RETURNING MATERIALS:
Place in book drop to remove this checkout from your record. FINES will be charged if book is returned after the date stamped below.

HOST-PARASITE RELATIONSHIPS AND MANAGEMENT OF HETERODERA SCHACHTII ASSOCIATED WITH BRASSICA OLERACEA VAR CAPITATA L.

By

Paul Muchena

A THESIS

Submitted to Michigan State University
in partial fulfillment of the requirements
for the degree of

MASTER OF SCIENCE

Department of Entomology

1984

ABSTRACT

HOST-PARASITE RELATIONSHIPS AND
MANAGEMENT OF HETERODERA SCHACHTII
ASSOCIATED WITH BRASSICA OLERACEA VAR CAPITATA L.

By

Paul Muchena

The distribution of Heterodera schachtii Schmidt, 1871 and Brassica oleracea var capitata L. roots were aggregated in the upper 20 cm of clay drainage tiles under greenhouse conditions. H. schachtii significantly (P=0.05) reduced B. oleracea capitata (cv. Roundup) marketable yield. The pathogenicity of Michigan H. schachtii and New York H. schachtii on B. oleracea capitata (cv. Roundup) was the same (P=0.05) under greenhouse conditions. Soil with Michigan H. schachtii, had significantly (P=0.05) more cysts, eggs, and second stage juveniles at the end of the growing season than soil with New York H. schachtii.

H. schachtii reproduced on B. oleracea capitata in greenhouse and field environments. Three generations of H. schachtii per season were observed on B. oleracea capitata under Michigan field conditions. H. schachtii had a P_{final} (P_f)/$P_{initial}$ (P_i) ratio of up to 14.0.

Phenamiphos (Nemacur®) at 6.0 kg ai/ha or 3.0 kg ai/ha at seeding and an additional 3.0 kg ai/ha at transplanting, significantly (P=0.05) increased B. oleracea capitata (cv. Roundup) marketable yield under field conditions. Phenamiphos application reduced the P_f/P_i ratio to 2.0. In the greenhouse, optimum B. oleracea capitata (cv. King Cole) marketable yield was obtained with phenamiphos rates between 4.8 and 6.0 kg ai/ha. Rates below 4.8 kg ai/ha were not effective in controlling H. schachtii and rates above 6.0 kg ai/ha were phytotoxic to B. oleracea capitata (cv. King Cole).

seed

house

phen

A positive linear relationship between B. oleracea capitata (cv. King Cole) seed germination and phenamiphos application rate was observed under greenhouse conditions. The seed germination loss was increased when equivalent phenamiphos application rates were applied in H. schachtii infested soil.

guida

My a

Grad

enthu

and

ackno

leade

memb

some

other

progr

frienc

Lorra

enjoya

enthus

for the

ACKNOWLEDGMENTS

I would like to thank my major professor, Dr. George Bird, for his excellent guidance and support during my graduate studies at Michigan State University. My appreciation is also extended to the members of my committee, Drs. Ed Grafius, Hugh Price, and Lal Tummala, for their time, assistance, and enthusiasm in sharing their knowledge and experiences with me.

I have enjoyed and benefited from my association with the faculty, staff, and students of the Entomology Department. In particular, I would like to acknowledge my respect and gratitude to Dr. James Bath for his outstanding leadership and ability to instill a sense of professionalism and camaraderie in all members of this department. He made this department look like my second home. I also thank Mr. Kenneth Dimoff and Ms. Susan Battenfield, and many other staff members for their patience and assistance during my graduate program.

All members of the "Nematology Group" deserve special thanks for their friendship and support of my research efforts. Mr. John Davenport and Mrs. Lorraine Graney were especially instrumental in making my stay at MSU both enjoyable and fruitful. Ms. Barbara Mullen is one of the many able and enthusiastic employees who assisted me in my laboratory and field experiments.

Finally, I would like to thank my parents and the government of Zimbabwe for their support to the fulfillment of my educational goals.

TABLE OF CONTENTS

TABL

TABLE OF CONTENTS (cont.)

TABL

2.

2.

2.

2.

2.

2.

2.

3. Ex

3.1

3.1

3.1

3.1

3.1

3.2

3.2.

3.2.

3.2.

3.2.

TABLE OF CONTENTS (cont.)

TABL

3

3.

3.

3.

3.

3.

3.

3.

3.

3.5

3.5

3.5

3.5

3.5

3.6

3.6

TABLE OF CONTENTS (cont.)

TABLE OF CONTENTS (cont.)

1.

2.

31.

32.

33.

34.

35.

36.

37.

38.

39.

40.

41.

42.

LIST OF TABLES

B11. H
ca
de
w

B12. H
re
ar
in

B13. H
ba
gr

B14. H
ar
pe

B15. H
cr
pe

B16. H
cr
pe

B17. H
cr
pe

B18. H
ag
cr

C1. Fr
ab
ab

C2. Fr
ab
ab

C3. N
co
st

C4. N
C5. N
C6. N
C7. N
C8. N
C9. N
C10. N
D1. F
D2. F
D3. N
D4. N
D5. N

LIST OF FIGURES

1. INTRODUCTION

1.1 GENERAL

Heterodera spp. (cyst nematodes) are important pests of many crops, principally in temperate climates (Dropkin, 1980). The primary hosts for selected species of economic significance are: Heterodera avenae Wollenweber, 1924--oats, barley, rye, wheat; H. glycines Ichinohe, 1952--soybeans, Phaseolus spp.; H. gottingiana Liebscher, 1892--peas, vetch, field bean; H. oryzae Brizuela, 1961--rice; Globodera rostochiensis Behrens, 1975--potatoes, tomatoes, eggplant; G. pallida Stone, 1973--potatoes, tomatoes, eggplant; H. schachtii Schmidt, 1871--beets, cabbage, rape; and H. trifoliae Goffart, 1932--red and white clover (Dropkin, 1980). All the 88 spp. of genera Heterodera (Dropkin, 1980; Mulvey and Golden, 1983) are phytoparasites and alter the physiology and ontogeny of host plants. Nematodes in this genus reduce growth, yield, and marketability of host plants at high infestation levels.

Plant stress and resulting crop loss caused by nematodes is governed by soil environment (especially physical structure and water content) and temperature, which in turn affect the population dynamics of the nematodes (Jones, 1957). Plant growth and H. schachtii (sugar beet cyst nematode) density population are negatively correlated (Abawi and Mai, 1980; Althof et al., 1974). The abundance of H. schachtii also influences the population dynamics and pathogenicity of many species and other organisms contributing to plant damage. For example, infection of plants by H. schachtii may decrease Meloidogyne hapla Chitwood, 1949 reproduction (Jatala and Jensen, 1976b), or increase the incidence of Rhizoctonia solani (Franklin, 1972).

Population dynamics of H. schachtii are influenced by the initial (P_i) nematode population density (Olthof, 1978); soil type (Brzeski, 1969; Jones, 1957; Olthof, 1978); temperature (Olthof, 1978; Thomason, 1962); pH (Brzeski, 1969); size of the roots (Olthof, 1978); complex biological associations (Jatala and Jensen, 1976b); and management practices (Abawi and Mai, 1977). To adequately assess the population dynamics of H. schachtii, it is necessary to understand the nature of the association among these factors and the life history of this nematode. This information is imperative for the development of predictive pest-crop ecosystem simulations and integrated nematode management programs.

The purpose of this research was to evaluate the host-parasite relationships of H. schachtii and Brassica oleracea var capitata L. and to assess the role of phenamiphos (Nemacur 3S) as a nemastat in cabbage production.

1.2 GOALS AND OBJECTIVES

Goal

Evaluate the host-parasite relationships of H. schachtii and B. oleracea capitata in relation to the development of future integrated nematode management programs.

Objectives

1.2-1 Evaluate the impact of H. schachtii on the ontogeny of B. oleracea capitata.

- Determine the spatial and temporal distribution of roots and H. schachtii.
- Describe the influence of H. schachtii on B. oleracea capitata emergence.

- Quantify the impact of H. schachtii on B. oleracea capitata growth and development.
- Compare the pathogenicity of Michigan and New York H. schachtii on cabbage.

1.2.2 Evaluate the influence of phenamiphos on the H. schachtii-B. oleracea capitata association.

- Determine the impact of phenamiphos on the emergence of B. oloracea capitata seeds.
- Quantify the response of B. oleracea capitata to different dosages of phenamiphos.
- Assess the role of phenamiphos as a nemastat on H. schachtii associated with cabbage.

1.3 RATIONALE AND RESEARCH APPROACH

The primary objective in sampling is to collect a sample that truly represents the population in a given plot or field at a given time (Barker et al., 1978). Most sampling schemes, however, are inadequate for characterizing the spatial and temporal distribution of nematodes within a growing season. This is particularly true for species that occur as aggregates (egg masses or cysts) which have skewed distribution because of plant and soil influences (Barker et al., 1978). To improve H. schachtii sampling schemes, it was essential to determine how cabbage roots are distributed throughout the growing season, and to examine how root distribution affects the distribution of H. schachtii.

The population dynamics of H. schachtii has been addressed in several studies, but some aspects of the nematode-environment relationship have not

been investigated. Lack of information on these relationships is apparent during the development of pest-crop ecosystem simulations. In the development of a computer simulation, many environmental variables must be assumed as optimal. Most simulations use temperature as the controlled variable. For these pest-crop models to be accurate predictive tools, it is necessary to simulate a "true environment" and to include all the "important interactions" with the nematode and crop. In my research, the influence of degree days and phenamiphos on the development of H. schachtii associated with cabbage was assessed.

The sugarbeet cyst nematode is an appropriate species for quantitative population studies due to its residency within root tissue, discernible life stages, and habits of oviposition (cysts--a single unit with eggs and second stage juveniles). Cabbage is a suitable host for these studies because it can be grown in the field or greenhouse, in clay drainage tiles, or clay pots. Also, cabbage is an important crop in most countries of the world. In the United States, it is fourth vegetable crop in volume, following, potato, lettuce, and tomato (Ryder, 1979).

H. schachtii can be controlled with several management tactics. Selection of a specific tactic is influenced by economics, biotic and abiotic environments, crop, and level of nematode infestation. When the level of infestation is above an action threshold, chemical control is generally an option because of its immediate reduction of the nematode population. Fumigant nematicides can be used to lower population densities of H. schachtii (Wright, 1981). Recently, however, fumigant nematicides have encountered several major problems, including the following setbacks--phytotoxicity and persistence of residues in the environment. Increasingly, nonfumigant nematicides have been adopted during

the last 20 years. They are less phytotoxic, relatively easier to apply than fumigants, require no special equipment, are effective in controlling nematodes at much lower dosages, and leave less persistant residues in the environment (Wright, 1981).

It is generally accepted that non-fumigants act by impairing nematode neuromuscular activity; thereby reducing movement, invasion, and feeding, and consequently the rate of development and reproduction (Evans, 1973). It is now also apparent that low concentrations of these compounds can affect the sensory behavior of nematodes, and that this is an important component in crop protection from nematodes (Wright, 1981). Most of the scientific literature indicates that at sublethal treatments, nonfumigant nematicides stimulate emergence of juveniles from cysts. On the other hand, concentrations that stimulate hatch may also disorient second stage juveniles sufficiently to interfere with invasion and development (Greco and Thomason, 1980; Steele and Hodges, 1975). The mode of action for control of the sugar beet cyst nematode with phenamiphos was assessed both in the field and greenhouse. Information on this will lead to the overall understanding of mode of action for nonfumigant nematicides. This information is imperative for the design of integrated pest management programs favorable to beneficial microorganisms.

2. LITERATURE REVIEW

2.1 HETERODERA SCHACHTII SCHMIDT, 1871

This nematode is commonly known as the sugar beet cyst nematode. It was first discovered in Europe by Schacht in 1859 (Maggenti, 1981; Thorne, 1961).

2.1.1 Description

Male: Body vermiform with terminus bluntly rounded; tail less than half body-width long; spear well developed with knobs concave anteriorly; esophageal glands overlying intestine ventro-laterally; excretory pore 2 to 3 body-widths behind medium bulb; and testis single.

Female: White, flask-shaped, with short neck embedded in host root and swollen body on root surface; terminal vulva on conical protuberance (vulva cone) covered with gelatinous matrix containing eggs. Median esophageal bulb prominant, spherical, glands overlapping intestine latero-ventrally. Paired ovaries long and much coiled; a few eggs laid into the matrix, but most retained in body.

Cysts: When the female dies the cuticle becomes tanned, brown, tough, and minutely rugose, forming a protective envelope, the cyst, containing the eggs. The cysts become detatched from the host root and remain in the soil, the contained eggs (often numbering 500 to 600) remain viable for at least 6 years. Cysts of H. schachtii can be distinguished from those of other species of the same genus by their shape and the features of the vulval cone. The terminal vulval slit is about as long as the vulval bridge. It can also be distinguished by its fenestral length (Abawi et al., 1973).

Second stage juveniles: Head is offset. Spear moderately heavy with prominent, forwardly-directed knobs; esophageal glands overlying intestine ventro-laterally; dorsal gland duct opening 3-4 μ behind spear base. Tail acutely conical with rounded tip; a distinct hyaline terminal section 1-1.25 times the stylet length.

2.1.2 Systematic Position

Tylenchida: Tylenchoidea: Heteroderidae: Heteroderinae: Heterodera Schmidt 1871: type species H. schachtii.

2.1.3 Distribution and Hosts

H. schachtii is distributed throughout Europe from Spain to Finland and Eire to Bulgaria. It is also recorded in USSR, Turkey, and Israel; in USA, both eastern and western States; in Canada and South Africa (Franklin, 1972).

The sugar beet cyst nematode is a polyphagous feeding species, mainly on plants in the families Chenopodiaceae and Cruciferae. In the former, it feeds on the cultivated varieties of Beta vulgaris and Spinacea oleracea; in the Cruciferae on Brassica oleracea of all varieties, B. napes, B. rapa, and Rhaphanus sativus. H. schachtii also infects Rheum rhaponticum, many species of Beta and Chenopodium, Brassica campestris, Arabis spp., Sisymbrium sp., and Stellaria media. Many of these are common weeds and may act as alternative hosts, carrying over soil infestation from one susceptible crop to the next (Abawi and Mai, 1977; Franklin, 1972).

2.1.4 Biology and Life History

H. schachtii has six developmental stages: egg, four juvenile stages, and adult. In addition, H. schachtii has a cyst stage which is a dead female body with eggs retained internally. Cysts are lemon shaped and 0.5-0.8 mm in length (Thorne, 1961).

In the cysts, the eggs undergo the process of embryogenesis, and the first stage juveniles molt to the second or infective stage. These may remain dormant in the eggs for several years, but some hatch every year and emerge from the cysts into soil (Franklin, 1972). The optimum temperature for hatching is 25°C (Thorne, 1961). Optimum movement of the second stage juveniles occurs when the size of the soil particle is 150 to 250 µ, humidity 10 to 20%, and temperature above 20°C (Decker, 1981). The optimum soil moisture is intermediate between saturated and dry (Wallace, 1963). Hatching is stimulated by exudates from the roots of host and non-host plants, but also takes place to a lesser extent in the absence of plants (Thorne, 1961; Franklin,1972).

Second stage juveniles of H. schachtii in soil are attracted to the host roots (Steele, 1975). They penetrate immediately basipetal to the subapical meristerm, and close to the stele. About 46% of the juveniles orient their anterior end towards the root tip, 44% toward the hypocotyl, and 10% orient perpendicular to the root axis (Steele, 1971). If the plant is a suitable host, it forms syncytia on which the nematode feeds and develops (Franklin, 1972). The syncytium, caused by the feeding of H. schachtii in young roots where no secondary growth has occurred, possess dense and multinucleate cytoplasm (Jatala and Jensen, 1976C). The syncytium is formed by a progressive dissolution of adjoining cell walls. This dissolution results in the merging of protoplasts

until the syncytium is one continuous mass (Jatala and Jensen, 1976C). M. hapla infection results in the formation of giant cells. A giant cell is characterized by hypertrophied cells containing many nuclei with a reticulate network of protoplasm (Jatala and Jensen, 1976C). Giant cells induced by M. hapla contrast strikingly with H. schachtii--induced syncytia in size and denseness of cytoplasm. The cytoplasm of syncytia is much more dense and granulated than that of giant cells. Individual M. hapla--induced giant cells are 2-8 times larger than individual H. schachtii--induced syncytia (Jatala and Jensen, 1976C).

The second stage juveniles molt and become third stage juveniles in about 5 days at 25°C (Decker, 1981). In 7-9 days, fourth stage juveniles are developed. Adult males emerge from the 4th larval cutile, and emerge from the roots 9-11 days after initial penetration (Decker, 1981). An adult male is 1.119-1.438 mm in length and 0.028-0.042 mm in width (Caswell, et al. 1981).

The activity of males after emergence from roots is of short duration. They live for only a few days. Males of H. schachtii are required for (obligatorially amphimictic) reproduction. H. schachtii males are attracted to nubile females by sex pheromones secreted more around the posterior region (Green and Greek, 1972; Wallace, 1958). Under normal conditions of development, the ratio of the sexes is 2 males:1 female (Decker, 1981). The presence of unfavorable factors such as inadequate nutrients, especially nitrogen, and inadequate water and light will cause a sharp increase in the number of males.

Females and males require different amounts of "living space" in the host roots for development to maturity and completion of the normal life cycle. An adult female requires a minimum living space of 0.070 mm^3 of root. Males require approximately 1/60 of this root volume or 0.0011 mm^3 to complete their development (Caswell, et al. 1981).

Development of developing females takes 13 days at 25°C (Johnson and Viglierchio, 1969). The female swells rapidly and breaks through the root cortex and epidermis, becoming visible as a white, adult female (referred to as the white cyst stage) on the root surface. The female remains attached to the root at the head and continues to feed in the syncytium. It is at this time that copulation occurs and females are inseminated.

The female continues to increase in size and ova develop into eggs. A gelatinous matrix, which is usually covered with dirt and debris, surrounds the posterior end of the adult female. Eggs deposited into this matrix vary from a few to 130. Eggs are also retained in the female body. The number ranges from a few to 600 (Decker, 1981; Thorne, 1961). Each cyst contains an average of 200 to 300 eggs. At a temperature of 25°C, the complete life cycle takes 27 days (Decker, 1981).

2.1.5 Pathogenicity

The economic importance of the sugar beet cyst nematode was recognized even in the last century when the discipline of nematology was still in its infancy (Franklin, 1972). With high infestation levels, H. schachtii can be a limiting factor to production of beets, cabbage, cauliflower, rape, and several other crops.

The general symptoms of plants infected by Heterodera spp. include retardation in growth of the aerial parts, leaves are smaller and lighter in color, and plants droop under the effect of sunlight and revive again during the night (Decker, 1981). The main root of infected plants is stunted and many lateral rootlets develop continuously on it to compensate for the infection (Decker,

1981). The root system is also discolored (Abawi and Mai, 1977). High infection levels can prevent germination of seeds. Infection also causes the formation of a syncytium which is typically formed within the stele and limited on the side toward the nematode by endodermis or in part by cortical cells (Jatala and Jensen, 1976C).

The action threshold for H. schachtii on cabbage is 6 to 9 eggs and juveniles per gram of soil (Abawi and Mai, 1980; Mai and Abawi, 1980). Marketable yields of cabbage can be decreased by 21, 28, 46, and 54% at P_is of 9, 18, 34, and 68 eggs and second stage juveniles of H. schachtii per gram of soil, respectively (Abawi and Mai, 1980; Mai and Abawi, 1980; Olthof et al., 1974). High pathogenicity also depends on optimum temperature conditions and soil type for development of the nematode (Olthof, 1978).

2.1.6 Interaction Between H. Schachtii and Abiotic Factors

There are many abiotic factors that affect the development of H. schachtii. The most important are temperature, moisture, soil texture, and soil pH.

2.1.6.1 Temperature

Temperature is one of the most thoroughly studied edaphic factors that affect Heterodera spp. Gradations in temperature may occur laterally in the field as well as vertically where there is a lag in diurnal fluctuation from the surface to the deeper layers. The degree of fluctuation and time lag at different depths are strongly influenced by soil texture and moisture (Norton, 1979).

Temperature affects all life stages of Heterodera spp. Eggs of H. schachtii hatch optimally at 25°C (Cooke and Thomason, 1979; Franklin, 1972; Steele, 1976b). Encysted eggs can survive 3 months of summer fallow in surface soils in which temperatures are as high as 52°C (Thomason and Fife, 1962). Hatch of the eggs peak in the second week when cysts are incubated at 25°C (Steele, 1976b). As a result, newly formed cysts are composed of almost 100% eggs without any second stage juveniles. The lowest recorded temperature for hatch is 10°C for cysts in vitro and 18°C for free eggs; and the upper limit for hatch is 35-36°C (Cooke and Thomason, 1979; Jenkins and Taylor, 1967). Hatched second stage juveniles of H. schachtii rapidly lose viability when stored at temperatures above 20°C (Steele, 1976b). Examination of sugar beets inoculated with second stage juveniles revealed that storage of second stage juveniles at 10°C soon after emergence more than doubled the number of viable juveniles. H. schachtii second stage juveniles optimally invade roots at 20°C (Davis and Fisher, 1976). The optimum temperature for movement of the juveniles in soil is 15°C (Franklin, 1972). The optimum temperature for juvenile development is 27.5°C (Thomason and Fife, 1962).

Accumulated heat units can be used to study nematode development. These units are usually calculated as the number of degrees centigrade times the number of hours or days above a temperature, below which nematode development does not occur or is negligible (Allen, 1976). The threshold temperature will vary with the nematode species, the host, and probably the environment (Norton, 1979). The base temperatures for G. rostochiensis and G. pallida are 6.2° and 3.9°, respectively (Norton, 1979); and H. schachtii basal temperature is ca 10°C (Thomason and Fife, 1962). Calculated degree days

should also have an upper threshold temperature, above which nematode development is negligible. The upper threshold temperature for H. schachtii is 32.5°C (Thomason and Fife, 1962). In California, H. schachtii requires ca 304 degree days at a base of 10^0C (DD_{10}) to complete a generation (Thomason and Fife, 1962). The actual number of days required to accumulate the required degree days for a generation will vary with temperature, for example 57, 44, 33, 27, 25, and 23 days were required to complete a generation at temperatures of 17.8, 20, 23, 26, 27, and 29°C, respectively (Decker, 1981).

Temperature is one of the factors which influence sex determination of Heterodera spp. Significantly smaller numbers of males than females were found in H. glycines cultures maintained at 24°C, whereas, the male to female ratio was approximately 1:1 at 28°C (Triantaphyllou, 1973). The low male to female ratio at 24°C is regarded as the norm, and the relatively increased sex ratio at 28°C is attributed to the influence of the higher temperature on sexual differentiation of female juveniles which then developed into males (Triantaphyllou, 1973). Further increases in the male to female ratio at 31°C or higher temperatures are associated with the degeneration of juveniles in the roots and are attributed to death of many female juveniles at these high temperatures (Triantaphyllou, 1973). In H. schachtii, the number of adult females decreases because of inhibition of their development in the juvenile stages due to external conditions (Kerstan, 1969).

H. schachtii reproduces most rapidly at soil temperatures of 21-27°C (Cooke and Thomason, 1979; Franklin, 1972). The upper limit for completion of a life cycle is 32.5°C (Cooke and Thomason, 1979). In California, H. schachtii can complete five generations during a growing season (Cooke and Thomason, 1979;

Franklin, 1972; Thomason and Fife, 1962), compared with two to three generations in more temperate areas like England (Thomason and Fife, 1962). In Michigan, H. schachtii can complete one and a half to three generations in a season depending on the growing season.

H. schachtii is well-suited to survival not only in areas where soil freezes in winter, but in hot desert areas where soil temperatures during summer are frequently above 40°C (Thomason and Fife, 1962). Encysted eggs can survive 3 months summer fallow in surface soils in which temperatures are as high as 52° C (Thomason and Fife, 1962).

2.1.6.2 Moisture

Moisture and temperature often interact. Consequently, it is usually difficult to separate the effect of the two. Overall, however, moisture is the most important abiotic parameter governing nematode populations, directly or indirectly (Norton, 1979). Constant soil moisture is difficult to maintain and thus there are few direct observations on the effect of moisture on nematode population dynamics.

Recovery of nematodes from dry soil is greater if the soil is moistened prior to sampling (Norton, 1979). Dryness also may promote maturation of nematodes (Norton, 1979). A higher percentage of brown cysts and more emergence of juveniles from brown cysts occurred when H. glycines was subjected to moisture stress after a period of favorable growth than when not (Hamblen and Slack, 1959). Similar results were found by Wallace (1959) who reported that maximum emergence of H. schachtii occurred when most soil pores were empty of water.

Optimum plant growth occurs between 75 and 100% of field capacity (Norton, 1979). Also optimum infection of seeding by H. schachtii occurs when soil is 80-100% of field capacity (Griffin, 1977). The optimum infection can be attributed to larger root area resulting in a greater chance for nematode-root proximity and a more favorable environment for migration of nematodes (Griffin, 1977).

Soil moisture often regulates the amount of aeration. Populations of nematodes are greatest in well-drained soils (Schmitt and Norton, 1972) and survival is least at low oxygen concentrations (Van Gundy et al., 1962). Death of the nematodes is believed to be due to suffocation and buildup of toxic substances.

Heterodera spp. can withstand a wide range of moisture stresses. Encysted eggs can withstand moisture stress for eight years or more. The cyst acts as a barrier against osmosis or evapotranspiration.

