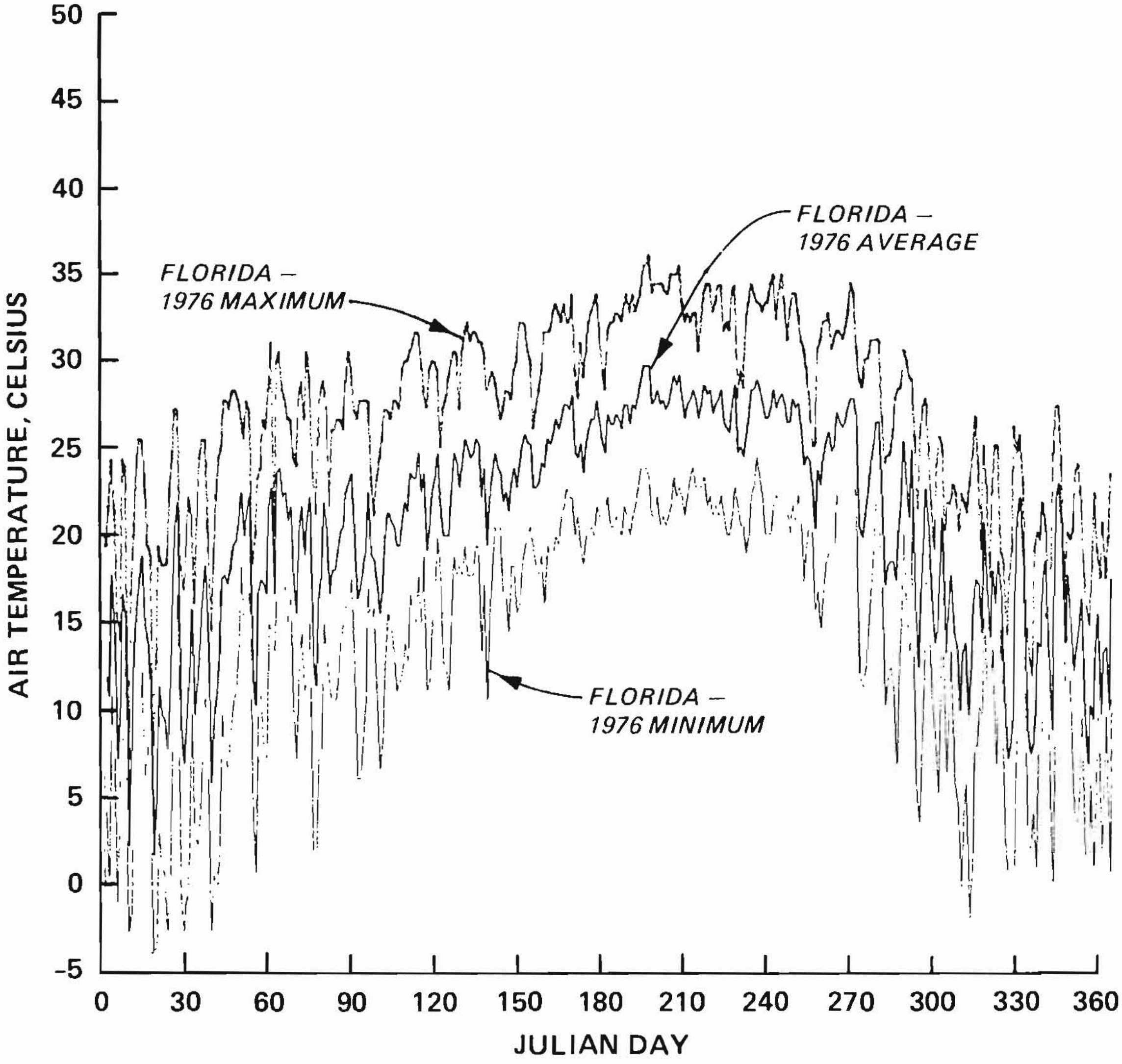

Figure C2. 1976 daily air temperatures at Gainesville, Fla.