2.1.6.3 Soil Texture

Studies by Wallace (1956) indicate that emergence of H. schachtii juveniles from cysts is related more to soil structure than soil type. He suggests that soil aeration is the single most important factor associated with soil structure. Soil structures that favor plant growth also favor activity of H. schachtii (Santo and Bolander, 1979). The oxygen consumption of the soil by the decomposition of organic substances and by microbiological activity has a big effect on aeration, and recent experiments with different soil types indicate that the rate of larval emergence can also be influenced by the oxygen availability in the soil (Wallace, 1956). H. schachtii reproduces best in silt loam (Santo and Bolander, 1979).

Light te

cabbage

occur wh

2.1.6.4 S

The

factor in

schachtii

optimum p

this pH co

positive co

from 5.0 t

developme

2.1.7 Con

Pla

tropical

Recogni

early m

tactics

nematod

fumigan

imperus

and availa

cides, increa

Light texture soil favors the development of H. schachtii associated with cabbage production in Poland (Brzeski, 1969). Optimum movement of juveniles occur when the size of the soil particles is 150 to 250 µ (Decker, 1981).

2.1.6.4 Soil pH

The literature suggests that the pH of the soils may well be a significant factor in nematode behavior (Norton, 1979). Brzeski (1969) showed that H. schachtii was associated with neutral acid or soils in cabbage production. The optimum pH for H. schachtii is 7.2 and ca 80% more cysts will be developed at this pH compared with a pH of 5.0 (Brzeski, 1969). Duggan (1963) found a positive correlation of H. avenae with pH from soil samples with a pH range from 5.0 to 7.5. Once infection has occurred, the influence of pH on nematode development is probably mediated through the host plant.

2.1.7 Control

Plant parasitic nematodes cause economically significant crop losses in tropical, subtropical, and temperate agricultural production systems (Bird, 1981). Recognizing the significance of plant parasitic nematodes is an important part of early modern nematology, 1845-1907 (Bird, 1981). In the last century, few tactics were available for protecting major food and fibre commodities from nematodes (Bird and Thomason, 1980). In the 1940's, the discovery of the soil fumigants, suitable for controlling phytopathogenic nematodes, gave added impetus to the science of nematology. Much more recently, the development and availability of non-fumigant organophosphate and organocarbamate nematicides, increased the range of agricultural crops where nematode populations can

be managed with chemicals. In the past 10 to 15 years, the effort to include all plant protection disciplines in a systems approach to integrated pest management (IPM) greatly enhanced nematological studies (Bird and Thomason, 1980). Integrated pest management can be defined as: a systems approach to reduce pest management to tolerable levels through a variety of techniques, including predators and parasites, genetically resistant hosts, natural environmental modifications, and when necessary and appropiate, chemical pesticides (Bird, 1981). Management procedures should usually be implemented when the marginal revenue derived from the management input is equal to or exceeds the marginal cost (Ferris, 1978).

$$MC = \frac{dTC}{dN}$$

where MC = marginal cost, TC = total cost of production, N = total yield, d = derivative, and

$$MR = \frac{dTR}{dN}$$

where MR = marginal revenue, TR = total revenue, N = yield or output and d = derivative. The economic threshold (MC=MR) is a dynamic concept. It depends on the cost of the management input, agricultural production system economics, nature of the nematode and population density, and other environmental parameters (Bird, 1981).

There are four primary means of controlling plant parasitic nematodes: cultural, chemical, biological, and physical.

a. Cu

Th

separate

time of

Fa

for vary

applicat

reductio

is prima

rainfall (

Fro

though it

the cyst

unhatche

It would

such a lon

Crop

control m

the introd

within the

difficult t

nematodes

H. sc

Mai and a

able beets

a. Cultural means of control

The cultural means of control can involve several different practices used separately or jointly. These are fallow, crop rotation, resistant varieties, and time of planting.

Fallowing. The land should be kept free of all vegetation, including weeds, for varying periods of time by frequent soil disking, plowing, harrowing or application of herbicides to prevent plant growth. The end result is the reduction of the nematode population through starvation and desiccation. Fallow is primarily effective under conditions of high soil temperature and no summer rainfall (Ayoub, 1980).

From a practical standpoint, this method is not generally viable even though it may be effective under specific circumstances. For example, some of the cyst nematodes, Heterodera spp., can survive as dormant juveniles or as unhatched eggs within the cyst in fallow soil for at least 14 years (Ayoub, 1980). It would not be economically feasible for growers to keep their land fallow for such a long period of time.

Crop rotation. Crop rotation is the oldest and still most widely used field control measure for nematodes (Mai, 1971). An effective crop rotation involves the introduction of a nematode-resistant plant which can be grown successfully within the same climatic conditions as the principle crop. Unfortunately, it is difficult to pick crops which will be compatible because many plant parasitic nematodes thrive on a wide range of host plants (Ayoub, 1980).

H. schachtii has a wide host range involving 218 plant species in 95 genera (Mai and Abawi, 1980). In New York, host crops in rotation are cabbage and table beets; and nonhost crops are corn, wheat and oats (Mai and Abwai, 1980).

Rotation of nonhost:host crops at a ratio of 2:1 or 5:1 decreased H. schachtii population density in the fields (Mai and Abawi, 1980). In California, nonhost crops used against the sugar beet cyst nematode are alfalfa, alsike clover, red clover, white clover, chicory, corn, flax, horse beans, and rye (Wright, 1950). In Utah, nonhost crops used are alfalfa, barley, bean, onion, potato, and wheat (Griffin, 1980).

Crop rotation has some limitations. Most notably, populations of nematode species which do not feed on one crop in the rotation may occur on the alternate crop. There are also some economic problems involved with this method since the nonhost crop grown in the rotation may be of low monetary value. Often the grower will have to wait several years before he is insured of a field sufficiently free of nematodes to plant his cash crop. The crop rotation method is also disadvantageous because the various crops in the rotation may require different equipment and different expertise.

Resistant varieties. The reaction of plants to plant parasitic nematodes range from complete resistance to high susceptibility. Over the years, plant breeders have noted that a plant's variation in resistance to plant parasitic nematodes is inherited. Plant breeders use this knowledge to develop stock which is nematode-resistant (Ayoub, 1980).

Many nematode-resistant plant varieties have been developed especially to Meloidogyne spp., Pratylenchus spp., and Xiphinema spp. (Ayoub, 1980). To date, no resistant varieties have been developed for H. schachtii associated with cabbage but experiments are in progress in USA, Britain, and Poland.

Time of planting. Since soil temperature plays a crucial role in the activities of certain plant parasitic nematodes, the time during which a crop is

planted is important. Nematode activity is inhibited during the winter season and early spring when soil temperature is still low enough to reduce the activity of nematodes.

There have been numerous successes with this preventive method of nematode control. In California, a field known to be infested with the sugar beet cyst nematode was planted at different times. The sugar beet yield proved to be much higher when the crop was planted in January-February than when planted in March-April (Ayoub, 1980).

b. Chemical means of control

A "good" nematicide should have most of these characteristics: (1) penetrate all barriers, such as soil, plant tissue, and nematode's body; (2) control all the major plant parasitic nematodes; (3) not injure the plants; (4) disperse or degrade within a reasonable time after application; (5) not leave harmful residues in soil or plant; (6) not react with soil constituents; (7) offer no hazard to man, domestic animals, or wildlife; (8) have a short waiting period or none at all between treatment and planting; (9) be easy and safe to apply; (10) be inexpensive and effective in small amounts; (11) not permit the nematode to build up an immunity to the toxic effects and (12) not disrupt soil community structure and balance.

There are two basic forms of nematicides: soil fumigants and non-fumigants. Soil fumigants are a class of nematicides which vaporize when mixed with soil. Non-fumigants do not vaporize and are applied as granules or liquid.

Soil fumigation is one of the most widespread forms of nematode control (Ayoub, 1980). This method of applying toxic chemicals originated in France in the early 1860's. The present effective soil fumigation, originated in 1943 with

the discovery of dichloropropene-dichloropropane (D-D). Soil fumigation can be divided into classes based on the method of application: pre-plant treatments and post-plant treatments. All of them are designed to inject the fumigant into the soil or to mix it with soil. The equipment used in pre-plant and post-plant fumigation is basically the same. There may be slight modifications in equipment to accommodate the root structure for existing plants during the post-plant treatment.

Pre-plant treatments. In some cases, a soil fumigant is too highly toxic to be applied directly in the presence of a plant. When this is true, the pre-plant method of application is used. The soil is fumigated before the crop is planted and significant time is allowed to elapse before planting so that the chemical vapors dissipate. Although this treatment may not completely eradicate the nematode population, a very high percentage can be killed.

Pre-plant treatments should only be applied after the land is properly prepared so that the volatile gases of the fumigant will be most effective. This involves plowing, chiseling, or disking the soil to the proper depth. The release of volatile gases requires maintenance of an adequate moisture level in the soil. The temperature of the soil is also important. Depending on the specific fumigant, the soil temperature at the depth of application should generally be at least $10^{o}C$. For maximum effectiveness, the soil should be sealed by ringroller, water, or tarpaulin immediately after the fumigant has been applied so that the nematicidal chemicals cannot escape.

Post-plant treatments. When a nematode infestation makes it necessary to fumigate a field after a crop is planted, the post-plant treatment method is used. The chemicals used in this treatment must not be toxic to the plant. The method is most widely used on perennial, long-lived crops.

Post-plant treatments are most effective on ectoparasitic nematodes since these nematodes are most likely to be exposed to the lethal effects of the chemical. Edoparasitic nematodes may also be killed when migrating from one plant to another. Often post-plant treatments are applied by either side-dressing or irrigation. Side-dressing involves application of the fumigant along the side of the plant with a hand injector or chisel applicator.

In Michigan, H. schachtii is controlled by the following fall soil fumigants (Grafius et al., 1982):

1,3-D

D-D: 124 gallons/ha (muck soil), 62 gallons/ha (mineral soil)

Telone II: 89 gallons/ha (muck soil), 37 gallons/ha (mineral soil)

Terr-o-cide 15D: 99 gallons/ha (muck soil), 38 gallons/ha (mineral soil)

or

1,3-D and methyl isothiocyanate

Vorlex: 37 gallons/ha (muck soil), 22 gallons/ha (mineral soil)

In California, H. schachtii is controlled by the following fumigants (Cooke et al., 1979):

1,3-D

D-D: 64 gallons/ha

Telone II: 59 gallons/ha

In Spain, H. schachtii is controlled by D-D applied at a rate of 50 gallons/acre (Franklin, 1972).

Non-fumigant treatments. No new fumigant nematicides have been developed for over 20 years, and with increasing concern over toxicological and environmental side effects, the number of fumigants in use and their applications

are likely to be reduced (Wright, 1981). Such problems already affect DBCP (1, 2 - dibromo - 3 - chloropropane) and may lead to restriction in the usage of EDB (ethlene dibromide), methylbromide, and D-D. Non-fumigant nematicides have several advantages when compared to fumigants which sometimes outweigh their greater basic cost: they are generally much less phytotoxic, relatively easier to apply, require no special equipment, are effective in controlling at much lower dosage rates, and have less persistent residues (Wright, 1981).

Non-fumigant nematicides can be divided into organophosphate and carbamate compounds. It is generally accepted that nematicides belonging to these groups act by impairing nematode neuromuscular activity, thereby reducing movement, invasion, feeding, and consequently the rate of development and reproduction (Starr et al., 1978; Steele, 1977; Steele, 1976a; Steele and Hodges, 1975; Wright, 1981). It is now also apparent that low concentrations of these compounds can affect the sensory behavior of nematodes, and this may be an important component in crop protection (Wright, 1981).

Inhibition of movement and feeding by organophosphate and carbamate nematicides would not in itself be expected to kill nematodes since they do not rely on respiratory movements for gas exchange and since many species of nematodes are able to withstand long periods of starvation and other unfavorable conditions (Wright, 1981). Eventually, however, affected nematodes in the soil would use up their food reserves, lose their infectivity, and die.

Organophosphates and carbamates act principally by inhibition of acetylcholinesterase (AChE) at cholinergic synapses in the nematode nervous system (Ware, 1978). AChE is thought to be the most important enzyme involved in transmitter destruction at cholinergic synapses, although pseudocholinesterase

(acylcholine acylhydrolase) may also contribute (Wright, 1981). One of the general features of the action of organophosphate and carbamate nematicides is that effects on the nematode are reversible on removal from the pesticide (Steele, 1977; Steele and Hodges, 1975; Wright, 1981). The recovery of nematodes can be more pronounced following treatment with carbamates than with organophosphates (Wright, 1981).

In Michigan cabbage production, H. schachtii can be controlled by phenamiphos (Nemacur) 15 G, applied at a rate of 39 kilograms/ha at planting as a broadcast and incorporate 5 to 15 centimeters (Grafius et al., 1982). Muchena and Bird (1983) have also shown that effective control can be achieved by applying phenamiphos at 7.2 kg ai/ha at planting or 3.6 kg ai/ha at planting and an additional 3.6 kg ai/ha four weeks after planting.

H. schachtii has been controlled by aldicarb (Temik®) in California (Hough and Thomason, 1975; Hough et al., 1975; Steele, 1976a); also phenamiphos is widely used in California (Greco and Thomason, 1980). In New York, oxamyl (Vydate®) is used to control the sugar beet cyst nematode (Starr et al., 1978). Griffin (1975) used phenamiphos and oxamyl to control H. schachtii in Utah. In Germany, aldicarb at 50kg/ha controlled H. schachtii (Franklin, 1972). Potter and Marks (1976b) used oxamyl to control the sugar beet cyst nematode in Canada.

2.2 BRASSICA OLERACEA L. VAR. CAPITATA

Cabbage is Brassica oleracea L. var capitata L., one polymorph of a group that also includes broccoli (var italica Plenck), cauliflower (var botrytis L.), kohlrabi (var caulorapa DC), Brussel sprouts (var gemimfera DC), and kale (var

acephhala DC) (Ryder, 1979). The cabbage group is part of the Brassicaceae (Cruciferae) and also includes radish (Raphanus spp.), turnip (B. campestris L. ssp. rapifera Sinsk), swedes and rapes (B. napus L. ssp. rapifera Metzg), mustards (B. juncea Coss and Czern., B. nigra (L.) Koch, and B. carinata A. Br.), rutabaga (B. napobrassica Mill), and Chinese cabbage (B. campestris L. ssp. pekinensis) (Ryder, 1979).

Cabbage is an important crop in most countries of the world. In the United States, it is fourth in volume after potato, lettuce, and tomato. In Western Europe, from 80-100,000 ha of cabbage are grown annually (Ryder, 1979). In Eastern Europe, the total annual area in vegetables is about 2 million ha, of which about one third is planted to cabbage. Japan grows more than 25,000 ha of cabbage annually, and Australia grows about 3000 ha (Ryder, 1979).

There are several uses for cabbage. Fresh market cabbage is for cooking or salad use. As a salad vegetable it is shredded and used either in a mixed salad or as the principle component of cole slaw. It may be cooked as a separate vegetable, as a component of stews, or in stuffed form, usually by wrapping leaves around meaty combinations.

Cabbage ranks high among vegetables for nutritive value. It contains 49 mg calcium, 130 I.U. vitamin A, and 4-7 mg ascorbic acid in 100 grams of raw product (Ryder, 1979). In the United States, cabbage ranks 15th among fruits and vegetables for nutrient concentration. However, in terms of total contribution to the diet, by virtue of the fact that it is consumed in large amounts, it ranks 8th (Ryder, 1979).

2.2.1 Life History

Growth of cabbage from seeding through transplanting and harvest follows a smooth and predictable growth curve (Strandberg, 1979). Four growth stages are detected when an average number of leaves per plant are plotted against cumulative degree days (Strandberg, 1979).

The four growth stages detected are: (1) Seedling--beginning with emergence to the 5-6 leaf stage. In this stage the cabbage plant is established. Leaves produced during this stage apparently do not reach a large size and are usually dropped as the plant begins to form a head. In seedbeds, severe competition from cohorts slows growth near the end of this stage. (2) Transplant--beginning at the 5-6 leaf stage and lasting through 6-8 leaf stage. Plants grow in size and new leaves begin to form a horizontal rosette type of growth. In transplanted cabbage, a period of re-establishment may slow growth and development for a period of 5-7 days during ideal conditions--longer if plants are not properly transplanted and cared for. (3) Cupping--plants have formed the basic frame that will support growth of the head. Leaves begin to enlarge, and the first upright leaves that will form the protective head wrapper leaves are produced. Biomass begins to accumulate rapidly. In the cupping stage, the leaves that will appear on the harvested product are developing, and plant protection activities must be adjusted accordingly. (4) Heading--the upright wrapper leaves enlarge and the head begins to develop from the inside out. The leaves that will become the outer head leaves curve over to cover the head, and like the wrapper leaves, these will appear on the harvested product and must be protected accordingly. No more leaves are evident because new ones are being produced from meristematic tissue inside the head and will continue to be produced until the

head is harvested. This is a period of very rapid biomass accumulation (Strandberg, 1979).

Time required to complete the entire growth cycle depends on the variety and environmental conditions. Hara and Sonoda (1979) suggest that the seedling stage takes 0-30 days after sowing; transplant stage, 30-60; cupping stage, 60-90; and heading stage, 90-120 days. There are several groups of cabbage and many varieties within each group. Perhaps the most practical method of classifying the varieties of cabbage is according to their use and the season in which they mature (Oyer, 1961). Becker (1978) and Holt (1971) classified some varieties according to time to reach maturity as follows:

MATURITY

Early	Mid-season	Late
Harvester Queen	King Cole	Roundup
Market Dawn	Superette	Titanic 90
Emerald Cross	Sanibel	Little Rock
	Market Topper	Cole Cash
	Head Start	Hybrid 8
		Shamrock
		Superboy
		Market Prize

Cabbage varieties have also been classified according to tipburn susceptibility (Becker, 1978):

Tipburn Susceptibility Classification

Slightly susceptible — Very susceptible

Harris W
Superboy
Harvester Queen
Titanic
Roundup
King Cole
Sanibel
Superette
Green Boy
Reo Verde

Quality. The important quality characteristics of fresh market cabbage are color, firmness, crispness, and freedom from decay or rot (Ryder, 1979). It is particularly important that stored cabbage retain its fresh look and texture, remaining green, firm, and crisp, as well as free of the organisms that cause decay. Proper storage conditions must, therefore, be maintained (Ryder, 1979). Optimum storage conditions are a temperature of $0^{o}C$ in a high humidity (for example, 97% R.H. or greater) and a controlled atmosphere consisting of 2.5% oxygen, 5% carbon dioxide, with the remainder nitrogen, trace gases, and other products of respiration (Davis, et al., 1980; Furry et al., 1981). Cabbage stored in these conditions can retain flavor characteristics of fresh cabbage for 22 weeks (Geeson and Browne, 1980). High ethylene concentrations can reduce market quality by loss of external green color and extensive leaf abscission (Pendergrass et al.,1975).

Planting methods. In California, cabbage is generally grown on standard 2-row beds on 102 cm centers. The rows are 36 cm apart, and plants are 31-36 cm apart within the row (Ryder, 1979). In other areas, distances vary according to cultivar and season. Early, small cultivars may be planted at distances of 40-50 cm, while summer and autumn cultivars which grow to larger sizes may be planted 60-70 cm (Ryder, 1979). Cabbage may be direct seeded or transplanted from seedbeds at the final spacings noted above. When direct seeded, seed is sowed at closer spacings of 2.5-5 cm and thinned to final stand at a later time.

Seedbeds for producing transplants for early production must be in protected locations, as they are started in late winter. These may be either in greenhouses kept above 15°C or in southern locations. For example, Florida supplies transplants for New York. For summer and fall production, transplants are grown in field nurseries. Nusery plants should receive adequate, but not high, amounts of water and fertilizer. Overwatering and excess nitrogen will cause plants to develop with too much top growth and insufficient root systems (Ryder, 1979). Transplants should be hardy with good root systems and only 4-5 expanded leaves for best results. They are usually in best shape for transplanting at 4-6 weeks in warm periods, 8-12 weeks in cooler periods (Ryder, 1979).

2.2.2 Interactions Between Brassica oleracea capitata and Abiotic Factors

There are several abiotic factors which affect the growth and development of cabbage. Of these, temperature, moisture, and soil type are the most important.

2.2.2.1 Temperature

Cabbage is a hardy, biennial plant, although grown as an annual crop. It is a cool-weather crop. Properly hardened plants are able to resist temperatures as low as -6°C (Weaver and Brunner, 1927; Wood, 1914). A light freeze, however, may damage or even kill young plants if they have not been hardened.

Prolonged periods of cool weather between freezing and 10°C will cause a large percentage of plants to initiate seed stalks. Research has shown that 30 days of cool temperatures in this range may be sufficient to initiate seed stalks (Wood, 1914).

Temperature affects the number of days for seed emergence. Wood (1914) showed that at 10, 15, 20, 25, and 30°C it takes 14.6, 8.7, 5.8, 4.5, and 3.5 days, respectively, for the seed to emerge.

Cultural practices which bring about an increase in soil temperature will advance emergence (Drew, 1982). Mulching fields with a southerly aspect increases soil temperature in the northern hemisphere. Flat fields can be given the advantages of a southerly aspect by ridging and sowing seeds in the south sides of the ridges (Drew, 1982).

2.2.2.2 Moisture

Cabbage does best in moist climates (Oyer, 1961; Thompson and Kelly, 1957). In California, cabbage is irrigated by sprinkler and furrow application. Several applications are needed, depending upon time of the year. In cooler periods when rainfall is regular and sufficient, little or no irrigation may be required. In the warmer, dryer periods, frequency of irrigation depends upon temperature during the growing period and soil texture. Lighter soils require

more frequent irrigation (Ryder, 1979). Cabbage in most other areas is dependent upon rainfall, although irrigation may be necessary at time of transplanting to ensure survival of the crop.

Although adequate soil moisture provided by irrigation or natural rainfall is essential for good yields of high quality, cabbage should not be irrigated heavily after heads begin to form, as severe splitting of maturing heads is likely to result (Miller, 1972).

Irrigation has a highly significant influence (P=0.001) on emergence rate of cabbage seedling (Drew, 1982). The seedlings emerge earlier on irrigated soil as compared to unirrigated soil. Seedlings emerged about a day earlier on irrigated soil (Drew, 1982).

2.2.2.3 Soil Texture

Cabbage can be grown successfully on a wide variety of soils (Miller, 1972; Ryder, 1979; Wood, 1914). Although cabbage does well on muck soils (Webster, 1953), it grows best on loam soils that are well drained (Miller, 1972). Cabbage has a relatively deep root system which can be as deep as 100 cm (Weaver and Brunner, 1927). Most of the lateral roots run outward and downward, often at an angle of ca 45 degrees or more (Weaver and Brunner, 1927).

Early cabbage is grown more frequently on sandy soils which are warmer and less likely to retain too much water (Ryder, 1979). Later production is on heavier soils to take advantage of their water-holding capacity (Ryder, 1979).

Cabbage does grow well in soils with pH values from 5.5 to 7.5. Optimum pH for cabbage growth is 6.0-6.5 (Miller, 1972; Ryder, 1979).

2.2.3 Interactions Between Brassica oleracea capitata and Plant Nutrients

Most soils on which cabbage is grown require different amounts of fertilizers. The most commonly required fertilizers should contain nitrogen, phosphorus, and potassium.

2.2.3.1 Nitrogen

Cabbage uses large quantities of nitrogen. The optimal amount depends upon soil type, climatic conditions, and other variables. A deficiency of nitrogen will depress yield, delay maturity, decrease keeping quality, and may cause a strong taste (Ryder, 1979). Excess nitrogen may promote too-rapid growth, leading to the development of coarse, loose heads with a tendency to crack earlier than normal and with susceptibility to internal tipburn. Keeping quality of stored cabbage may also be impaired (Ryder, 1979).

Early cabbage and late cabbage require different amounts of nitrogen on different soil types (Wood, 1914):

Soil type	Nitrogen (kg/ha)	
	Early	Late
Sandy loam	80-90	50-60
Silt loam	70-80	40-50
Muck	**	30-40
Silt clay loam	**	40-50

** = Early crop is usually not raised on these soils.

2.2.3.2 Phosphorus

Cabbage does not grow well on a highly acid soil. Thompson and Kelly (1957) showed an increase in yield as acidity decreased from pH 4.3 to about 6.0. They stated that maximum availability of phosphorus may be expected between pH 5.5 and 6.4. Where clubroot is very serious, (Thompson and Kelly, 1957), recommend application of caustic lime or hydrated lime to bring the soil to a neutral or alkaline reaction.

It is important that the amount of phosphorus in the soil is tested before any additional applications. If the soil is classified as having low or high phosphorus content, Wood (1914) recommended that the following be applied to early and late cabbage growing on different soil types:

Soil Type	kg/ha of Phosphorus	
	High P	Low P
Sandy loam	90	180
Silt loam	90	180
Muck	90	180
Silty clay loam	90	180

2.2.3.3 Effect of Nutrients on Growth and Development

There is positive correlation between plant nutrients in the soil just prior to harvest and yield of marketable cabbage (Volk, et al., 1947; Akratanakul et al., 1977). The critical point in nitrate content of the soil is approximately 17 kg/ha. Above this value the response to larger amounts of nitrate decrease rapidly (Volk et al., 1947).

According to Ryder (1979), yield may range from 10-100 m tons/ha. Red and savoy cultivars produce the lowest yields, 10-40 m tons/ha; and green cabbages produce the highest yields, ranging from 60-80 m tons/ha. The average yield for fresh cabbage in the United States in 1976 was 26.6 m tons/ha (Ryder, 1979).

Yield of cabbage varies with different cultivars (Kretchman and Jameson, 1978). The following are examples of yields obtained with the respective cultivars:

Cultivar	Tons/ha	Kg/Head
King Cole	103.5	3.65
Roundup	94.5	3.15
Titanic 90	88.6	2.96
Hybrid N	104.7	3.54
BRR 51317	44.7	2.05
Sanibel	94.1	3.06

2.2.4 Pest Management

There are several important pests associated with cabbage. The most important are clubroot, nematodes, yellows, blackleg, blackrot, and insects. A serious infection can be sufficient to make cabbage growing unprofitable and result in total loss of the crop (Thompson and Kelly, 1957).

CLUBROOT is produced by the invasion of a slime mold (Plasmodiophora brassicae Wor.) on the roots. Plants affected by this disease show, in the earlier stages of growth, a wilting of the foliage on sunny days with recovery toward evening. The roots of affected plants show characteristic swellings which often

become very large. The mass of thickened, malformed roots presents a clubbed appearance.

The organism is a soil parasite which thrives best in an acid soil. Thompson and Kelly (1957) summarize the control measures as follows: (1) Badly infested areas should be abandoned for cruciferous crops. (2) Select clean soil for plant beds to avoid infestation of new areas, and avoid contamination of new areas by implements, farm animals, plants, and surface drainage water. (3) Keep the soil alkaline if possible. A pH of 7.2 is optimal for control of clubroot. Lime, preferably hydrated, for clubroot control should be applied in the spring rather than during the previous fall. (4) A long rotation, in which no cruciferous plants are grown, is of value in controlling the disease in the field.

NEMATODES (Meloidogyne spp. and Heterodera schachtii) invade the roots of cabbage and cause galls and formation of syncytia, respectively. Symptoms of infection are wilting of cabbage leaves during hot periods and retardation of shoot and root growth.

Crop rotation was the only means of control for many years. Soil fumigants and non-fumigants are now available for control. Small grains, most grasses, corn, velvet beans, and some varieties of cowpeas are nearly immune (nonhost) to the nematodes. These crops should be used in crop rotation. Seedbeds should be fumigated with methyl bromide, chloropicrin, or chlorobromopropene. Post-planting control of the nematodes can be achieved by a non-fumigant (phenamiphos and aldicarb).

YELLOWS. This disease is recognized in the field by the lifeless, yellowish-green color which shows up in 2 to 4 weeks after transplanting. The plants are stunted and often warped and curled because the attack is more

severe on one side of the plant than on the other. The vascular bundles of the stem and lower leaves become darkened, the color deepening as the disease progresses.

This disease is caused by Fusarium oxysporum. When the soil is seriously infested with the fungus, a large part of the crop may be destroyed. This fungus is especially destructive to cabbage when grown as a summer crop. The fungus does not develop at temperatures lower than 20°C, and it is at its maximum rate of growth when temperatures reach 26°C to 32°C (Thompson and Kelly, 1957).

The organism persists indefinitely in the soil; therefore, ordinary crop rotation does not control the disease. Seedbed infection is one of the worst dangers; hence, care should be taken to plant the seed in clean soil. Where the disease is present and is serious, the only practicable control measure is to grow resistant strains or varieties. There are resistant strains of the various important cabbage types: Jersey Queen (Wakefield type); Resistant Detroit, Resistant Golden Acre, Racine Market, Marion Market, Medium Copenhagen Resistant (all of the Copenhagen Market type); all Head Select, Globe, Improved Wisconsin All Seasons (all of the Glory type); and Wisconsin Ballhead, Wisconsin Hollander, Bugner, Empire Danish, and Red Hollander (all of the Danish type).

BLACKLEG. This disease is caused by a fungus parasite (Phoma lingam). It may invade almost any portion of the plant, but the worst damage occurs when it kills the stems of the young plants in the seedbed or in the field. Infection often occurs on the stem near the ground, causing dark sunken areas. The disease spreads from these areas, gradually killing the base of the stem and roots, so that the plant wilts. The wilting of the entire plant is characteristic of the advanced stages of this disease, and the leaves adhere to the stem instead of falling off as in the yellows.

Crop rotation and seed treatment are the methods of control generally recommended. The rotation should cover at least 3 years. Hot water treatment, 50°C for 25 to 30 minutes, is effective in destroying the parasite on the inside as well as on the outside of the seed.

BLACKROT. This is caused by the bacterium Xanthomonas campestris and appears in the plant at any stage of growth. The yellowing of affected leaves followed by a blackening of the veins is the first indication of the disease. Later the plants show a dwarfing or one-sided growth of the head, or if the disease is severe and starts early in the season, there may be no head formed. The heads sometimes rot and fall off.

Seed infection is the major means of overwintering, but it may also live over in the stems of the diseased cabbage. Seed treatment by the hot-water method described for blackleg destroys the bacteria on the seed. The use of clean seed, crop rotation, and seedbed sanitation are recommended. The rotation should be one in which no cruciferous crops or cruciferous weeds are allowed to grow for at least 3 years.

OTHER DISEASES. Many other diseases attack cabbage, including alternaria leaf spot, damping-off, bacterial leaf spot, sclerotinia rot, white rust, downy mildew, anthracnose, and several others.

INSECTS. Cabbage and closely related plants are attacked by many insects, including both those with chewing and those with sucking mouth parts. The important chewing insects of cabbage are the cabbage maggot, green-cabbage worm, Southern cabbage butterfly, cabbage looper, diamondback moth, cross-striped cabbage worm, cabbage webworm, garden webworm, purple-backed cabbage worm, and zebra caterpillar. The important sucking insects attacking

cabbage are cabbage aphid, turnip aphid, and harlequin cabbage bug (Thompson and Kelly, 1957).

CABBAGE MAGGOT (Delia brassicae). The cabbage maggot is a small whitish larva of a black fly and is smaller than the common housefly. The fly deposits eggs just below the surface of the ground, on or near the roots of cruciferous plants. The eggs hatch in a few days, and the larvae feed on the plants for about 3 weeks. They first attack the rootlets and then burrow into the main root, causing the plant to wilt and, in most cases, to die.

Cabbage maggot can be controlled by several insecticides, namely: Diazinon 50 WP, Guthion 50 WP, Dyfonate 4 EC, or Lorsban 4 EC (Grafius et al., 1982).

GREEN CABBAGE WORM OR IMPORTED CABBAGE WORM (Pieris rapae). This worm is the larva of a small white butterfly. The larva is about 2.5 cm long and velvet green in color. It is one of the most destructive of the common cabbage insects, eating holes in the leaves and often burrowing into the head (Thompson and Kelly, 1957).

The most popular materials for control of this worm and days which the chemical can be applied before harvest are: Endosulfan 3EC (7 days), Carbaryl (3 days), Guthion 50WP (21 days), Methomyl 90SP (2 days), Monitor 4EC (35 days), Diazinon 4EC (7 days), Parathion 6EC (10 days), Penncap-M 2F (21 days), Dibrom 8EC (1 day), Dylox 80SP (21 days), Malathion 5EC (7 days), or Bacillus thuringiensis (0 days) (Grafius et al., 1982).

CABBAGE LOOPER (Trichoplusia ni). The larva of a moth, resembling the cutworm moth, feeds on the foliage of cabbage and related plants. This worm can be distinguished from the others by its peculiar looping or doubling up as it

crawls. The control measures are much the same for the looper as for the imported cabbage worm.

CABBAGE APHID (Brevicoryne brassicae). This is one of the species of insects commonly called plant lice. These insects are more injurious during the latter part of the season than earlier. The cabbage aphid is covered with a coat of fine waxy powder, very much like the bloom on cabbage leaves. This covering protects the insects from spray material since the liquid runs off their waxy surface.

2.3 SIMULATION OF HETERODERA SCHACHTII ON BRASSICA OLERACEA CAPITATA

A simulation of H. schachtii associated with cabbage was developed spring 1983 as a requirement for a Michigan State Univ. course entitled, Ecosystem Analysis and Design (SYS 843). The model was developed by Hu, R., D. Kayakawa, P. Michalak, and P. Muchena. It is presented here to summarize literature review on H. schachtii associated with cabbage. The simulation also uses some of the results that I obtained in summer 1982.

2.3.1 Objectives

Our objectives in developing the simulation were to: (1) assimilate information previously published on the biology of H. schachtii; (2) identify research gaps concerning the interaction between H. schachtii and cabbage; (3) develop a mathematical description of the: spatial and temporal distribution of roots and nematodes, population dynamics of H. schachtii, and the impact of H. schachtii on cabbage growth and development using the existing data base and my 1982 research.

2.3.2 System Identification

The model simulates the spatial and temporal distribution of cabbage roots and H. schachtii, the population dynamics of H. schachtii, and the impact of H. schachtii on cabbage growth and development with a single cabbage. The daily development of H. schachtii life stages and cabbage is predicted by the model according to soil temperature using information previously cited. Other abiotic factors such as soil moisture, texture, nutrient levels, and pH are not currently included in the model due to the lack of quantitative data but can be added when an appropriate data base is developed. Similarly, little information on the relation of root volume and shoot weight was available.

Model Overview. In the model, the nematode population is divided into cyst, juvenile, and adult stages (Figure 1). Flows from one stage to another are dictated by temperature-dependent developmental rates and by natural mortality factors.

The user is prompted for initial H. schachtii density, planting date, and length of growing season. Field soil temperature is read from a tape at each daily iteration. Degree days (base $10^{o}C$) for nematode life stages, (base $25^{o}C$) for natural mortality factor, and (base $0^{o}C$) for cabbage root growth are accumulated and the various subroutines are called. Model output is stored at the end of each daily iteration.

2.3.3 Subroutines

Three subroutines are called by the main program. These subroutines are DDAY (Degree Days), INIT (Cylinder Initiation), UPDATE (Updates cabbage and H. schachtii development).

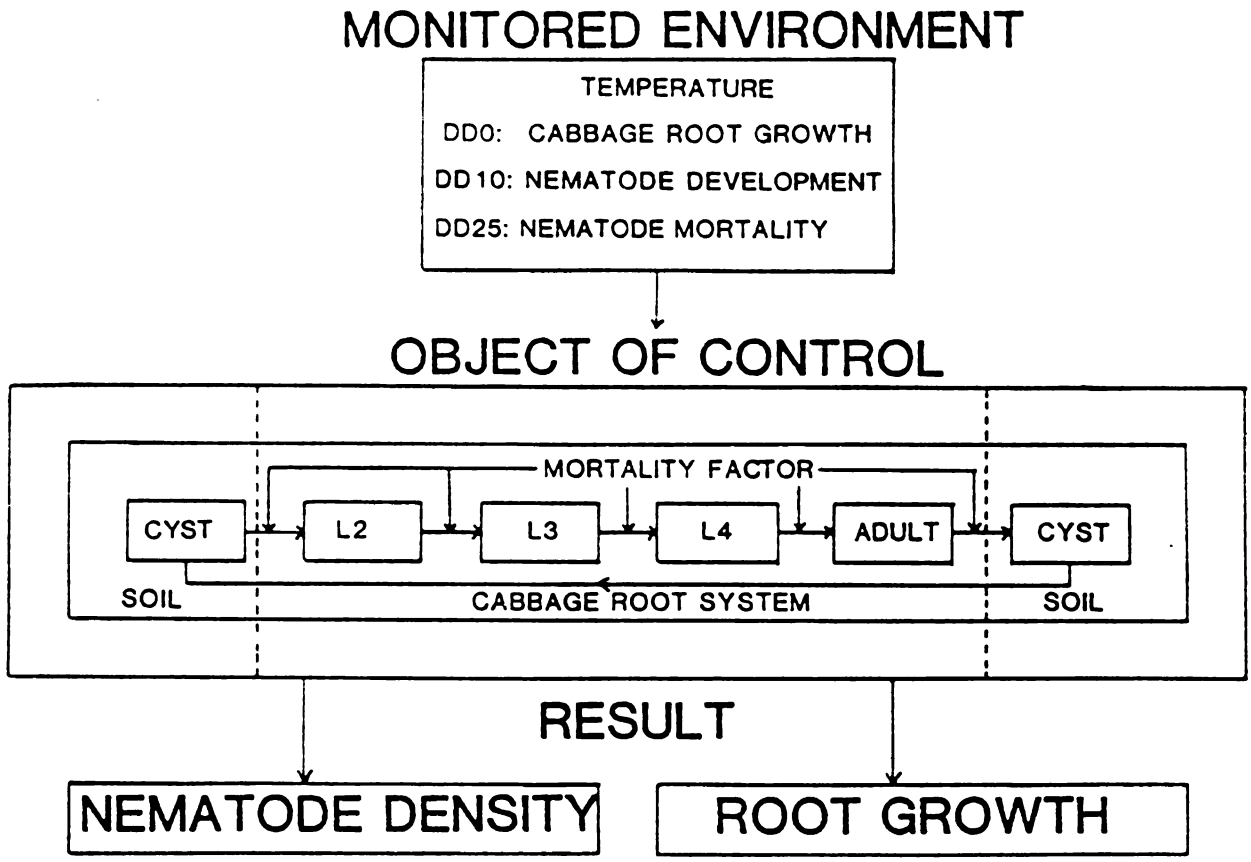

Fig. 1. Conceptual diagram of H. schachtii-B. oleracea v. capitata ecosystem.

2.3.3.1 Degree Days

A Fortran program was used to calculate heating and cooling degree days (Allen, 1976). This program is based on the assumption that the temperature cycle is approximated by a sine wave.

2.3.3.2 Cylinder Initiation (INIT) Subroutine

This subroutine cylinder initiation determines the cumulative growth of the cabbage root system and loss in root volume due to nematode density and penetration (Figure 2). Cabbage growth is described by the equation:

$$R(K) = R(K-1) + 14\ U(K)$$

$$D(K) = D(K-1) + 3.5U(K)$$

Where R is radius of the cylinder, D is depth of the cylinder, K denotes present time, K-1 denotes past time, and U(K) is a proportion value which varies between 1.0 and 0.001. When U(K) = 1.0 it means the radius and depth are optimal hence there is no H. schachtii effect on the root system. When U(K) = 0.001 it means the radius and depth are reduced because of H. schachtii infestation. In the simulation, values for U(K) varied between these two extreme values depending on the Pi.

The proportion of optimal growth is determined by X.

$$X = (.1*L2 + .2*L3 + .3*L4 + Adult) \div Volume$$

Percent of optimal growth is 40, 60, 77.5, 82.5, 85, 87.5, 92.5, or 100 when X is greater than or equal to 2.0, 1.0, 0.5, 0.3, 0.1, 0.05, 0.001, or 0, respectively. The increase in radius, depth, and volume will be:

$$R = 9.0*\text{percent of optimal growth}$$

$$D = 7.0*\text{percent of optimal growth}$$

$$\text{Volume} = 6.2831*R^2*D - \text{previous volume}$$

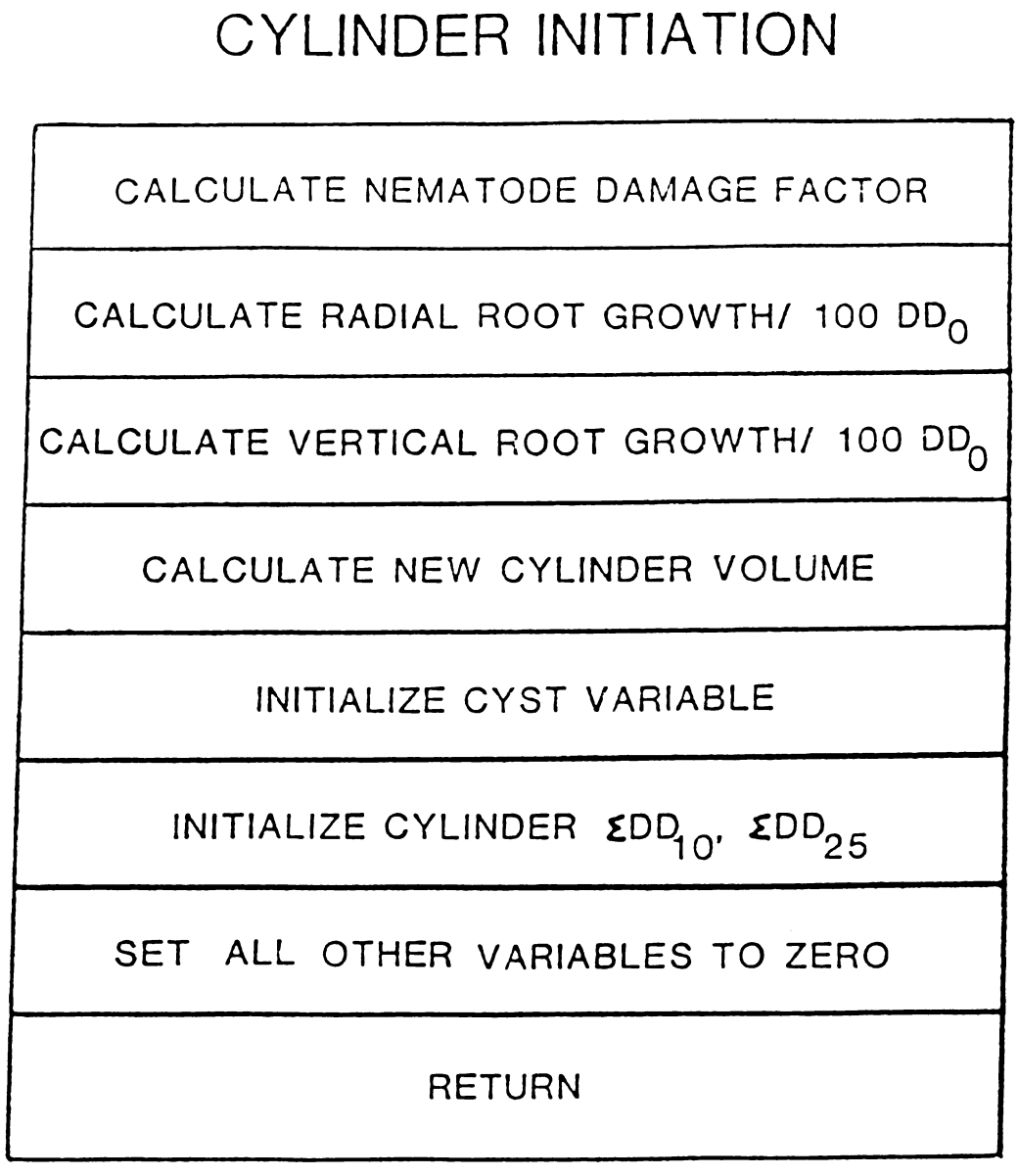

Fig. 2. Overview of Subroutine Cylinder Initiation.

2.3.3.3 Update Subroutine

This subroutine (Figure 3) determines the number of juveniles hatching from cysts, the number of juveniles surviving to adult stage, and the proportion of adult males to females with eggs.

-Number of second stage juveniles hatched

Hatch = 0.5 - MORTDD ÷ 1000.0 where

MORTDD = Mortality degree days calculated as below.

-Number of second stage juveniles penetrating the roots

L2Surv = 0.5 - MORTDD ÷ 1000.0

-Number of third stage juveniles surviving

L3Surv = 1.0 - MORTDD ÷ 5000.0

-Number of adult surviving

ADSurv = 1.0 - MORTDD ÷ 5000.0

-Percentage of females

% of females = .05 - (Adult count $*10^{-8}$)

MORTDD = $2CDD_{25} + HDD_{25}$ This is the deviation of temperature from 25°C, calculated as heating and cooling degree days. When temperature is suboptimal, this will enhance mortality of the nematodes. CDD_{25} = number of cooling degree days deviating from the optimal temperature of 25°C, HDD_{25} = number of heating degree days deviating from the optimal temperature of 25°C.

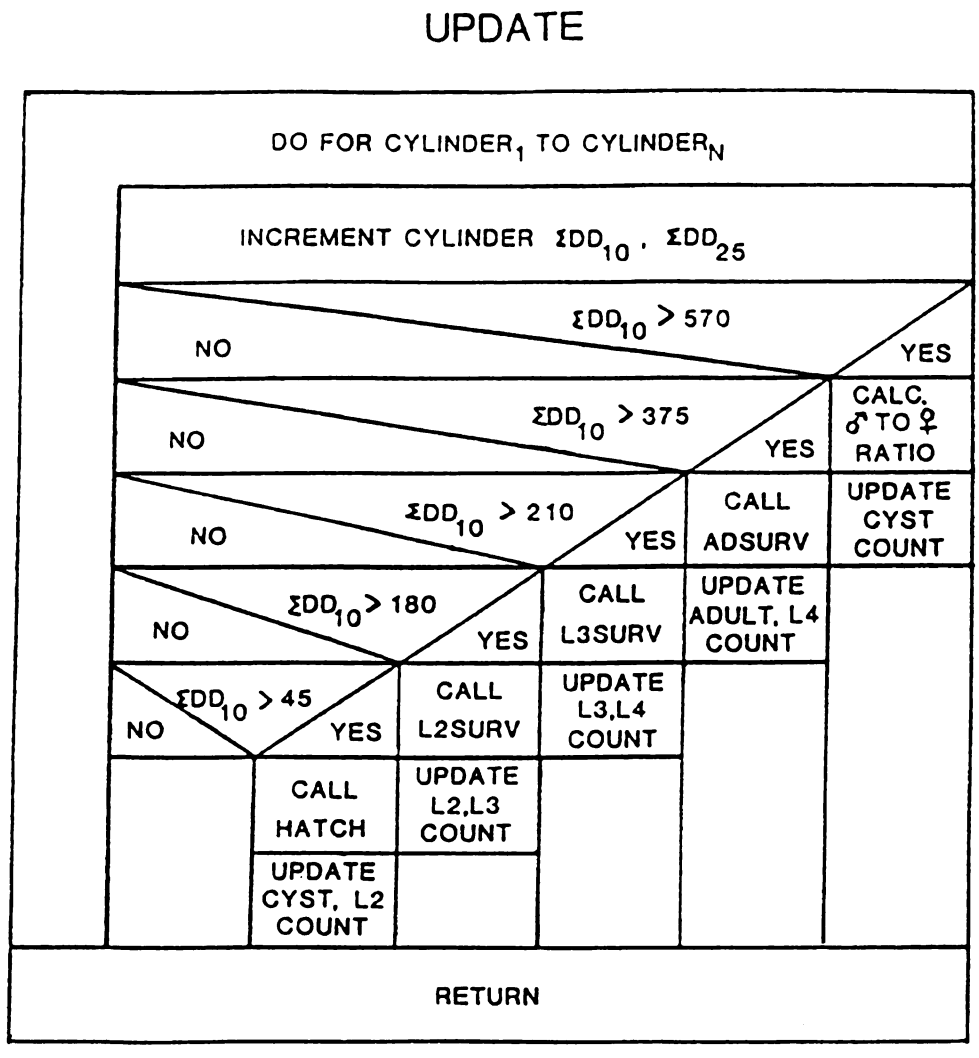

Fig. 3. Flow chart of a Subroutine Update.

2.3.4 Driver Program

During the growing season, daily temperatures are input, and degree days (DD) are determined and summed at bases 0, 10, and 25°C (Figure 4). Degree day bases correspond to the lower threshold temperature for cabbage development, the lethal low temperature for nematode development, and the optimal temperature for H. schachtii development, respectively.

If 100 DD_0 have accumulated, a soil cylinder is initiated to measure the cumulative growth of the root system. This is done with the cylinder initiation subroutine. The cylinder update subroutine is activated each calendar day, and nematode population dynamics are calculated.

2.3.5 Simulation Output

The simulation keeps track of the development of H. schachtii and growth of cabbage roots. This is updated every calendar day and stored in a matrix until 100 DD_0 have been accumulated. The results are output both in terms of Julian days and degree days.

2.3.5.1 Second stage juveniles in roots

Second stage juveniles emerged from cysts after accumulating a specific number of DD_{10}. The number of second stage juveniles that emerged depended upon the total number of accumulated degree days and the initial cyst population density (P_i). Effects of root exudate and availability of attackable sites were assumed to be non-limiting.