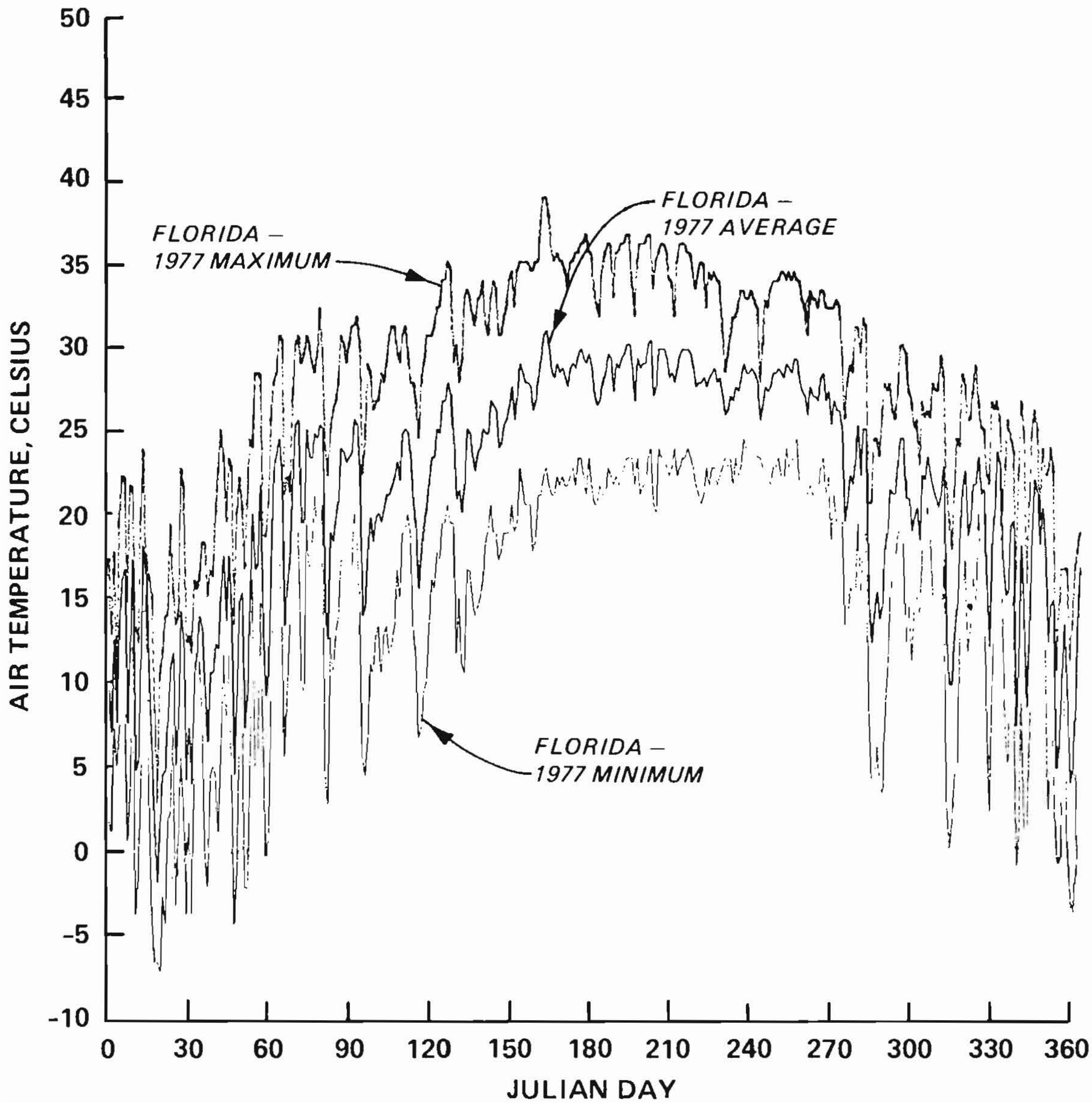

Figure C3. 1977 daily air temperatures at Gainesville, Fla.