The number of second stage juveniles per gram root decreased until day 30 (Figure 5). This decrease can be attributed to: (1) second stage juveniles

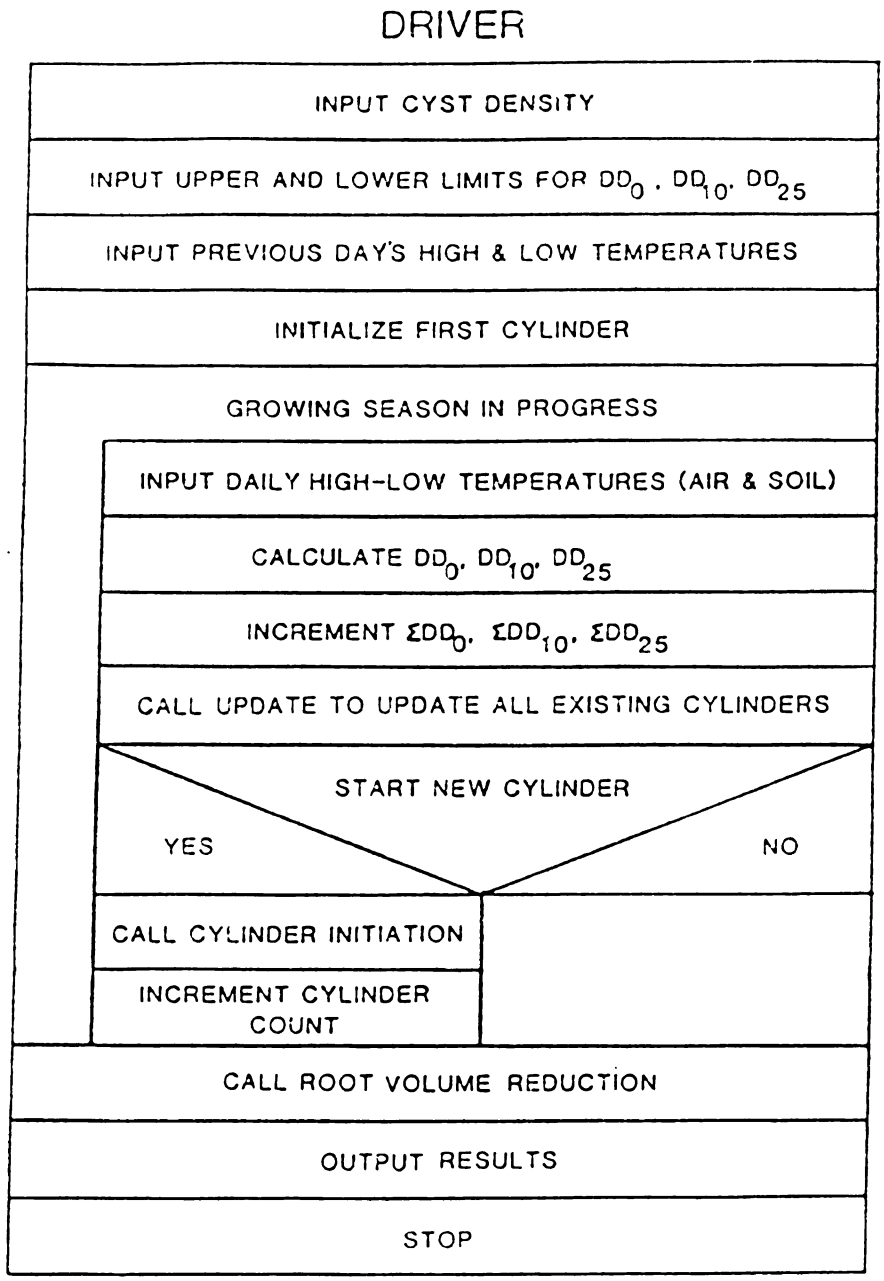

Fig. 4. Flow chart of the main Program Driver.

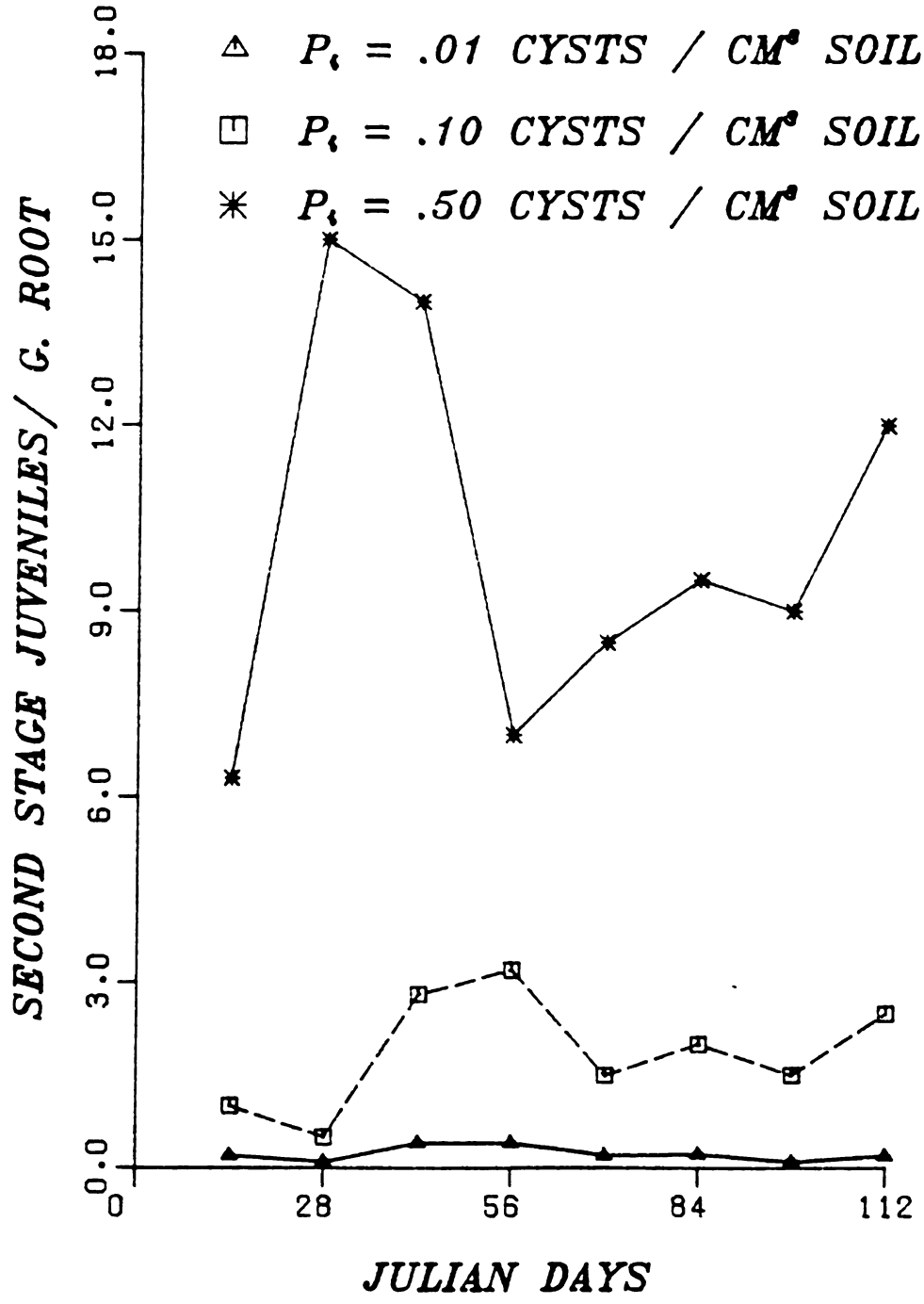

Fig. 5. Relationship between the initial population density of H. schachtii and second stage juveniles found in cabbage roots during the growing season.

developing into third stage juveniles, and (2) unfavorable temperatures which reduced the number of juveniles penetrating the roots and increased mortality of the second stage juveniles because of increased deviation from the optimal temperature.

When conditions were favorable, the number of second stage juveniles per gram root increased to peak around day 50 (Figure 5). After day 50, the number of second stage juveniles in roots decreased again. This decrease could have resulted from:

1. Second stage juveniles developing into third stage juveniles,
2. depletion of second stage juveniles in the soil, and/or
3. unfavorable temperatures.

At the end of the growing season, the number of second stage juveniles increased again. This increase can be attributed to second stage juveniles coming from fresh cysts formed after the end of the first generation.

2.3.5.2 Females with eggs in the roots

It took about 55 days before females with eggs were observed in the simulation. The number of females with eggs per gram root increased until day 95 (Figure 6). After day 95, the number of females with eggs in roots decreased. This is because females with eggs were developing into cysts.

2.3.5.3 Cysts in the soil

The number of cysts in the soil decreased from the initial population density at the beginning of the growing season (Figure 7). This decrease is because some of the cysts were hatching and releasing second stage juveniles

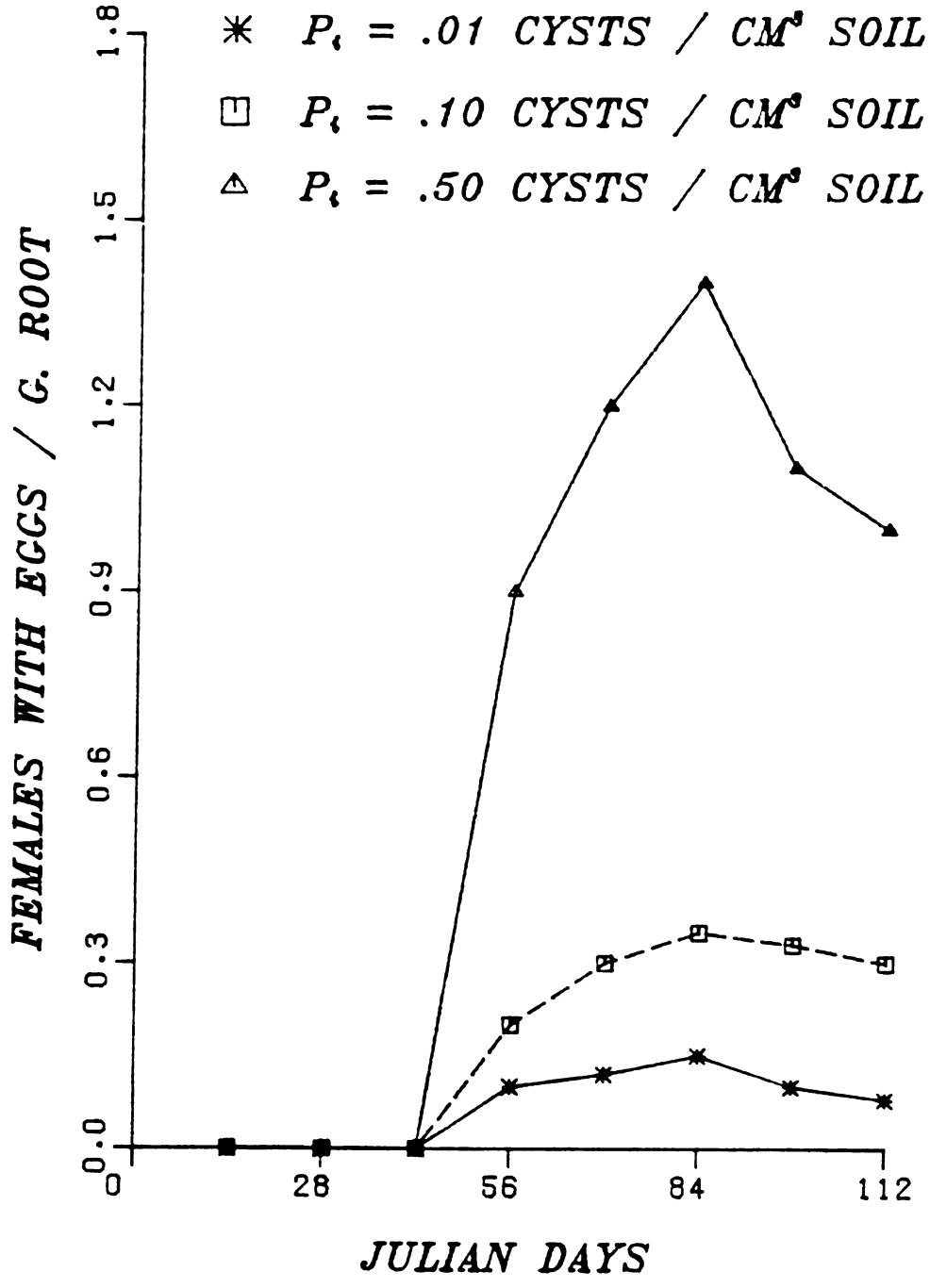

Fig. 6. Relationship between initial population density of H. schachtii and females with eggs found in cabbage roots during the growing season.

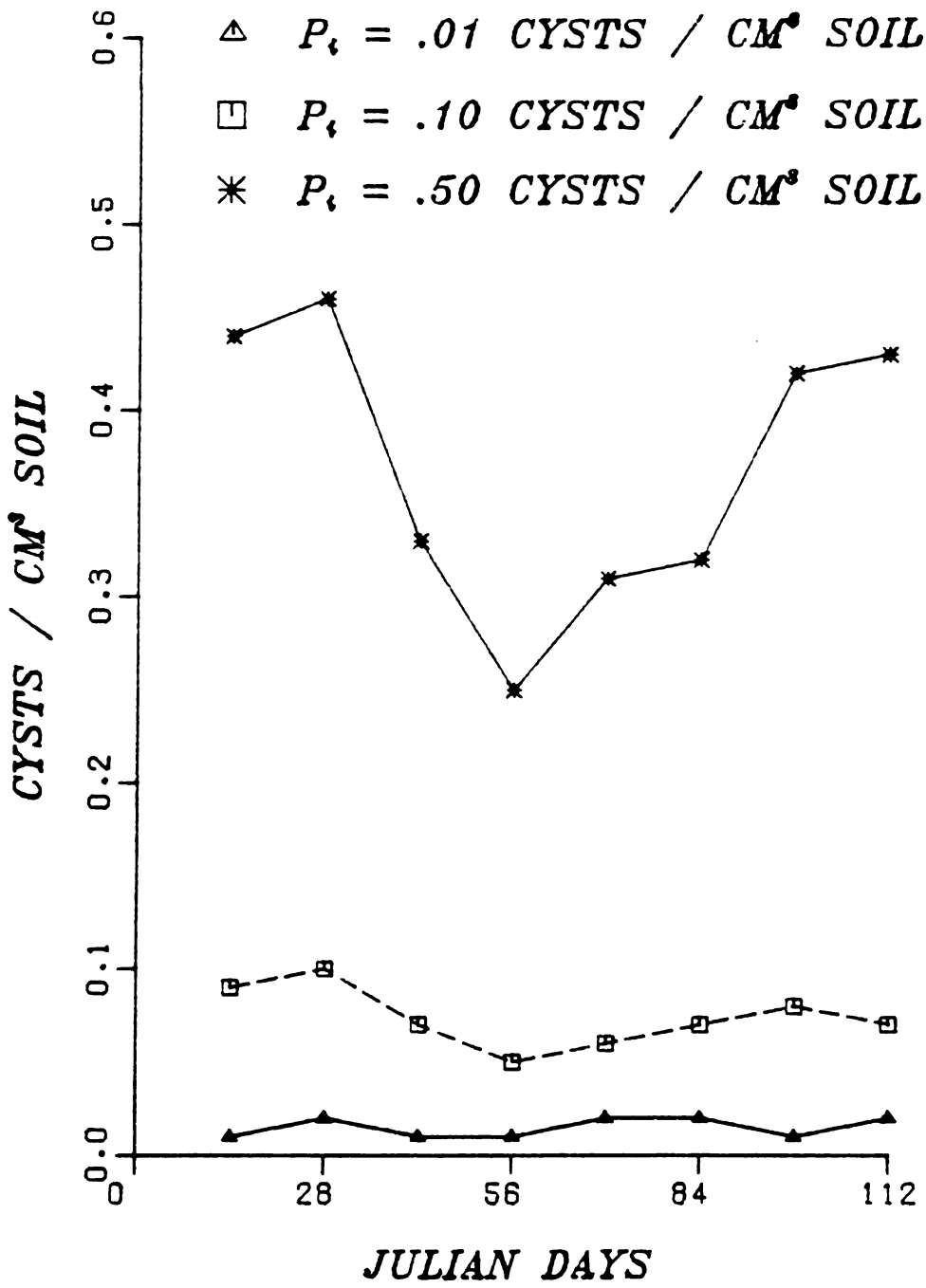

Fig. 7. Relationship between the initial population density of H. schachtii and cysts found in the soil during the growing season.

into the soil. This continued until day 60 (Figure 7). After this day, the number of cysts per cm^3 of soil gradually increased as females with eggs developed into new cysts. The number of cysts/cm^3 of soil tapered off at the end of the growing season because some of the mature cysts started to hatch.

2.3.5.4 Distribution of cysts in the soil

Distribution of cysts/cm^3 of soil at the end of the growing season showed an aggregation in the upper 50 cm, and as depth increased, the density of cysts per cm^3 of soil suddenly decreased (Figure 8a). The high concentration of cysts in the upper 50 cm of soil is because the nematodes in this zone completed a generation. At the end of a generation, a high number of cysts is produced.

The nematodes did not complete a generation on roots which were at lower depths. There is a time lag before nematodes in this section will have roots to penetrate. This time lag increases with depth. If the cabbage had been allowed to grow for a longer period, the aggregation of cysts would have been at lower depths than 50 cm. It is quite apparent in Figure 8b that females with eggs just below the cysts' peak will have developed to cysts after a short time.

2.3.5.5 Cabbage growth

In the simulation, cabbage growth responded to H. schachtii infection. Root volume was reduced by 22, 42, and 85% at P_i of 2, 20, and 100 eggs and juveniles per cm^3 of soil, respectively (Figure 9). This ties reasonably well with yield losses of 21, 46, and 54% at P_i of 9, 34, and 68 eggs and juveniles per cm^3 of soil, respectively (Abawi and Mai, 1980). We assumed a linear relationship between root volume, root weight, and shoot weight. This relationship has to be verified.

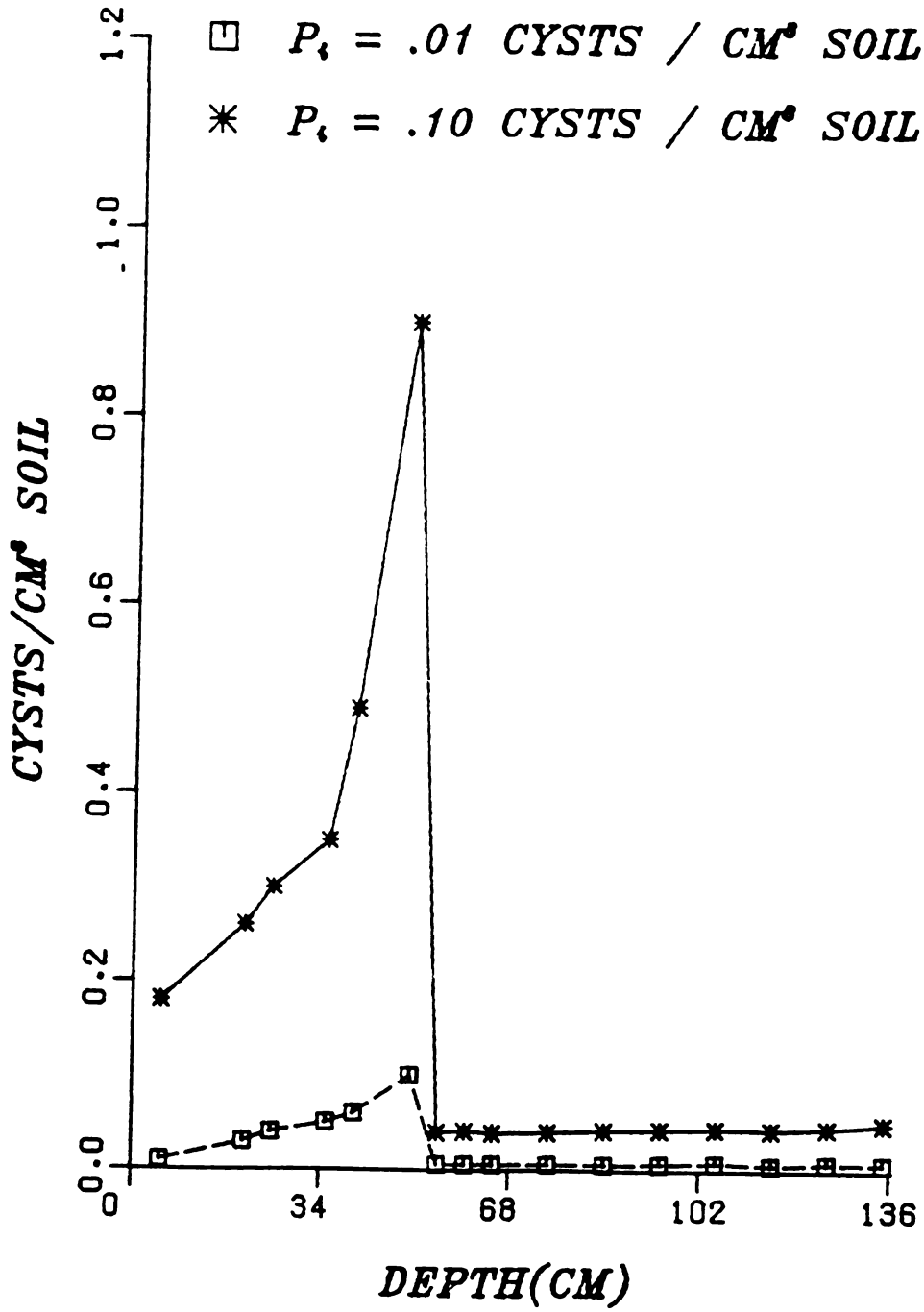

Fig. 8a. Relationship between initial population density of H. schachtii and the density of H. schachtii cysts at different depths at the end of the growing season.

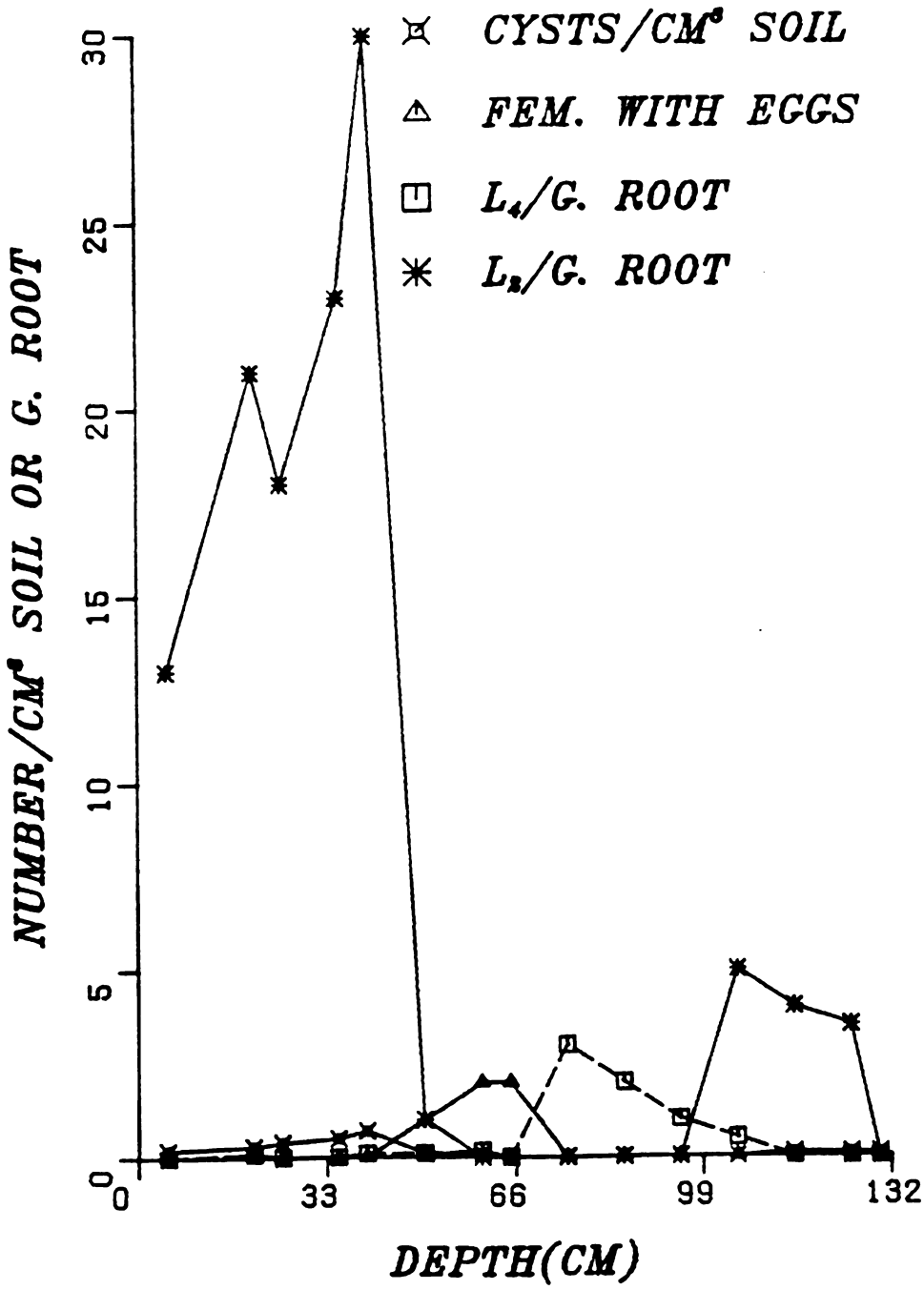

Fig. 8b. Vertical distribution of H. schachtii cysts, females with eggs, fourth stage juveniles and second stage juveniles per unit weight of soil or root, at the end of cabbage growing season.

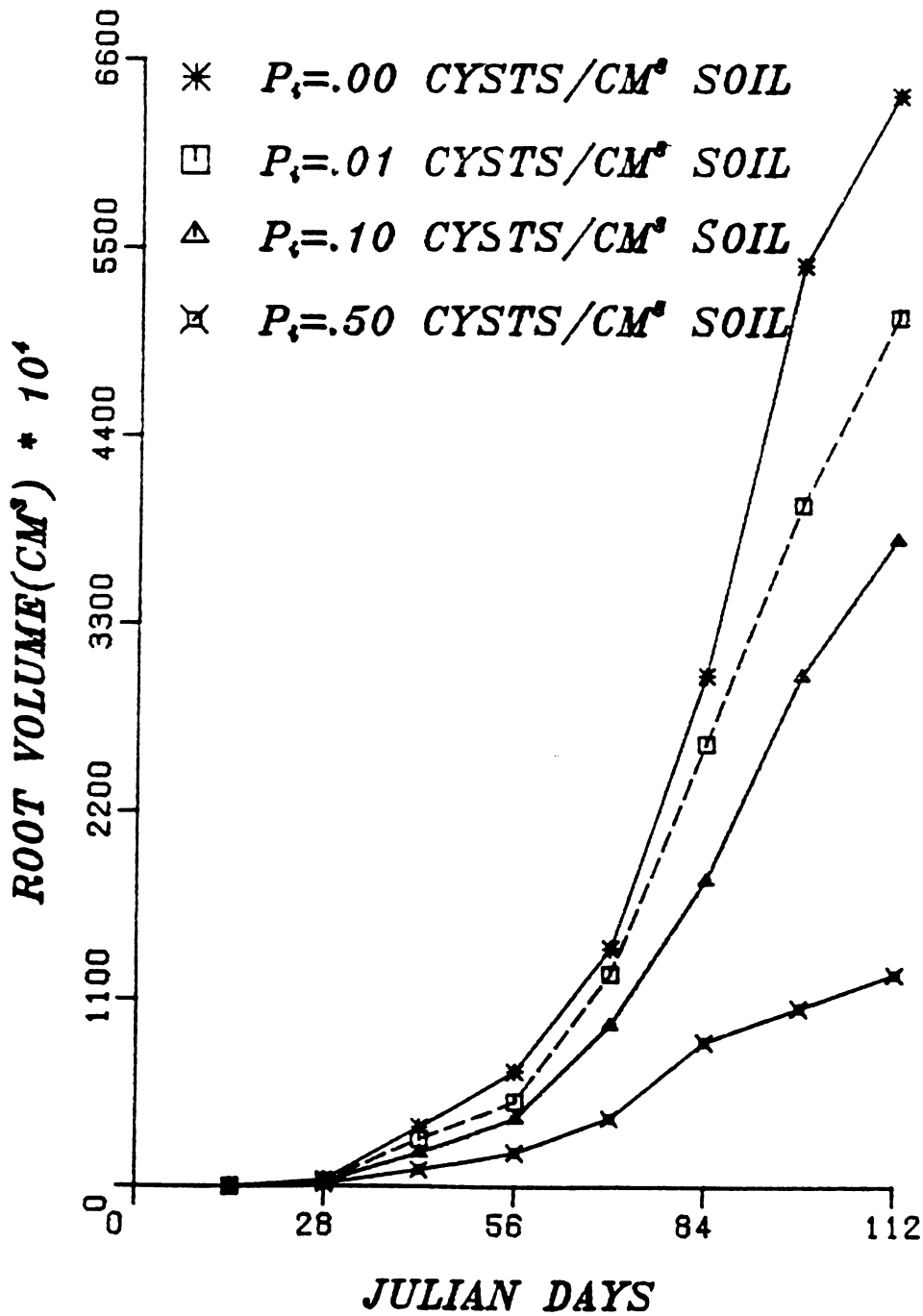

Fig. 9. Influence of H. schachtii initial population density on cabbage root volume.

2.3.6 Conclusions

The following conclusions were derived from the simulation.

1. H. schachtii is a limiting factor for cabbage production.
2. Distribution of cysts is aggregated in the upper 50 cm of soil, at the end of the growing season of an annual crop like cabbage.
3. Reduction in yield is dependent on the initial population density. As the initial population density increases, yield losses also increase.
4. H. schachtii completed 1.5 generations during the growing season. The development is dependent upon accumulated DD_{10}.
5. The simulation is relatively accurate since the results are comparable to previous research data.

2.3.7 Recommendations

For the simulation to be used as a predictive tool for the design of management strategies, more variables have to be input into the model. The following variables should receive the highest priority:

1. Environmental variables
    a. Soil moisture
    b. Soil texture
    c. Soil pH
    d. Interaction of the variables
2. Nematode
    a. Factors affecting mortality
    b. Factors affecting cyst distribution
    c. Determination of male and female ratio as it is affected by nematode density
    d. Hatching rate of eggs

3. Cabbage

   a. Relationship between root volume, root weight, and shoot weight

   b. Factors affecting cabbage growth

   c. Effect of crop density

3. EXPERIMENTATION

STUDIES ON HOST-PARASITE RELATIONSHIPS AND MANAGEMENT OF *HETERODERA SCHACHTII* ASSOCIATED WITH *BRASSICA OLERACEA* VAR *CAPITATA* L.

Heterodera schachtii is a limiting factor to several agricultural crop productions. It is one of the key pests in Michigan sugar beet production. Several studies were conducted to clarify the interaction between *H. schachtii* and *Brassica oleracea capitata*. The goals of this research were to: (1) assess the impact of *H. schachtii* on the ontogeny of cabbage and (2) to determine the influence of phenamiphos on the *H. schachtii*-cabbage association. The specific objectives of the experiments to be described were:

1. Determine the spatial and temporal distribution of cabbage roots and *H. schachtii*.
2. Assess the influence of *H. schachtii* and phenamiphos on cabbage seed emergence.
3. Determine *H. schachtii* influence on cabbage growth and development.
4. Compare Michigan and New York *H. schachtii* pathogenicity on cabbage.
5. Assess effect of phenamiphos on cabbage seed emergence.
6. Assess yield response of cabbage associated with *H. schachtii* when treated with different rates of phenamiphos.
7. Assess the role of phenamiphos as a nemastat on *H. schachtii* associated with cabbage.

3.1 SPATIAL AND TEMPORAL DISTRIBUTION OF CABBAGE ROOTS AND *HETERODERA SCHACHTII*

3.1.1 Introduction

The spatial and temporal distribution of *H. schachtii* is influenced by several factors. Some of the factors are root system of the host plant, soil type, and methods used to prepare the field for the crop. An understanding of the distribution of *H. schachtii* both in soil and roots will help in designing sampling schemes and sampling units. With accurate estimates of the population and its distribution, this will help in the design of good management tactics. The infection court of *H. schachtii* is a region behind the subapical meristem. Therefore, the distribution of these attackable sites should dictate where second stage juveniles are penetrating the roots. The younger developmental stages of *H. schachtii* are associated with newly penetrated roots and the older *H. schachtii* stages are associated with roots, in which second stage juveniles penetrated for an equivalent developmental period. Roots generally grow vertically, therefore, vertical distribution of *H. schachtii* is influenced by the time which has elapsed between root penetration and sampling data. Thus, in recently infested fields, the cysts are more or less confined to the topsoil whereas in older infestations, the cysts occur at much greater depths (Webster, 1972). For a young focus, 90% of the cysts are in the upper 10 cm (Webster, 1972). These differences in vertical distribution have a remarkable influence on the effect of control measures (Webster, 1972).

The major objective of this study was to determine the spatial and temporal distribution of cabbage roots and *H. schachtii* under greenhouse

conditions. In addition to the objective, it was of interest to find sections of the root system which will yield the most representative population structure.

3.1.2 Methods and Materials

B. oleracea capitata (cv. Roundup) was direct seeded in clay drainage tiles (24 cm diameter and 42 cm deep) on April 4, 1983, in a greenhouse with day and night temperatures of 27°C and 22°C, respectively. The tiles were first filled with certain proportions of steamed sandy-clay loam soil mixed with soil containing H. schachtii cysts so that the initial population density (P_i) would be 20 eggs and second stage juveniles per cm^3 of soil. The soil was mixed with a cement mixer. The inoculum was cultured in the greenhouse in wooden culture boxes 1.5 m long, 1.0 m wide and 0.3 m deep. The culture boxes were first filled with sandy-clay loam soil containing H. schachtii cysts, and then B. oleracea capitata (cv. King Cole) seedlings were transplanted into the culture box. The culture was maintained for about 8 months before use. About 100 cm^3 of soil from the culture box contained ca 100 cysts. Each cyst was estimated to have ca 200 eggs and second stage juveniles.

Tiles were arranged in a completely randomized block design with 1 treatment and 10 replications per treatment. Each tile received 30 kg/ha of 20-20-20 fertilizer at seeding. The seeds were watered daily until the seedlings were fully established. Emergence occurred as early as 4 days after seeding.

Plants were sampled at 2, 4, 6, and 8 weeks after seeding. On each sampling date, the soil and root system in the tile were divided into 9 sections. The soil and root system were first divided into 3 sections ca 14 cm deep (top, middle, and bottom). Then from each section 3 cylinders were drawn out with

diameters of 4, 8, and 12 cm (center, middle, and outer cylinders). Soil and roots were collected from each section. The following parameters were evaluated:

1. Fresh weights of root system were obtained by direct weighing.
2. About 0.1 gram of the root system was stained in a solution of lactophenol with 0.01% acid fuchsin, to determine the number of second stage juveniles, third and fourth stage juveniles, developing females, adult males, and females with eggs (Goodey, 1963).
3. Soil, 100 cm^3, was processed using the centrifugation-flotation technique to determine the number of cysts, second stage juveniles, eggs, and adult males (Goodey, 1963 and Jenkins, 1964).

3.1.3 Results

Root weight at depths 0-14, 14-28, and 28-42 cm, varied with time (Figure 10). Two weeks after seeding, a very limited root system was present in the 0-14 cm region, and no roots were present in the deeper regions. After four weeks, roots were found in 0-14 and 14-28 cm regions. No roots were found at this time in the 28-42 cm region. Six weeks after seeding, roots were found in all regions, but the highest root weight ($P=0.05$) was in the top section and the least in the bottom section. Also eight weeks after seeding, roots were found in all regions, still the highest root weight was in the top section. The root system in the middle region was less than the root system in the bottom section. Root system in the bottom section was higher because by this time the roots were pot bound.

Cysts per 100 cm^3 soil in the zones 0-14, 14-28, and 28-42 cm deep, were most numerous at the end of the growing season (Figure 11). Two weeks after seeding, number of cysts per 100 cm^3 soil was the same ($P=0.05$) in all the three

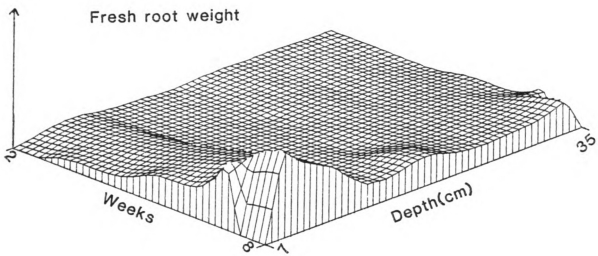

Fig. 10. Fresh root weight of cabbage collected at depths 0-14 cm, 14-28 cm, and 28-42 cm of a clay drainage tile in an 8 week growing period.

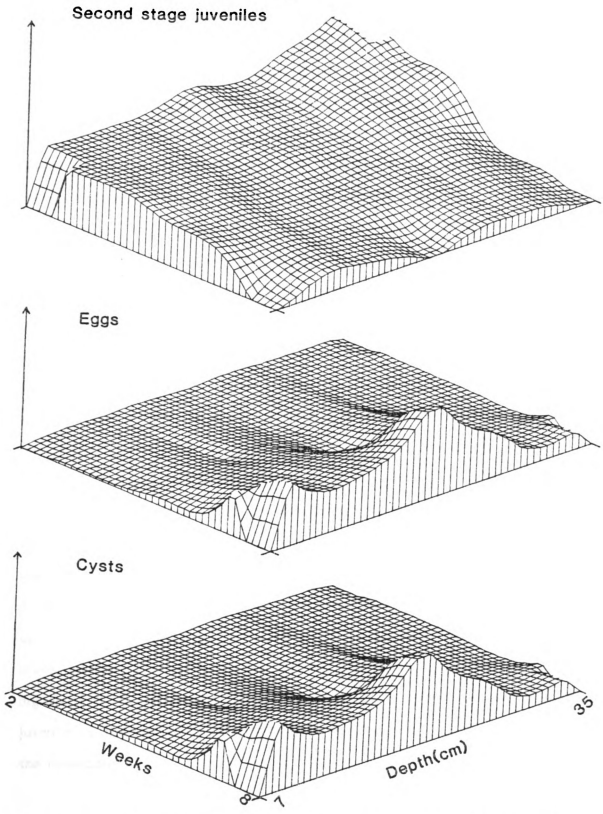

Fig. 11. H. schachtii cysts, eggs, and second stage juveniles in 100 cm^3 soil collected at depths 0-14 cm, 14-28 cm, and 28-42 cm of a clay drainage tile in an 8 week growing period.

zones. Four weeks after seeding, the number of cysts per 100 cm^3 soil was the same in all three zones. Two weeks later, the number of cysts in the top and middle zone, increased significantly (P=0.05). At the end of the eighth week, the number of cysts per 100 cm^3 soil increased in all the three zones. The highest density was in the top and middle zones. Density of cysts in these two zones were ca 4 times greater than the density in the bottom section.

Eggs per 100 cm^3 soil in the zones 0-14, 14-28, and 28-42 cm deep, also had the highest density at the end of the growing season (Figure 11). The bottom zone had the highest number of eggs per 100 cm^3 soil and the top zone had the least two weeks after seeding (P=0.05). After another two weeks, the density of eggs in all the three zones were the same (P=0.05). Six weeks after seeding, the top section had the highest number of eggs per 100 cm^3 soil (P=0.05). At the end of the growing season, the density of eggs in the soil increased in all the three zones. The highest density (P=0.05) was in the top and middle zones.

Second stage juveniles per 100 cm^3 soil in the zones 0-14, 14-28, and 28-42 cm deep were most numerous at the beginning of the growing season (Figure 11). The highest density of second stage juveniles were recorded two weeks after seeding. All the three zones had the same (P=0.05) density of second stage juveniles. After an additional two weeks, the density decreased and was the same in all the three zones. Six weeks after seeding, the bottom zone had the lowest number of second stage juveniles per 100 cm^3 soil, and the top zone the highest (P=0.05). At the end of the growing season, the density of second stage juveniles in the soil decreased further. The density was the same (P=0.05) in all the three zones.

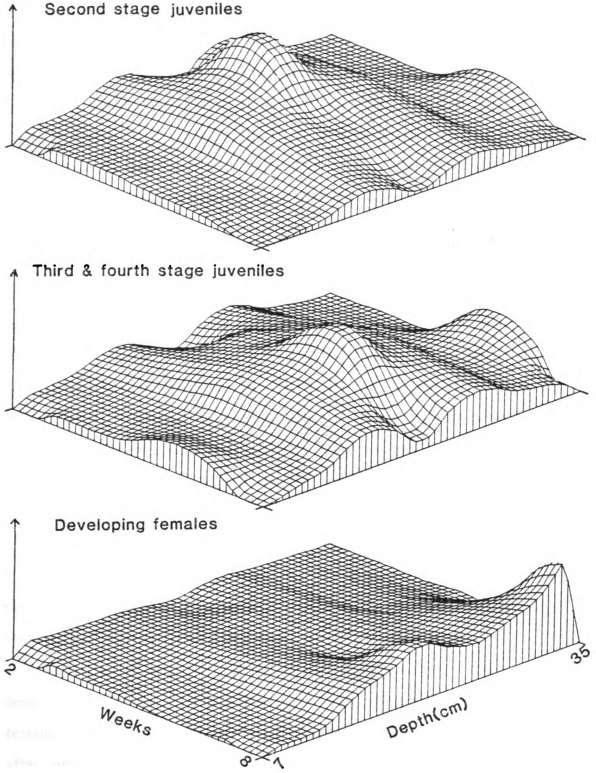

Fig. 12. H. schachtii second stage juveniles, third and fourth stage juveniles, and developing females found in 0.1 gram roots of cabbage from depth of 0-14 cm, 14-28 cm, and 28-42 cm of a clay drainage tile in an 8 week growing period.

Second stage juveniles per 0.1g root in the zones 0-14, 14-28, and 28-42 cm deep had the highest density four weeks after seeding (Figure 12). No second stage juveniles were observed in roots in the middle and bottom sections two weeks after seeding. Second stage juveniles were observed in roots from the top zone, two weeks after seeding. After an additional two weeks, the highest density of second stage juveniles was recorded in roots from the middle zone and the lowest in roots from the bottom zone (P=0.05). Six weeks after seeding, the highest density of second stage juveniles was recorded in roots from the middle and bottom zones and the least in roots from the top zone. At the end of the growing season, the density of second stage juveniles in the roots decreased in all the three zones. The density was the same (P=0.05) in roots from all the zones.

The distribution of third and fourth stage juveniles has its highest density per 0.1g root in week six (Figure 12). Two weeks after seeding, third and fourth stage juveniles were observed in roots from the top zone. After an additional two weeks, third and fourth stage juveniles were observed in roots from all the three zones. The highest density was in roots from the middle zone and the least in roots from the bottom zone (P=0.05). Six weeks after seeding, the highest density of the juveniles per root weight was still in roots from the middle zone but the least density was now in roots from the top zone (P=0.05). At the end of the growing season, the highest density of third and fourth stage juveniles was in roots from the bottom zone and the least in roots from the top zone.

Developing females per 0.1g root in the zones 0-14, 14-28, and 28-42 cm deep, had the highest density in the eighth week (Figure 12). No developing females were observed in roots from the middle and bottom zones two weeks after seeding. A few developing females were recorded in roots from the top

zone. Four weeks after seeding, still no developing females were observed in roots from the bottom zone. A few developing females were observed in roots from top and middle zones, four weeks after seeding. Developing females were observed in roots from all zones six weeks after seeding. The highest density (P=0.05) was in roots from the middle zone and the least in roots from the bottom zone. At the end of the growing season, the highest density was recorded in roots from the bottom zone and the least in roots from the top zone (P=0.05).

Adult males per 0.1g root in the zones 0-14, 14-28, and 28-42 cm deep, had the highest density six weeks after seeding (Figure 13). In week two, no adult males were observed in roots from the middle and bottom zones. A few adult males were observed in roots from the top zone, two weeks after seeding. After an additional two weeks, still no adult males were observed in roots from the bottom zone. A few adult males were observed in roots from the top and middle zones four weeks after seeding. In week six, adult males were observed in roots from all the three zones. The highest density of adult males were in roots from the middle zone and the least in roots from the bottom section (P=0.05). At the end of the growing season, still the highest density of adult males were observed in roots was the same (P=0.05) in all the three zones.

Females with eggs per 0.1g root in the zones 0-14, 14-28, and 28-42 cm deep had the highest density eight weeks after seeding (Figure 13). No females with eggs were observed in roots from all the zones two weeks after seeding. In week four, still no females with eggs were observed in roots from the bottom zone. Females with eggs were observed in roots from the top and middle zone four weeks after seeding. The density was higher (P=0.05) in roots from the top zone. Six weeks after seeding, still no females with eggs were observed in roots

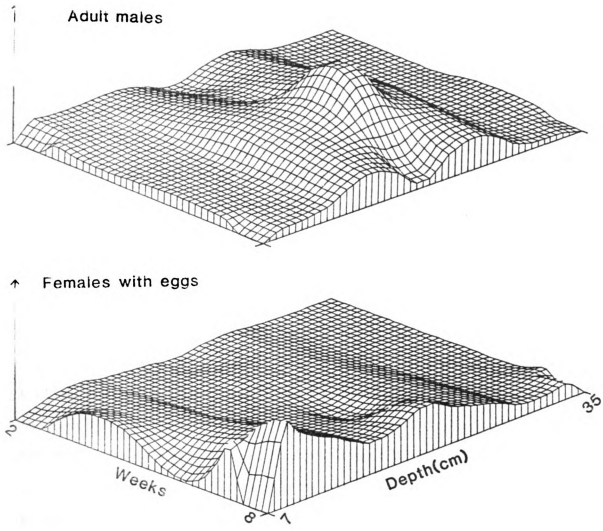

Fig. 13. H. schachtii adult males and females with eggs in 0.1 gram roots of cabbage from depths 0-14 cm, 14-28 cm, and 28-42 cm of a clay drainage tile in an 8 week growing period.

from the bottom section. The density of females with eggs in roots from top and middle sections decreased in week six. At the end of the growing season, females with eggs were observed in roots from all the three zones. The highest density was recorded in roots from the top zone and the least in roots from the bottom zone (P=0.05).

Root weight in cylinders of radius 0-4, 4-8, and 8-12 cm varied with time and depth at which the root weight was measured (Figure 14). The root weights were measured at depths of 0-14 and 28-42 cm. At depth 0-14 cm, no roots were observed in the middle and outer cylinders, two weeks after seeding. Very few roots were observed in the inner cylinder. No roots were observed in all the cylinders at depth 28-42 cm, two weeks after seeding. After an additional two weeks, roots were observed in all the cylinders at depth 0-14 cm. The inner cylinder had the highest root weight and the middle the least (P=0.05). Still no roots were observed in all the cylinders at depth 28-42 cm, four weeks after seeding. In week six, all the cylinders at depth 0-14 cm and 28-42 cm had roots. At depth 0-14 cm, the highest root weight was in the inner cylinder (P=0.05) and the least in the middle cylinder, at depth 28-42 cm, the highest root weight was in the outer cylinder and the least in the middle cylinder. At the end of the growing season, the highest root weight was in the inner cylinder and the least in the middle cylinder at depth 0-14 cm (P=0.05) and the highest root weight was in the outer cylinder and the least in the middle cylinder (P=0.05) at depth 28-42

Cysts per 100 cm^3 soil from the cylinders of radius 0-4, 4-8, and 8-12 cm and depths of 0-14 and 28-42 cm, were most numerous at the end of the growing season (Figure 15). At depth 0-14 cm, all the cylinders had the same (P=0.05)

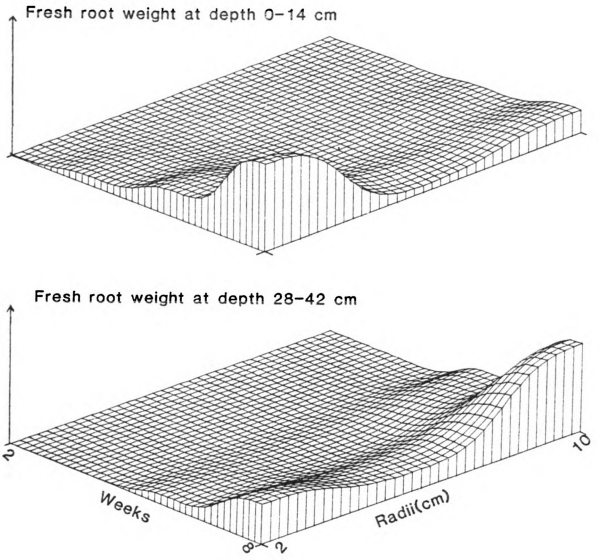

Fig. 14. Fresh root weight of cabbage collected at radii 0-4 cm, 4-8 cm, and 8-12 cm and at depths 0-14 cm and 28-42 cm of a clay drainage tile in an 8 week growing period.

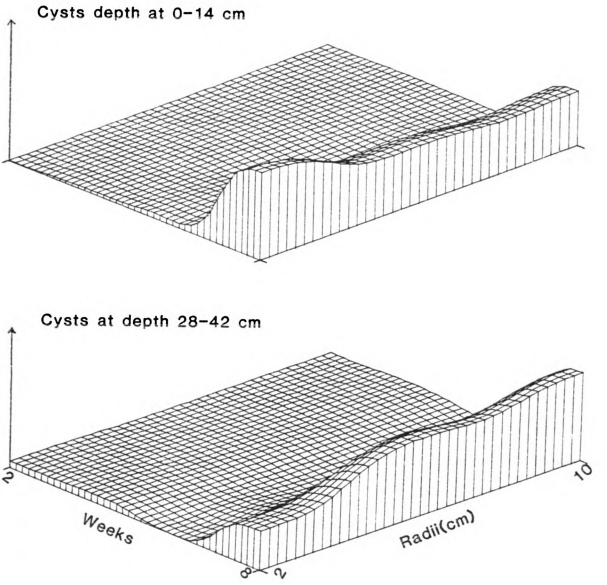

Fig. 15. H. schachtii cysts in 100 cm^3 soil collected at radii 0-4 cm, 4-8 cm, and 8-12 cm and at depths 0-14 cm and 28-42 cm of a clay drainage tile in an 8 week growing period.

density of cysts and at depth 28-42 cm, all the cylinders also had the same cyst density, but the cyst density at depth 28-42 cm was higher than the density at depth 0-14 cm, two weeks after seeding. After an additional two weeks, the cyst density in all the cylinders were the same. In week six, the cyst density was highest in the inner cylinder and least in the middle cylinder at depth 0-14 cm (P=0.05). The cyst density at depth 28-42 cm was very low and was the same in all the cylinders. At the end of the growing season, the cyst density in all the cylinders increased by at least four-fold. At depth 0-14 cm, the highest density was in the inner cylinder and the least in the outer cylinder (P=0.05). At depth 28-42 cm, the cyst density was highest in the outer cylinder and least in the inner cylinder (P=0.05). The distribution of eggs was similar to the distribution of cysts in all the cylinders and at both depths (Figure 16).

The distribution of second stage juveniles per 100 cm^3 soil was different from the distribution of cysts or eggs (Figure 17). The highest density of second stage juveniles was observed two weeks after seeding. At depth 0-14 cm, all the cylinders had the same second stage juvenile density. At depth 28-42 cm, all the cylinders also had about the same density of second stage juveniles, but it was slightly higher than the density at 0-14 cm. The density of second stage juveniles decreased throughout the growing season, and it was the same (P=0.05) in all the cylinders and at both depths.