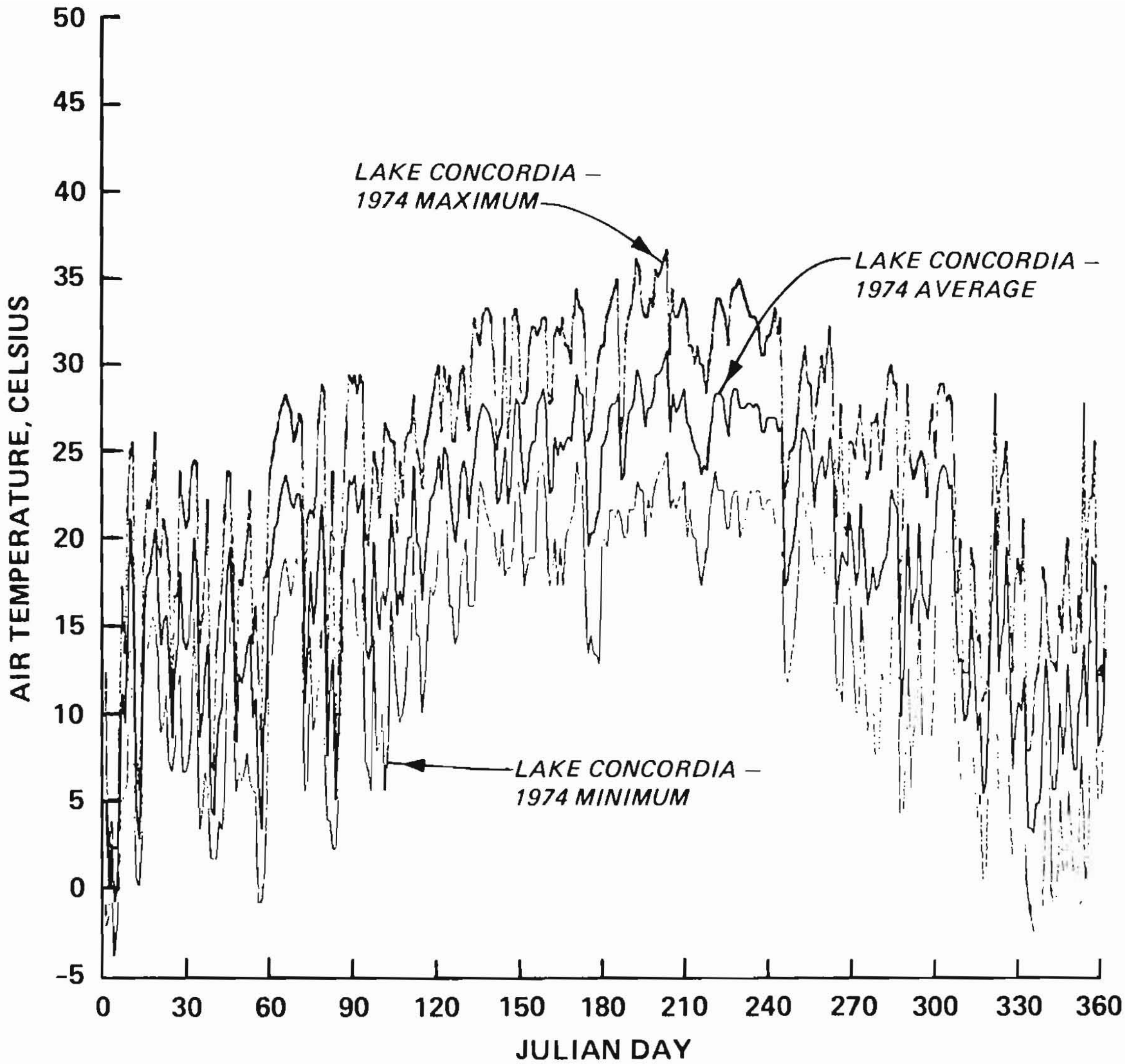

Figure C4. 1974 daily air temperatures at Jonesville Locks, Louisiana