Second stage juveniles per 0.1g root had their highest density in week four and six at depths 0-14 and 28-42 cm, respectively (Figure 18). Two weeks after seeding, second stage juveniles were observed in roots from the inner cylinder only at depth 0-14 cm, and at depth 28-42 cm, no second stage juveniles were observed in roots from all cylinders. After an additional two weeks, second

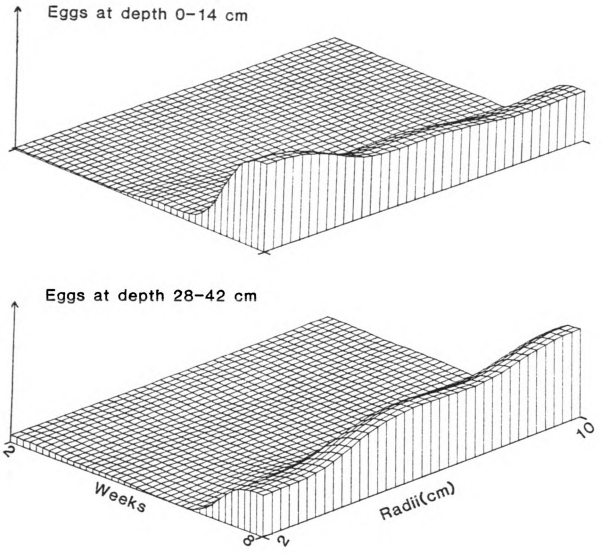

Fig. 16. H. schachtii eggs in 100 cm^3 soil collected at radii 0-4 cm, 4-8 cm, and 8-12 cm and at depths 0-14 cm and 28-42 cm of a clay drainage tile in an 8 week growing period.

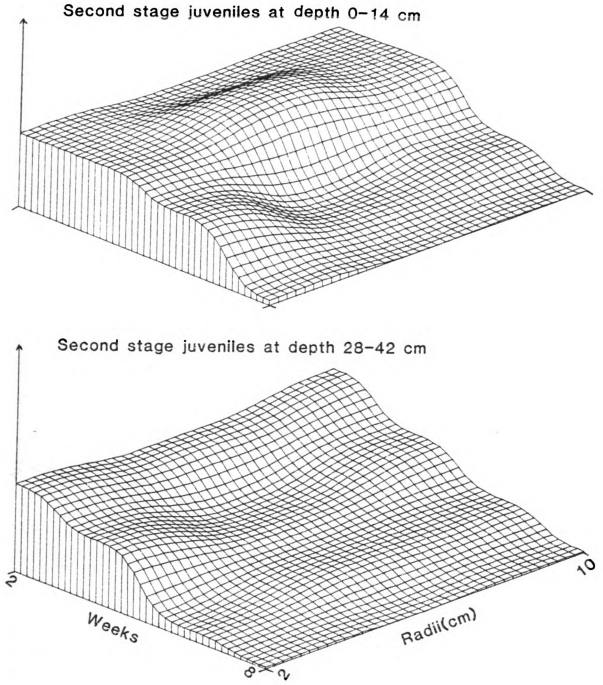

Fig. 17. H. schachtii second stage juveniles in 100 cm^3 soil collected at radii 0-4 cm, 4-8 cm, and 8-12 cm and at depths 0-14 cm and at 28-42 cm of a clay drainage tile in an 8 week growing period.

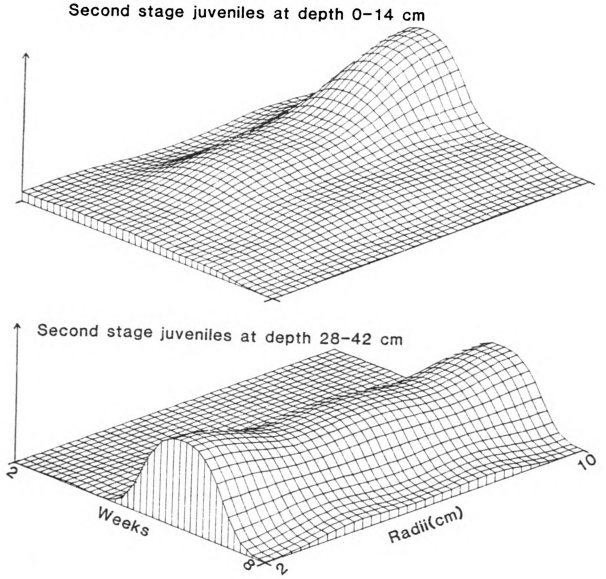

Fig. 18. H. schachtii second stage juveniles in 0.1 gram roots of cabbage collected at radii 0-4 cm, 4-8 cm, and 8-12 cm and at depths 0-14 cm and 28-42 cm of a clay drainage tile in an 8 week growing period.

stage juveniles were observed in roots from all cylinders at depth 0-14 cm. The highest density was in roots from the outer cylinder and the least in roots from the inner cylinder (P=0.05). At depth 28-42 cm, second stage juveniles were observed in roots from the inner cylinder only. In week six, the highest density was in roots from the middle cylinder and least in roots from the inner cylinder at depth 0-14 cm, and highest density was in roots from the inner cylinder and least in roots from the middle cylinder at depth 28-42 cm. At the end of the growing season, no juveniles were observed in roots from the outer cylinders at both depths. The density in the other cylinders was about the same at both depths. Third and fourth stage juveniles had a distribution similar to the distribution of second stage juveniles per root weight (Figure 19).

Developing females had their highest density at the end of the growing season at depth 28-42 cm (Figure 20). Two weeks after seeding, at depth 0-14 cm, developing females were observed in roots from the inner cylinder only, and at depth 28-42 cm, no developing females were observed in roots from cylinders. In week four, developing females were observed in roots from all cylinders at depth 0-14 cm. The inner cylinder had roots with the highest density of developing females and the outer cylinder had the least. Still no developing females were observed in roots from all cylinders at depth 28-42 cm. After an additional two weeks, developing females were observed in all cylinders at depth 0-14 cm, and at depth 28-42 cm developing females were observed in roots from the inner and middle cylinders but not the outer cylinder. In week eight, developing females were observed in roots from all cylinders and at both depths. The density of developing females was higher at depth 28-42 cm than at depth 0-14 cm (P=0.05).

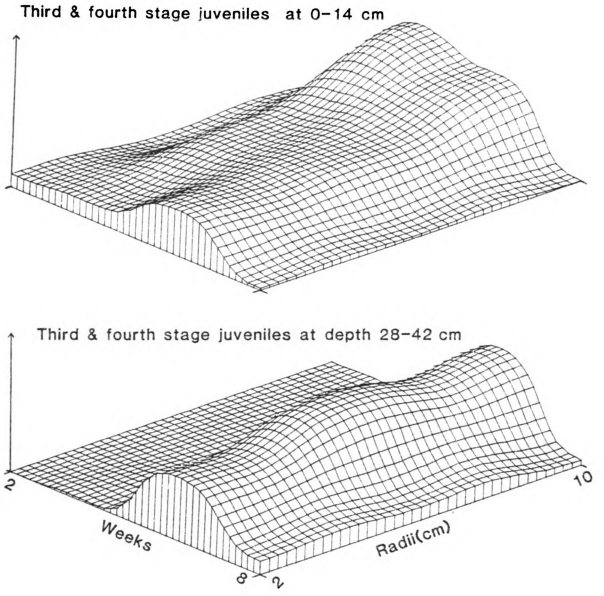

Fig. 19. H. schachtii third and fourth stage juveniles in 0.1 gram roots of cabbage collected at radii 0-4 cm, and 8-12 cm and at depths 0-14 cm and 28-42 cm of a clay drainage tile in an 8 week growing period.

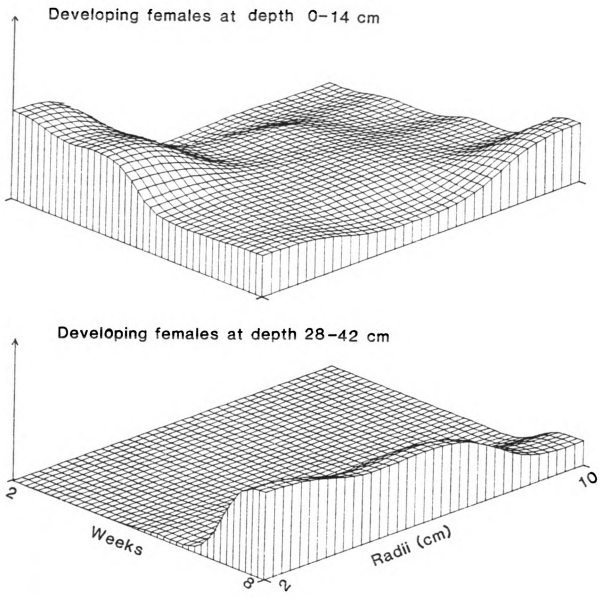

Fig. 20. H. schachtii developing females in 0.1 gram roots of cabbage collected at radii 0-4 cm, 4-8 cm, and 8-12 cm and at depths 0-14 cm and 28-42 cm of a clay drainage tile in an 8 week growing period.

Adult males per 0.1g root were only observed in roots from the inner cylinder at depth 0-14 cm two weeks after seeding (Figure 21). Two weeks after seeding, no adult males were observed in roots from all cylinders at depth 28-42 cm. After an additional two weeks, adult males were observed in roots from middle and inner cylinders at depth 0-14 cm. Still no adult males were observed in roots from all cylinders at depth 28-42 cm (Figure 21). In week six, adult males were observed in all cylinders and at both depths. Cylinders at depth 0-14 cm had a slightly higher density than cylinders at depth 28-42 cm. At the end of the growing season, cylinders at depth 28-42 cm had a higher density of adult males per root weight than cylinders at depth 0-14 cm.

Females with eggs per root weight had their highest density in week eight at both depths (Figure 22). No females with eggs were observed in roots from all cylinders and at both depths two weeks after seeding. In week four, females with eggs were only observed in roots from the inner cylinder at depth 0-14 cm and no females with eggs were observed in roots from cylinders at depth 28-42 cm. After an additional two weeks, females with eggs were observed in all cylinders at depth 0-14 cm. Still no females with eggs were observed in roots from all cylinders at depth 28-42 cm. At the end of the growing season, females with eggs were observed in roots from all cylinders and at both depths. The highest density of females with eggs was in the inner cylinder at both depths ($P=0.05$).

3.1.4 Discussion

Vertical distribution of the cabbage root system showed an accumulation in the upper 14 cm of soil, especially during the early stages of growth. Weaver

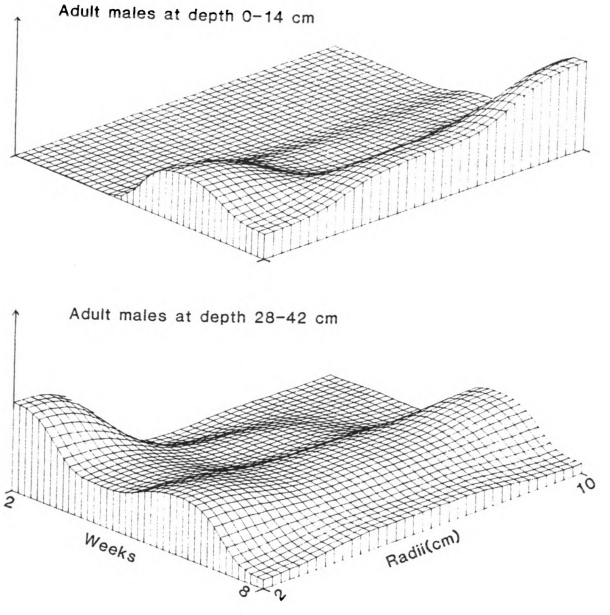

Fig. 21. H. schachtii adult males in 0.1 gram roots of cabbage colledted at radii 0-4 cm, 4-8 cm, and 8-12 cm and at depths 0-14 cm and 28-42 cm of a clay drainage tile in an 8 week growing period.

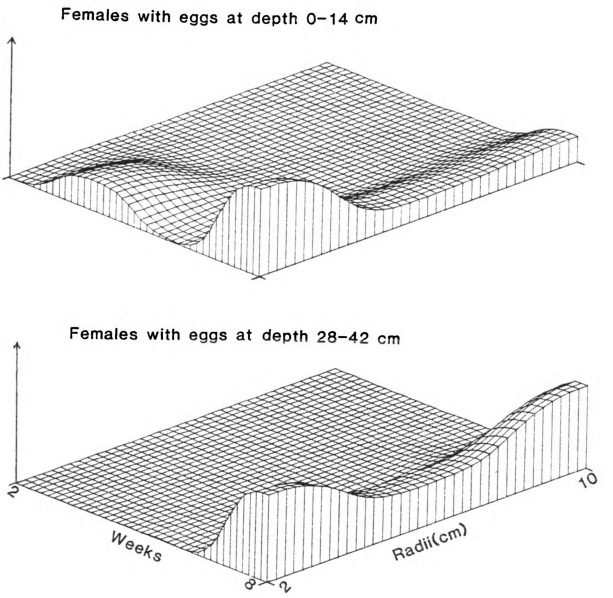

Fig. 22. H. schachtii females with eggs in 0.1 gram roots of cabbage collected at radii 0-4 cm, 4-8 cm, and 8-12 cm and at depths 0-14 cm and 28-42 cm of a clay drainage tile in an 8 week growing period.

and Brunner (1927) reported that about 90% of the cabbage root system is within the upper 20 cm of soil 55 days after seeding. The cabbage root system started to accumulate at lower layers at the end of the season. Weaver and Brunner (1927) also reported that 90% of the cabbage root system is within the upper 50 cm of soil 75 days after seeding. The depth to which the cabbage root system can reach is a function of time and other variables like soil type, moisture and temperature. Under ideal conditions, the cabbage root system can grow to a depth of ca 100 cm (Weaver and Brunner, 1927). In this study, the cabbage root system showed a slight accumulation at the base of the tile because roots were container bound.

Horizontal root distribution of the cabbage root system showed an accumulation in a radius of 8 cm on all sides of the plant. Weaver and Brunner (1927) reported that 90% of the cabbage root system is within a radius of 40 cm 55 days after seeding. The roots branch many times within this radius so that the soil is quite thoroughly filled with roots (Weaver and Brunner, 1927). Most of the lateral roots run outward and downward, often at an angle of approximately 45 degrees (Weaver and Brunner, 1927). Lateral roots frequently reach a lateral spread of 90 cm on all sides of the plant. In this study full lateral spread was stopped because of the tile, hence the root system started to accumulate along the wall of the tile. The root crowding was more pronounced at depth 28-42 cm because most of the roots grow downward at an angle of 45 degrees.

The vertical distribution of H. schachtii is influenced by the age of infestation (Webster, 1972). Thus, in recently infested fields, 85% of the cysts are confined to the upper 10 cm whereas in older infestations the cysts occur almost uniformly to a depth of 50 cm (Webster, 1972). In this study, about 90%

of the cysts were confined to the upper 30 cm. H. schachtii in upper layers completed two generations and H. schachtii at lower levels completed only one generation. This accounts for the difference in cyst density between the layers. H. schachtii in lower levels completed only one generation primarily because there was a time delay of 14-28 days before these nematodes were exposed to root tissue. It appears that an infected rootlet ceases to grow and gives rise to another branch which still continue to grow. This phenomenon gives rise to the whiskered appearance of the root system.

Horizontal cyst distribution at a depth of 0-14 cm showed an aggregation within a radius of 8 cm. About 75 of the cysts are within this radius. Again the primary reason for the aggregation is that H. schachtii in this radius completed two generations whereas H. schachtii out of this radius only completed one generation. The cyst density at a depth of 28-42 cm was highest in the outer cylinder because this cylinder had more root tissue than the other two primarily because the root system grew at an angle. Cyst density within a radius of 4 cm was about four times higher at a depth of 0-14 cm compared to cyst density at depth of 28-42 cm, whereas cyst density in the radius 8-12 cm was the same at depth 0-14 cm and 28-42 cm. Distribution of eggs in the soil was similar to cyst distribution. The above explanation is also true for egg distribution.

Second stage juveniles in the soil showed a vertical distribution with very little variation. At the beginning of the season slightly more juveniles were in soil at a depth of 28-42 cm. Second stage juveniles at depth 0-14 cm started to penetrate roots much earlier than juveniles at a depth of 28-42 cm. Second stage juveniles in the soil decreased throughout the growing season as the inoculum source was being used up. Newly formed cysts in the zone 0-14 cm

deep did not produce many second stage juveniles. Eggs in a cyst can have a time lag of up to a week or more before a complete development of second stage juveniles (Franklin, 1972). Horizontal distribution of second stage juveniles in the soil showed little variation between cylinders and the two depths. Juveniles in the soil decreased throughout the growing season. If the cabbage had been allowed to grow longer, a large influx of second stage juveniles in the soil from newly formed cysts was expected.

Vertical distribution of second stage juveniles in roots appeared to be a function of attackable sites and the density of second stage juveniles in the soil. The highest density per root weight is attained when both variables are optimal. Attackable sites per root weight depend on the age of the root system. Young roots have more attackable sites per unit weight compared to old roots. At the beginning of the season, the density of second stage juveniles per root weight was low because attackable sites were a limiting factor. In the middle of the season, the highest density of second stage juveniles was recorded. It appears both attackable sites and second stage juveniles in the soil were optimal. At the end of the season, the density of second stage juveniles per root weight decreased because the number of second stage juveniles in the soil was at its lowest. Horizontal distribution of second stage juveniles per root weight exhibited a trend similar to vertical distribution of second stage juveniles per root weight for similar reasons.

Third and fourth stage juveniles per root weight had a similar distribution to second stage juveniles per root weight but had a 1-2 week time shift. This time shift is associated with the delay required to develop from second stage to third or fourth stage. The time delay is about 9 days (Caswell et al., 1981;

Decker, 1981). Developing females exhibited a similar trend but with a longer time shift from the second stage juveniles per root weight. The time delay is about 11 days (Caswell et al., 1981; Decker, 1981).

Adult males per root weight had a slightly different distribution. The maximum density per root weight is not very high both for vertical and horizontal distributions. Probably the reason why the numbers are not so high is because after copulation, the adult males moved out of the root into the soil. But in general, adult male distribution per root weight also shows a time shift from the distribution of second stage juveniles per root weight. The time delay is about 11 days (Caswell et al., 1981; Decker, 1981).

The distribution of females with eggs per root weight is similar to the distribution of developing females per root weight except that there is a time lag. The time lag from developing females to females with eggs is about 9 days (Caswell et al., 1981; Decker, 1981). The distribution of females with eggs has two peaks at weeks four and eight. This implies that about two generations were completed in the eight-week growing period. The relatively fast rate of development might have been facilitated by optimal developmental temperatures under greenhouse conditions. The developmental period can be as short as 23 days at 29^{o}C (Decker, 1981).

This research shows that the distribution of cabbage roots is dictated by the length of the growing period. For short growing periods, the root system is mainly confined in the upper layers. The root system can spread to deeper layers if the growing period is prolonged. Horizontally, the root system is confined in the center for short growing periods, but the root system can spread to greater radii if the growing period is prolonged. The distribution of roots in turn dictate

the distribution of H. schachtii. The highest density of H. schachtii cysts is associated with the oldest root system which is in the upper layers and in the center. On the other hand, second stage juveniles will be in the deeper layers and in the periphery. For management purposes, it is apparent that when controlling H. schachtii in cabbage fields, management tactics should only be concentrated in the upper 50 cm.

3.2 INFLUENCE OF HETERODERA SCHACHTII AND PHENAMIPHOS ON CABBAGE SEED EMERGENCE

3.2.1 Introduction

Nonfumigant nematicides are generally not phytotoxic when used at low concentrations (Wright, 1981). At high concentrations, phenamiphos is phytotoxic and can inhibit seed emergence (Griffin, 1975). Also high levels of H. schachtii infestation can inhibit seed emergence or cause death of young plants (Mai et al., 1972). At high concentrations, phenamiphos effectively controls H. schachtii therefore loss of seed emergence will be primarily due to phenamiphos. On the other hand, at very low phenamiphos concentrations, H. schachtii will be primarily responsible for loss of seed emergence. Little is known about the interaction between phenamiphos and H. schachtii on cabbage seed emergence. This information is essential in the design of good management tactics.

In this study, loss of seed emergence was assessed in soil: (1) with a constant initial population density of H. schachtii and (2) treated with different rates of phenamiphos.

3.2.2 Methods and Materials

Pregerminated B. oleracea capitata (cv. King Cole) seeds were seeded in 20 cm diameter clay pots on November 14, 1982, in a greenhouse with day and night temperatures of 27°C and 22°C, respectively. The pots were first filled with certain proportions of steamed sandy-clay loam soil mixed with soil containing H. schachtii cysts so that the initial population density (P_i) would be 20 eggs and second stage juveniles per cm^3 of soil. The soil was mixed with a cement mixer. The inoculum was cultured in the greenhouse in wooden culture boxes 1.5 m long, 1.0 m wide, and 0.3 m deep. The culture boxes were first filled with sandy-clay loam soil containing H. schachtii cysts and then B. oleracea capitata (cv. King Cole) seedlings were transplanted into the culture box. The culture box was maintained for about 5 months before use. The culture contained about 130 cysts in 100 cm^3 of soil. Each cyst was estimated to have ca 200 eggs and second stage juveniles.

Pots were arranged in a completely randomized block design with 9 treatments and 20 replications. The treatments received 20-20-20 fertilizer at 30 kg/ha on the seeding day. All the treatments had the same H. schachtii initial population density (20 eggs and second stage juveniles per cm^3 of soil) but different phenamiphos rates--0, 1.2, 2.4, 3.6, 4.8, 6.0, 7.2, 9.6, and 14.4 kg ai/ha, respectively. The seeds were watered daily. Emergence occurred as early as 4 days but all the treatments were assessed for emergence after 14 days.

3.2.3 Results

Emergence loss was assessed by noting pots in which the seed did not emerge and the sum of these were expressed as a percentage for each treatment.

Treatments 1, 2, 3, 4, 5, 6, 7, 8, and 9 had 20 eggs and second stage juveniles per cm^3 of soil plus 0, 1.2, 2.4, 3.6, 4.8, 6.0, 7.2, 9.6, and 14.4 kg ai phenamiphos/ha, respectively. The highest concentration of phenamiphos had the lowest seed emergence (Table 1). Emergence loss ranged from 20% to 65%. There is a high correlation (R=0.823) between phenamiphos concentration and cabbage seed loss of emergence (Figure 23).

3.2.4 Discussion

Emergence of cabbage seeds was influenced both by H. schachtii and phenamiphos. An initial population density of 20 eggs and second stage juveniles per cm^3 of soil caused 20% reduction in cabbage seed emergence. The penetration of second stage juveniles into the young root system, disrupted the absorption of nutrients and water by the root system, and as a result the seed or seedlings died.

H. schachtii plus phenamiphos caused more cabbage seed emergence loss. At low rates of application, phenamiphos is not expected to be phytotoxic or to control H. schachtii. In fact, at low rates, phenamiphos stimulates hatch of second stage juveniles and results in higher numbers of second stage juveniles penetrating host plant roots (Steele and Hodges, 1975). It appears at 1.2 and 2.4 kg ai/ha, increase in emergence loss resulted from increase in second stage juvenile invasion rather than phytotoxicity of phenamiphos. At 3.6 kg ai/ha, phenamiphos started to impair juvenile penetration into the roots such that emergence increased slightly. It is unlikely that phenamiphos was phytotoxic at this rate too.

Table 1. Emergence loss of cabbage seeds grown in clay pots in the presence of H. schachtii (20 eggs and second stage juveniles/cm^3 soil)and phenamiphos.

Phenamiphos rate (kg ai/ha)	Number of seeds which did not emerge out of 20	% emergence loss
0	4	20
1.2	9	45
2.4	9	45
3.6	7	35
4.8	10	50
6.0	9	45
7.2	9	45
9.6	12	60
14.4	13	65

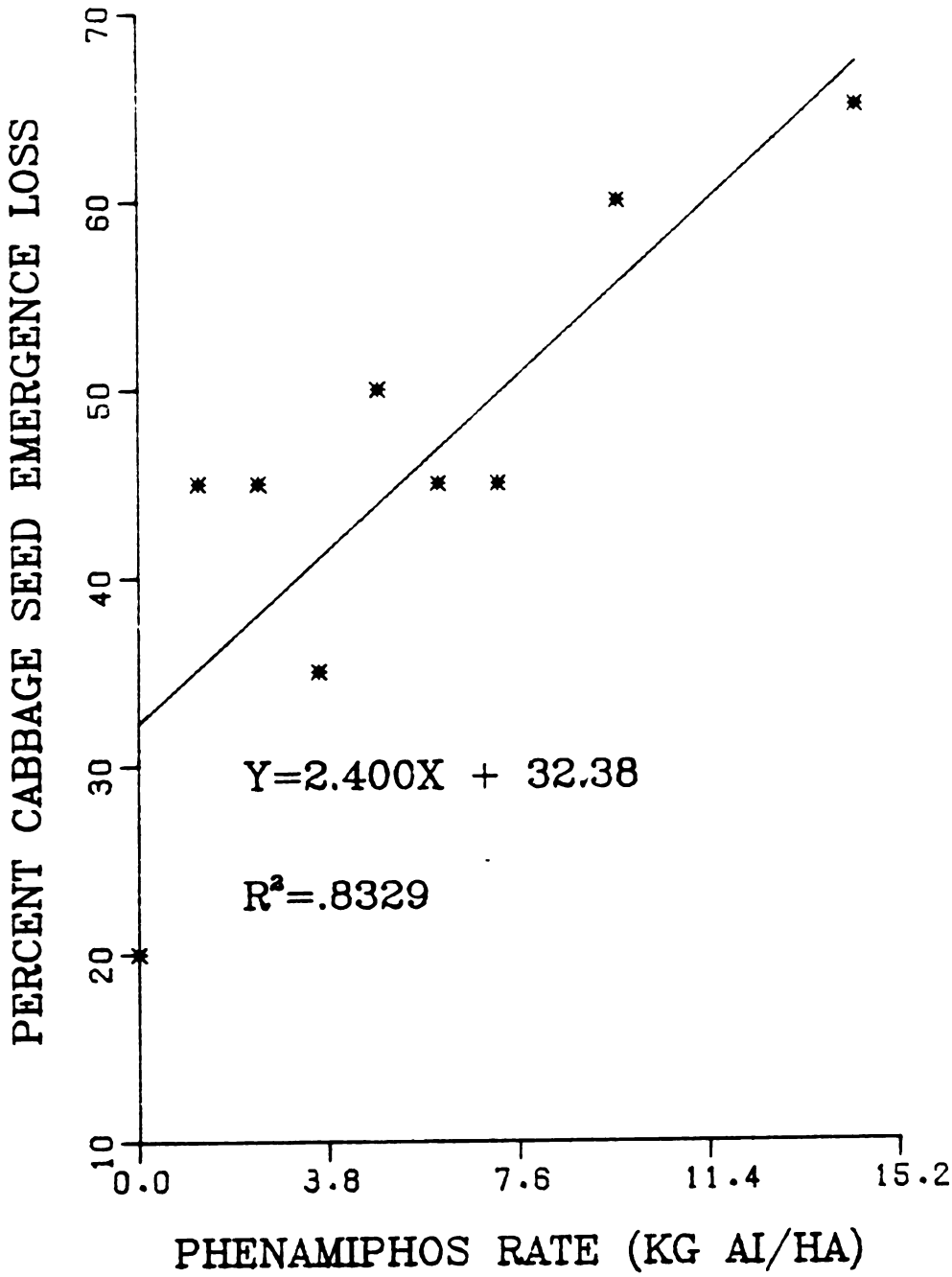

Fig. 23. Relationship between cabbage seeds emergence loss and phenamiphos concentration in the presence of *H. schachtii* (P_i = 20 eggs and second stage juveniles/100 cm^3 soil).

From an application rate of 4.8 kg ai/ha to 14.4 kg ai/ha, phenamiphos could have been phytotoxic. At these rates the effect of H. schachtii on emergence is minimal to nil since very few juveniles can penetrate roots at these rates. At 9.6 kg ai/ha and 14.4 kg ai/ha, second stage juveniles in the soil may even be killed.

Overall it appears that at low rates of phenamiphos application, H. schachtii was primarily responsible for cabbage seed emergence loss and at very high rates of phenamiphos applications, the nematicide was primarily responsible for the loss in cabbage seed emergence. At intermediate rates, H. schachtii and phenamiphos may have had an additive effect on cabbage seed emergence loss.

The phytotoxic effect detected at high rates of application may have been faciiitated by the confinement of the plant in a pot. In the field, the phytotoxicity may not be detected at equivalent rates. It is likely that much higher rates may be required for the detection of phytotoxicity under field conditions.

3.3 INFLUENCE OF H. SCHACHTII ON CABBAGE GROWTH AND DEVELOPMENT

3.3.1 Introduction

H. schachtii limits cabbage production in Michigan (Chitwood, 1953), where about 3200 acres are under annual production (Federva and Pscodna, 1983). The sugar beet cyst nematode primarily stunts cabbage growth and development (Abawi and Mai, 1980; Abawi and Mai, 1977; Barker and Olthof, 1976; Brzeski, 1969; Jones, 1957; Mai and Abawi, 1980; Mai et al., 1972; Olthof et al., 1974) and

results in up to 70% yield losses depending with the initial population density. An initial population density as low as six to nine H. schachtii eggs and second stage juveniles per cm^3 of soil can significantly reduce marketable yield (Abawi and Mai, 1980; Barker and Olthof, 1976; Mai and Abawi, 1980).

Relationships between initial population density of H. schachtii and cabbage yield losses are important in the development of predictive pest-crop ecosystem models. Also important are relations between the environment and nematode/crop development. The objective of this study was to determine the relationships between initial population density of H. schachtii and cabbage yield losses. Also it was of interest to determine the life cycle of the nematode during the growing season as influenced by physiological time (degree days).

3.3.2 Methods and Materials

B. oleracea capitata (cv Roundup) was direct seeded in small paper cups (Volume=50 cm^3) on July 9, 1983. The cups were set into flats filled with soil to conserve moisture in the cups. The experiment was run in a greenhouse with day and night temperatures of 27°C and 22°C, respectively for four weeks and then the seedlings in the cups were transplanted into clay drainage tiles (24 cm diameter and 42 cm deep) in the field.

Cups and tiles were filled with similar proportions of steamed sandy clay loam soil mixed with soil containing H. schachtii cysts so that the initial population density would be 20 eggs and second stage juveniles per cm^3 of soil. The inoculum was cultured in the greenhouse in wooden culture boxes 1.5 m long, 1.0 m wide, and 0.3 m deep. The culture boxes were first filled with sandy-clay loam soil containing H. schachtii cysts and then B. oleracea capitata (cv. King

Cole) seedlings were transplanted into the culture box. The culture box was maintained for about 8 months before use. The culture contained about 80 cysts in 100 cm^3 of soil. Each cyst has 200 eggs and second stage juveniles (Mai and Abawi, 1980; Olthof et al., 1974).

Tiles were arranged in a completely randomized block design with 4 treatments and 10 replications for each treatment. The treatments received 15 kg/ha and 30 kg/ha of 20-20-20 fertilizer at seeding and transplanting, respectively. Two additional fertilizer applications at 100 kg/ha of 20-20-20 fertilizer were made at 4-week intervals.

After seeding, the soil was sprayed with a fungicide Lesan 70W (Dexon) at 1.0 kg/ha to control damping off. When the seedlings were transplanted into the field, they were treated with a fungicide manganese ethylenebisdithiocarbamate (maneb) and an insecticide 0,S-dimethyl acetylphosphoramidothioate (orthene) at 1.4 kg/ha and 1.6 kg/ha, respectively. The fungicide and insecticide were applied biweekly throughout the growing season to minimize the effect of pests other than nematodes.

Air temperature was monitored using a Biophenometer TA51 for the entire growing season. The weather computer was programmed to give degree days with a lower limit of 10°C and an upper limit of 45°C.

Plants were sampled biweekly. On each sampling date the entire plant, including the root system, was dug. Soil was also collected from the cups or tiles. The following parameters were evaluated:

(1) Fresh weights of root and shoot systems were obtained by direct weighing.

(2) About 0.1 gram of the root system was stained in a solution of lactophenol with 0.01% acid fuchsin to determine the number of second stage juveniles,

third and fourth stage juveniles, developing females, adult males, and females with eggs.

(3) Soil 100 cm^3 (50 cm^3 for the first two samplings) was processed using the centrifugation-flotation technique to determine the number of cysts, eggs, and second stage juveniles.

3.3.3 Results

H. schachtii infection reduced (P=0.05) total shoot weight (Figure 24), marketable yield, and root weight (Figure 25). Marketable yield was reduced (P=0.05) by 70%, 50%, and 30% in treatments in which cabbage seed was direct seeded into: H. schachtii infested soil and then transplanted into H. schachtii infested soil four weeks after seeding (Hs-Hs), noninfested soil and then transplanted into H. schachtii infested soil four weeks after seeding (Ck-Hs), and H. schachtii infested soil and then transplanted into noninfested soil four weeks after seeding (Hs-Ck), respectively. Root weight was reduced (P=0.05) by 36%, 28%, and 14% in treatments Hs-Hs, Ck-Hs, and Hs-Ck, respectively.

The number of cysts in the soil fluctuated (P=0.05) throughout the growing season (Figure 26). Treatments Hs-Hs and Hs-Ck have three peaks of cysts. The peaks follow accumulations of 540, 1180, and 1600 DD_{10}. The number of eggs in the soil also followed the same trend (Figure 27). Second stage juveniles in the soil followed a different trend (Figure 28) which peaked after 1730 DD_{10}.

Second stage juveniles in the roots peaked 3 times (Figure 29). The peaks follow accumulations of 220, 820, and 1730 DD_{10}. Third and fourth stage juveniles followed the same trend (Figure 30). Developing females followed a different trend with two peaks after an accumulation of 540 and 1730 DD_{10}

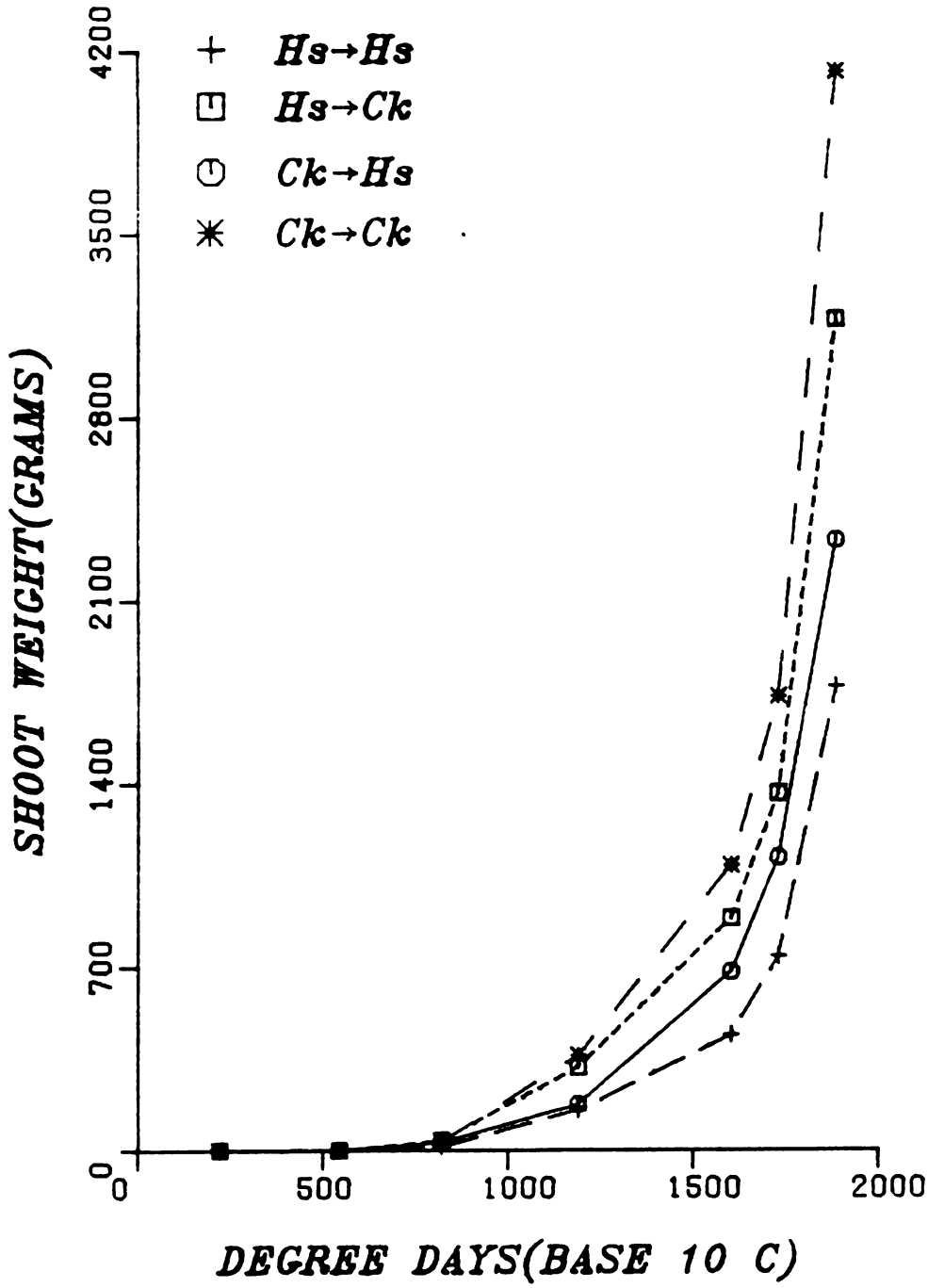

Fig. 24. Fresh shoot weight of cabbage grown in the presence and absence of H. schachtii for a period of about 1900 DD_{10}.

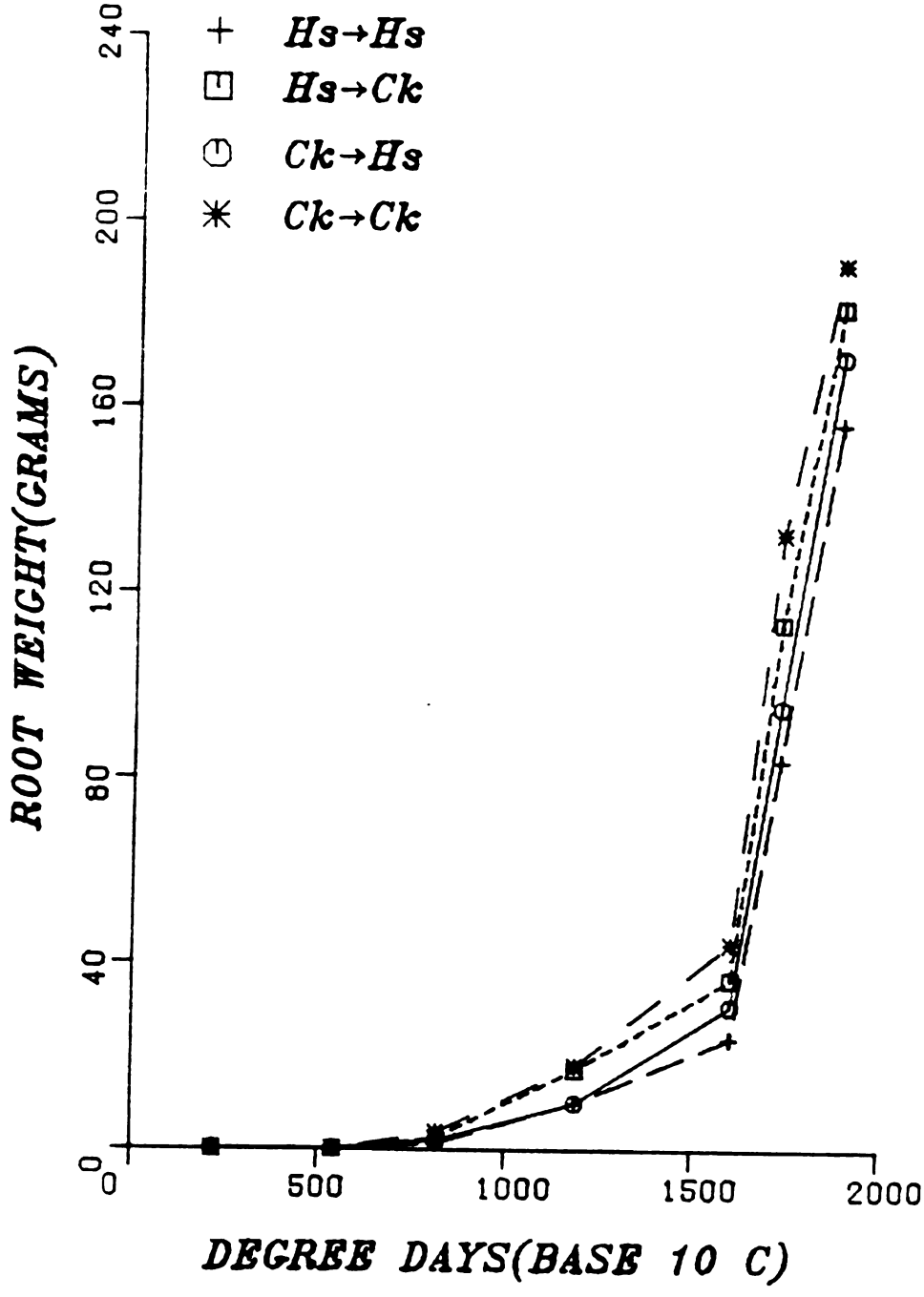

Fig. 25. Fresh root weight of cabbage grown in the presence and absence of H. schachtii for a period of about 1900 DD_{10}.

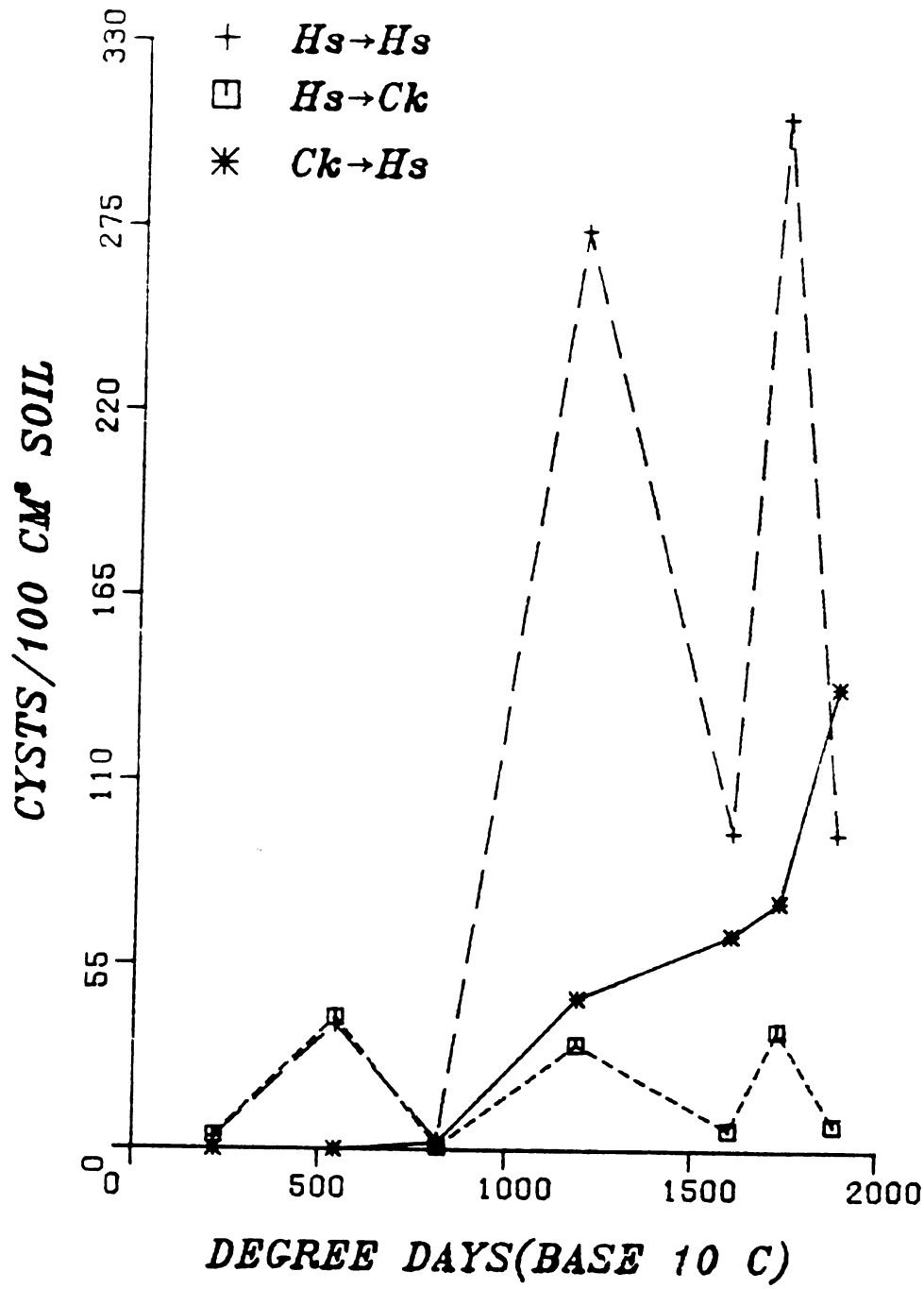

Fig. 26. Number of H. schachtii cysts in 100 cm^3 soil surrounding cabbage grown in the presence and absence of H. schachtii for a period of 1900 DD_{10}.

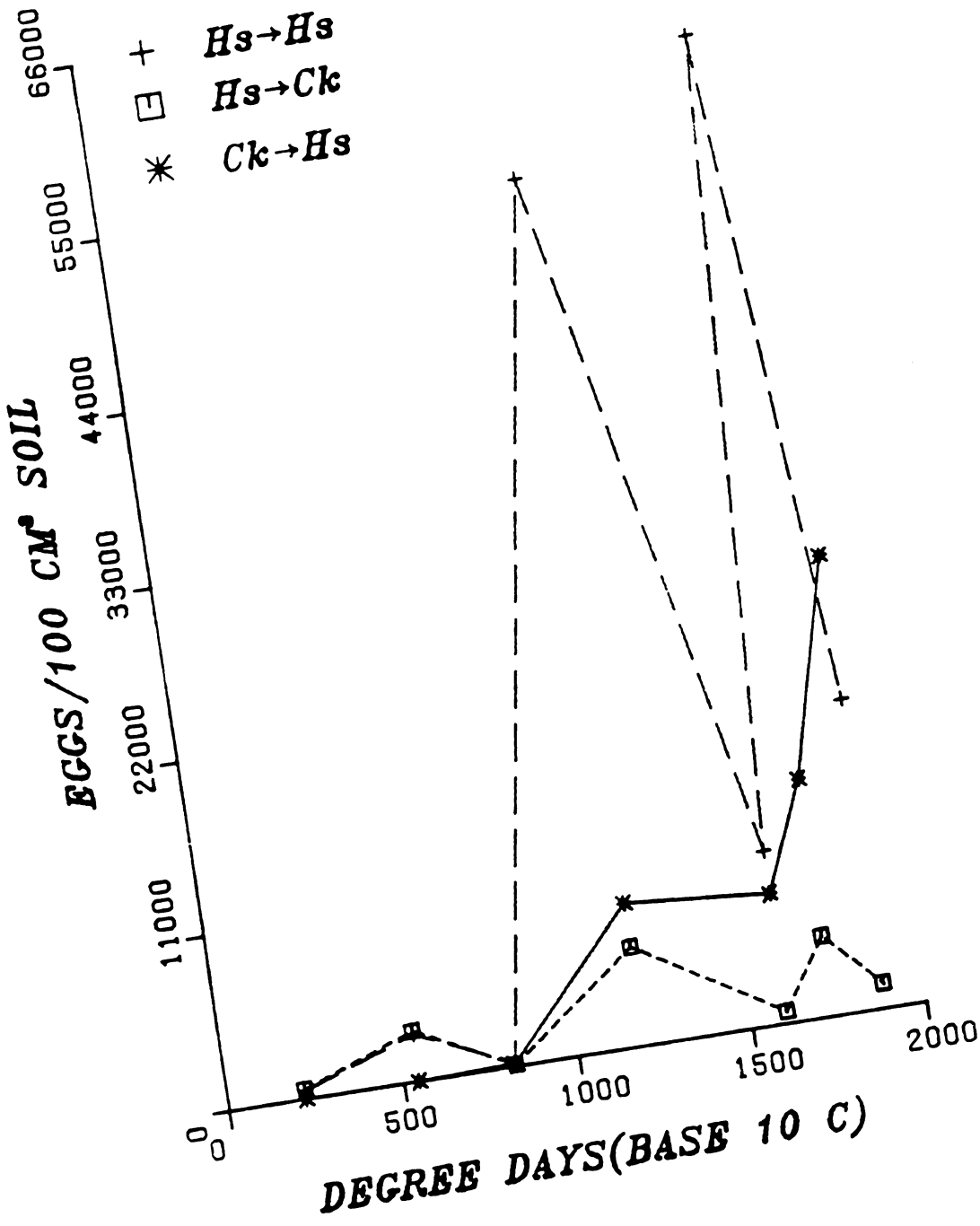

Fig. 27. Number of H. schachtii eggs in 100 cm^3 soil surrounding cabbage grown in the presence and absence of H. schachtii for a period of 1900 DD_{10}.

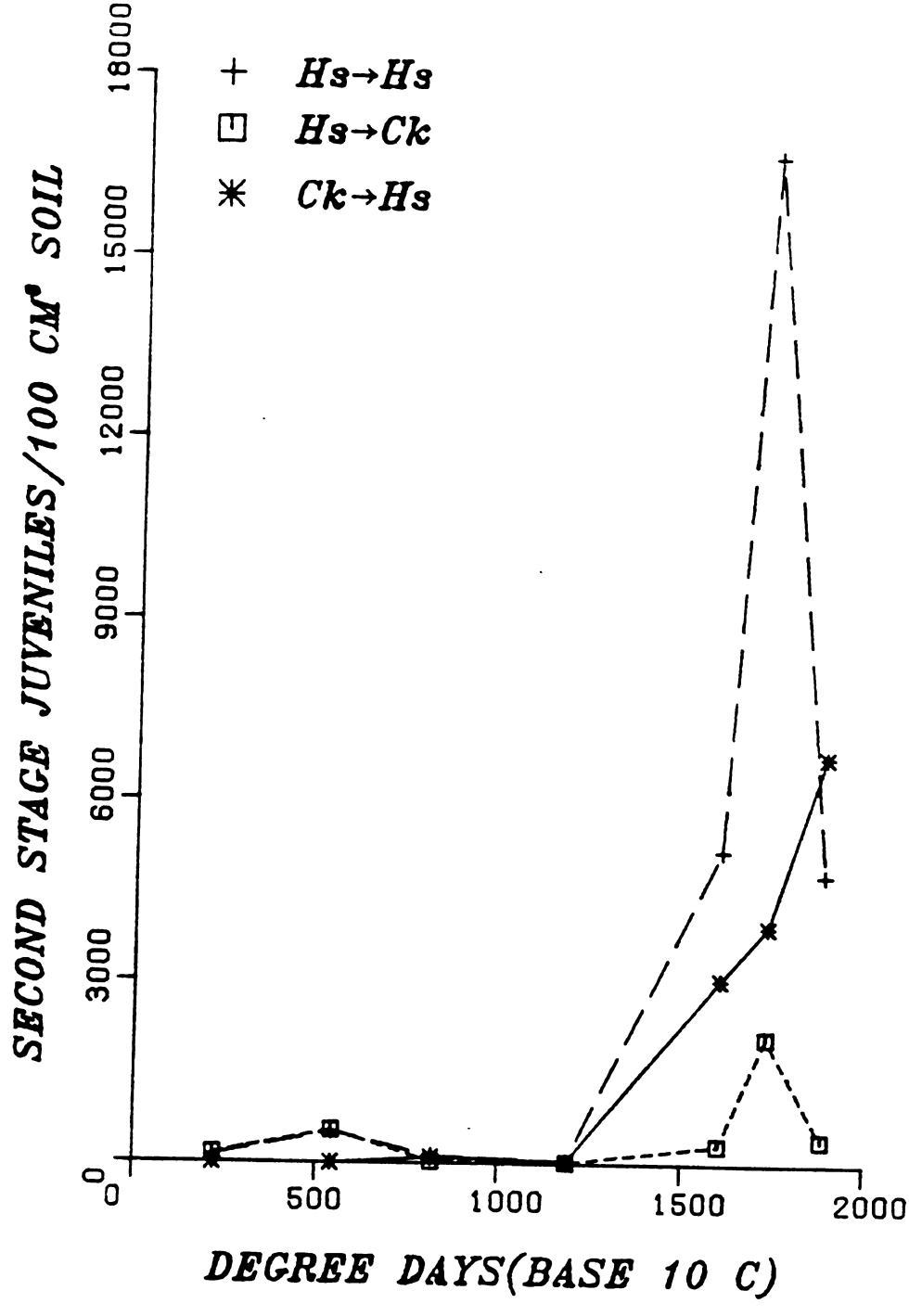

Fig. 28. Number of H. schachtii second stage juveniles in 100 cm^3 soil surrounding cabbage grown in the presence and absence of H. schachtii for a period of 1900 DD_{10}.

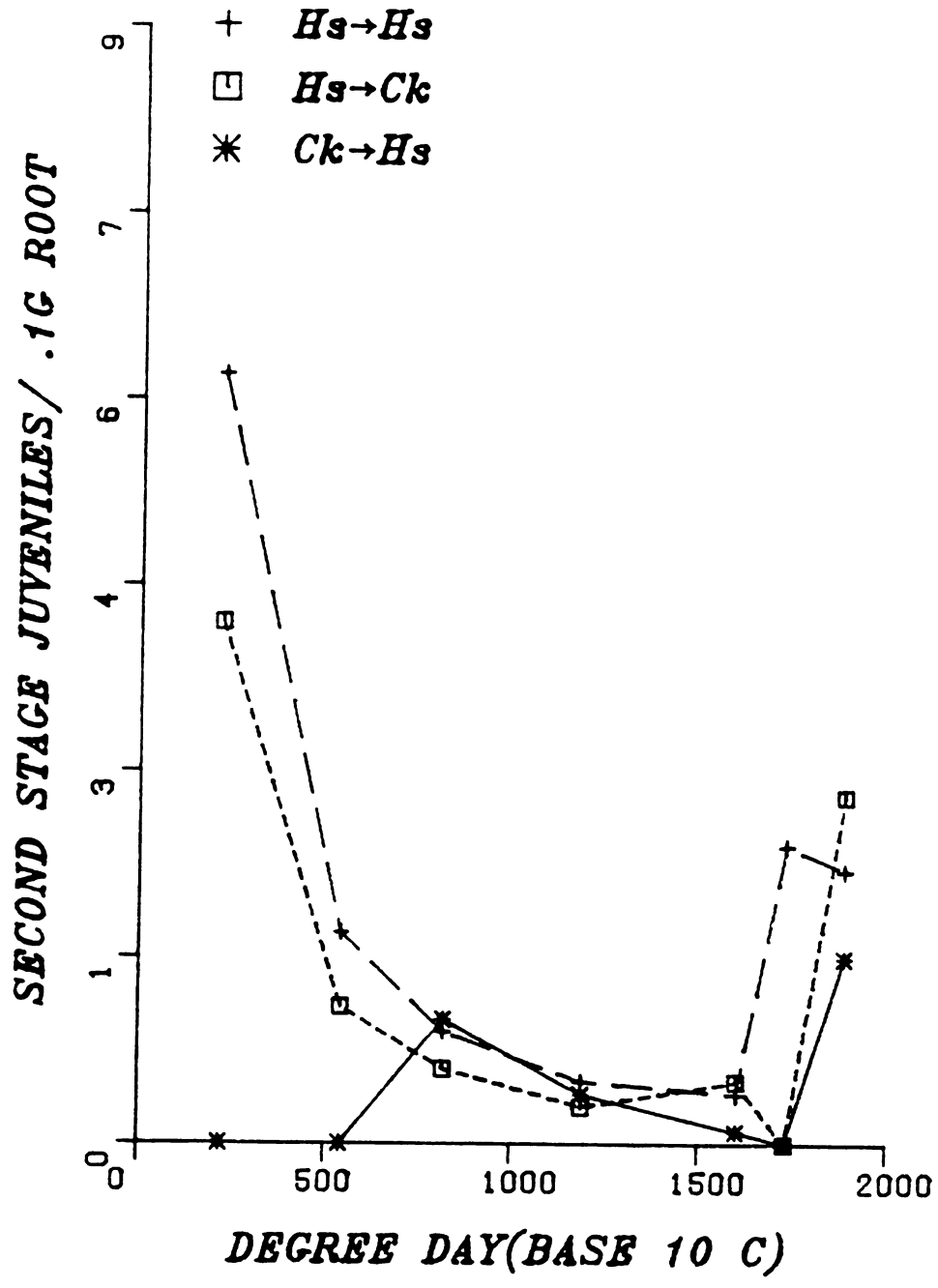

Fig. 29. Number of H. schachtii second stage juveniles in 0.1 gram roots of cabbage grown in the presence and absence of H. schachtii for a period of about 1900 DD_{10}.

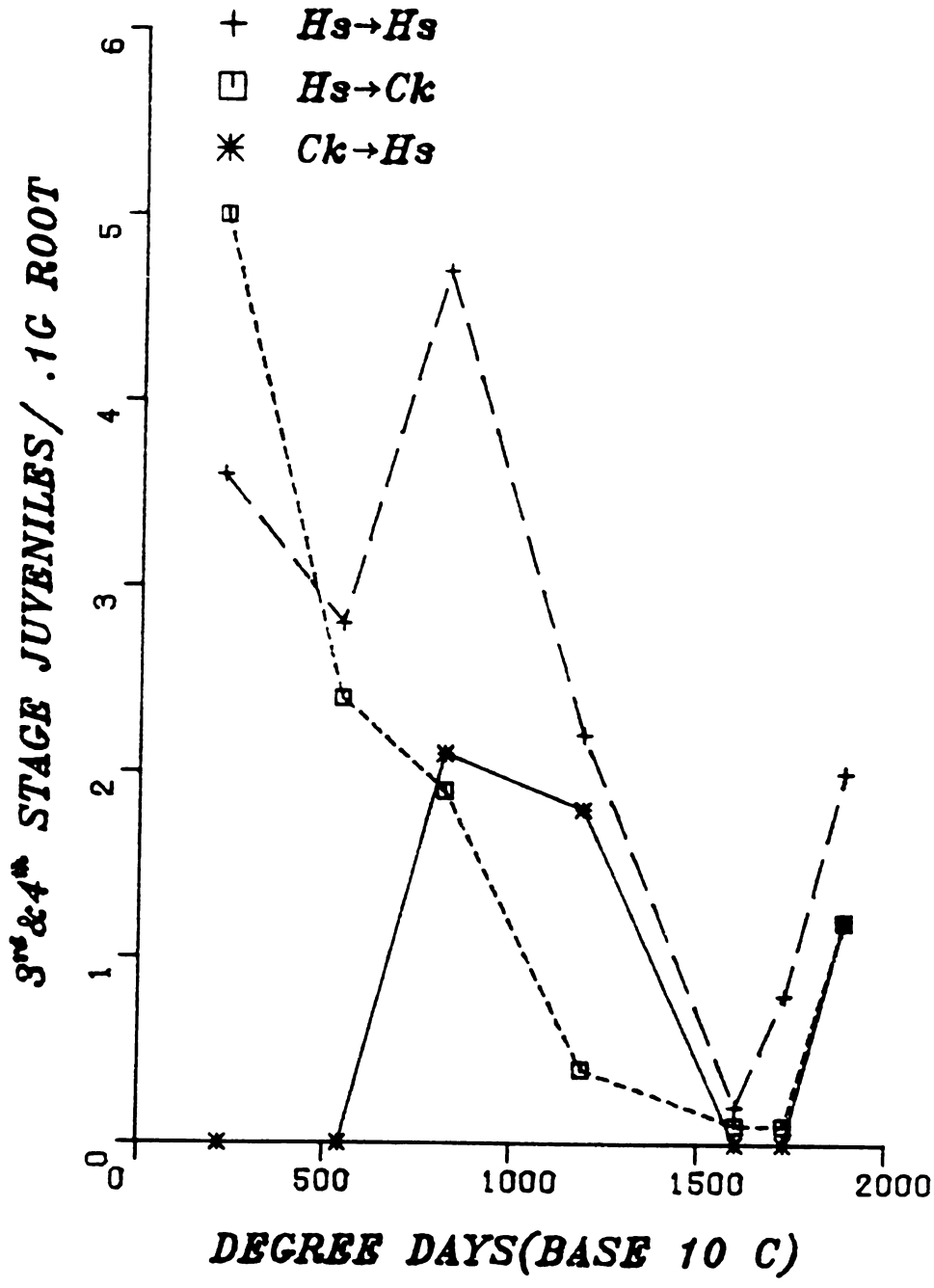

Fig. 30. Number of H. schachtii third and fourth stage juveniles in 0.1 gram roots of cabbage grown in the presence and absence of H. schachtii for a period of 1900 DD_{10}.

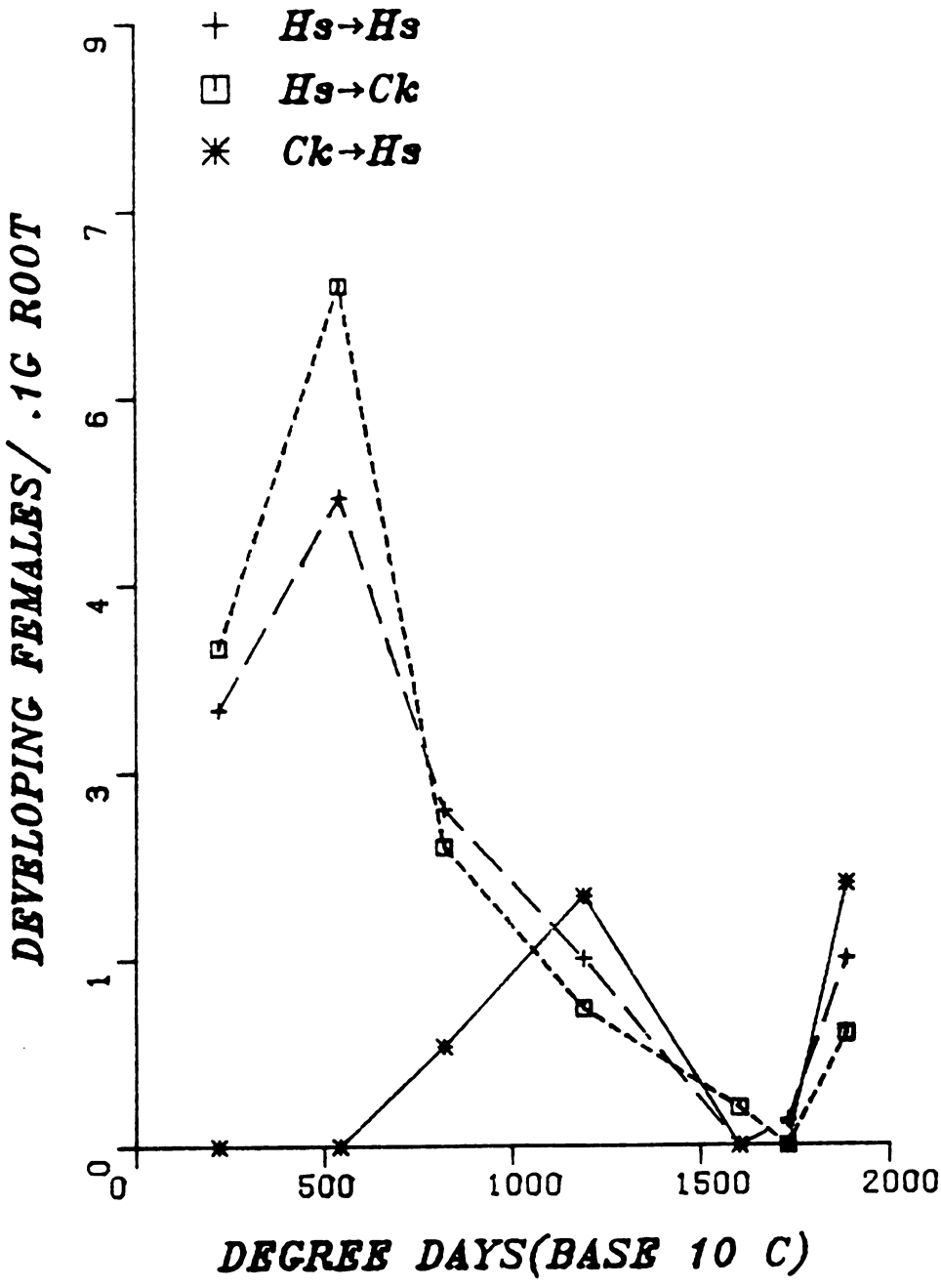

Fig. 31. Number of H. schachtii developing females in 0.1 gram roots of cabbage grown in the presence and absence of H. schachtii for a period of 1900 DD_{10}.

(Figure 31). Adult males peaked after an accumulation of 540, 1180, and 1730 DD_{10} (Figure 32). Females with eggs have three peaks (Figure 33). The peaks follow accumulations of 540, 1180, and 1730 DD_{10}.

3.3.4 Discussion

H. schachtii greatly retarded cabbage growth by mechanically and chemically disrupting feeder roots and vascular parenchyma, and directly feeding on the nutrients of the cabbage. This reduces yield by as much as 70%. Retarded cabbage growth by H. schachtii also occurs in New York, California, Canada, and Europe (Abawi and Mai, 1980; Abawi and Mai, 1977; Brzeski, 1969; Mai and Abawi, 1980; Olthof et al., 1974, Radewald et al., 1971).

Cabbage growth appears to have been greatly hampered by the containers used at the beginning of the season. The paper cups in which the cabbage was seeded were too small for four-week-old plants. Seedlings generally have a shoot weight of 10 grams after four weeks but in this experiment, four-week-old seedlings had a shoot weight of less than a gram.

At the end of the season, cabbage plants transplanted to infested soil had higher (P=0.05) populations of H. schachtii. This also occurs in New York (Abawi and Mai, 1980). The number of nematodes that will penetrate roots is related to the amount of root tissue at transplanting (Webster, 1972). Greater root tissue per nematode allows more penetration and development of nematodes. When infected cabbage was transplanted to uninfested soil, the nematode population experienced a transplant shock, and in some of the plants the nematodes died. Death could have resulted from partial dehydration in the roots while the roots were developing new root hairs. For these plants, yield increased by 20%.

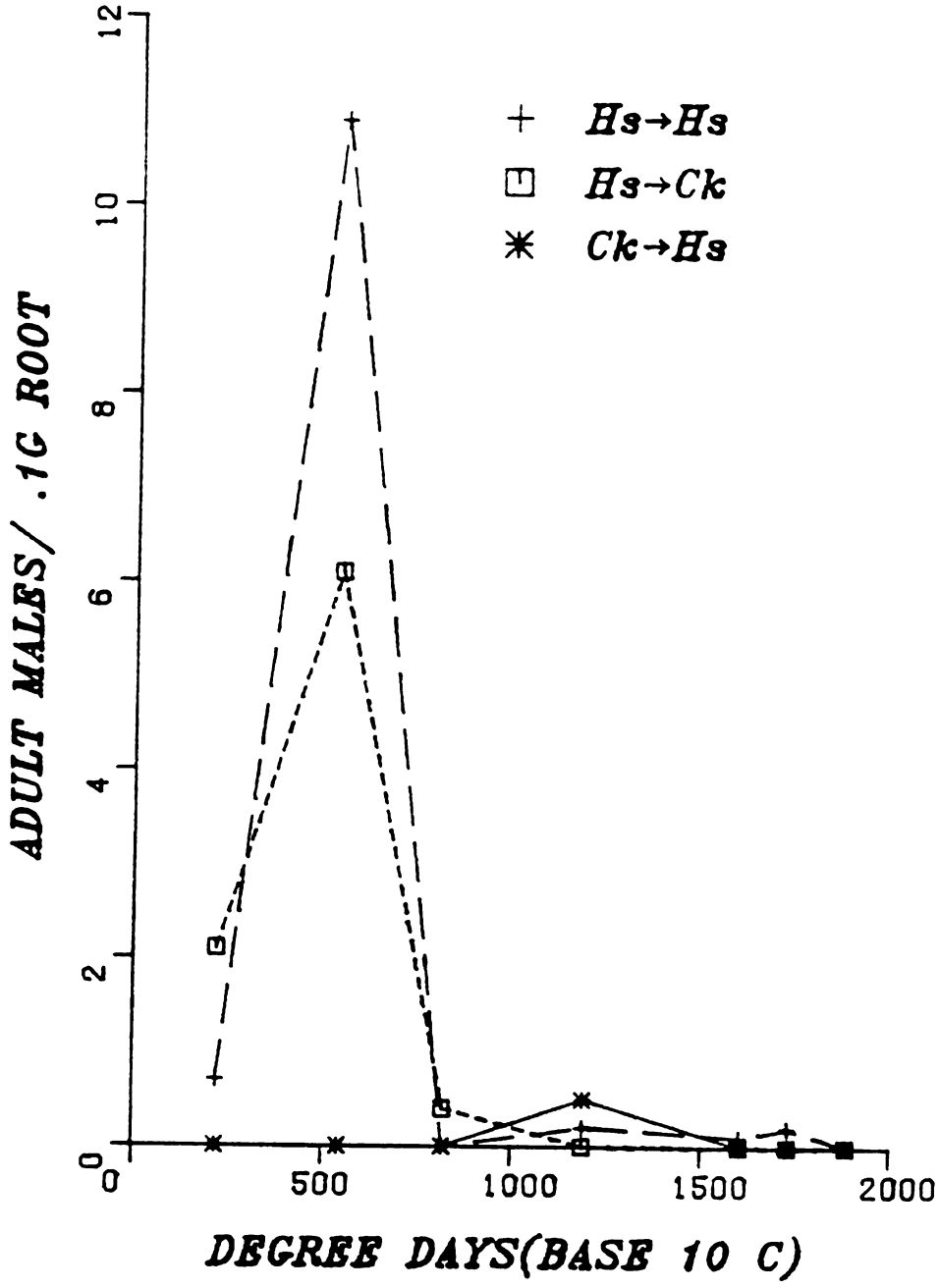

Fig. 32. Number of H. schachtii adult males in 0.1 gram roots of cabbage grown in the presence and absence of H. schachtii for a period of 1900 DD_{10}.

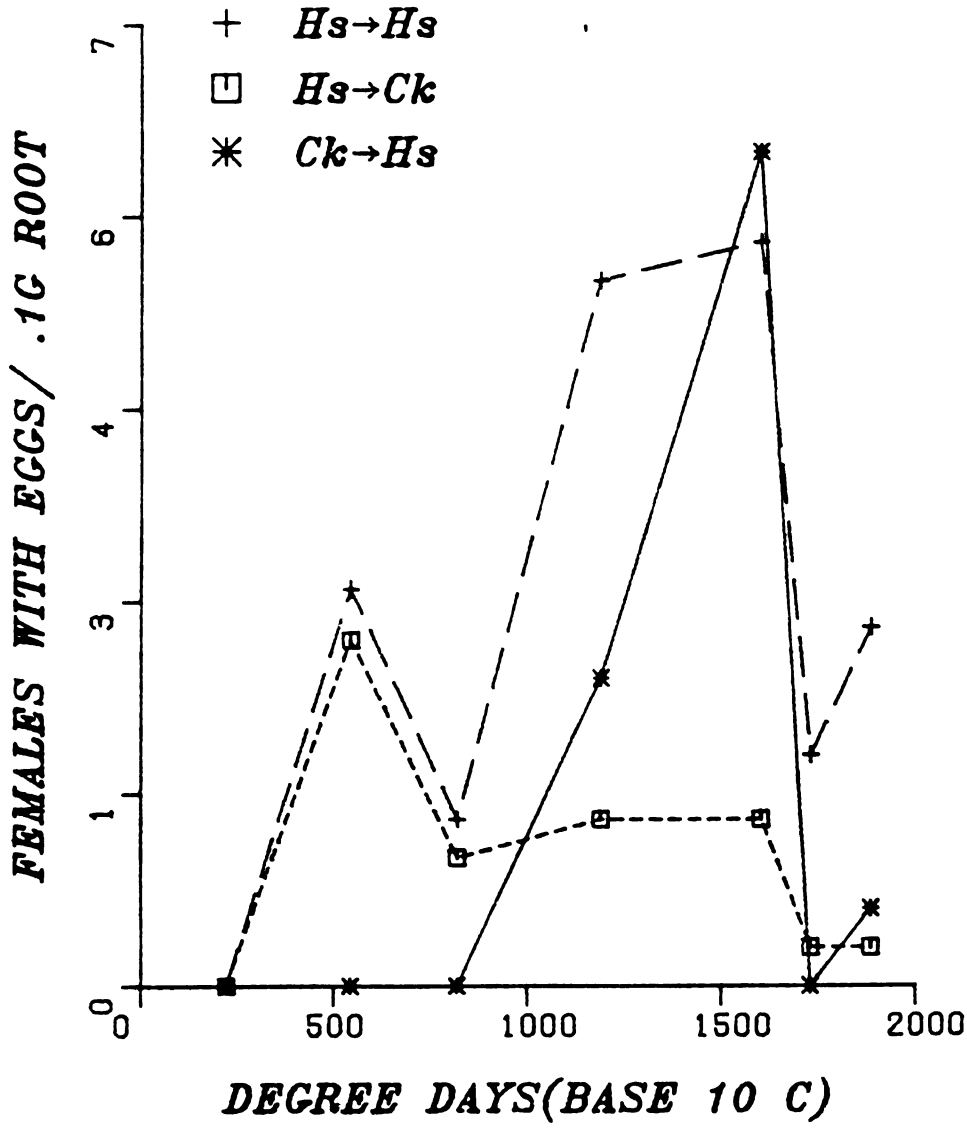

Fig. 33. Number of H. schachtii females with eggs of 0.1 gram roots of cabbage grown in the presence and absence of H. schachtii for a period of 1900 DD_{10}.

Therefore, it may be better to transplant infected seedlings to uninfested soil rather than transplanting uninfected seedlings to infested soil. It is also apparent that to avoid economic yield losses, cabbage seedlings will have to be protected from H. schachtii for a period greater than four weeks.

H. schachtii had a $P_{midseason}/P_{initial}$ of 27 and $P_{final}/P_{initial}$ of 14 in some treatments, suggesting that B. oleracea capitata (cv Roundup) is a very susceptible host to H. schachtii. Therefore, this variety should not be grown in fields infested by high populations of H. schachtii. The high fecundity of this nematode appears to enhance its pathogenicity.

In Michigan, H. schachtii completed three generations. Under ideal conditions, H. schachtii can have 3 to 5 generations (Thomason and Fife, 1962). The number of generations per season is controlled mainly by DD_{10} accumulated. In California the first, second, and third generations required 320, 396, and 349 DD_{10} (Thomason and Fife, 1962), but if plants were seeded in September when the soil temperature fell low enough for nematode activity, then 502 DD_{10} were required to complete the first generation (Thomason and Fife, 1962). Apparently at both ends of the temperature range, the response of the nematode to temperature was distorted, and one degree day was not as effective in promoting growth as in the optimal range (Thomason and Fife, 1962). Since more degree days are required in Michigan for completion of a generation, it can be asserted that Michigan summer temperatures deviate more from H. schachtii optimal temperature range than do California summer temperatures.

3.4 COMPARISON OF MICHIGAN AND NEW YORK H. SCHACHTII PATHOGENICITY ON CABBAGE

3.4.1 Introduction

Pathogenicity of nematodes is a function of many variables of which the environment is one (Ferris, 1981). The environment can be subdivided into: (a) physiographic and soil textural conditions and (b) temperature conditions as influenced by location and planting date (Ferris, 1981). Soil temperatures are very important in the reproduction of H. schachtii. In the Imperial Valley of southern California, H. schachtii can complete 5 generations during the growing season, compared with one to three generations in more temperate areas like England (Cooke and Thomason, 1979). H. schachtii is more pathogenic in areas where it can reproduce well.

Michigan State University and Cornell University have joint nematode projects because these universities are under similar climatic conditions. To interpret data correctly from these two stations, it is essential to know whether there are any other factors that might influence pathogenicity differently other than the environment. Graney (1983) noted differences between Michigan cysts and New York cysts (personal communication). These differences might be a result of inherent genetic differences.

The objective of this study was to determine whether the pathogenicity of Michigan H. schachtii was different from that of New York H. schachtii when the two are subjected to similar environmental conditions. In addition to this objective, it was of interest to determine whether the nematode life cycle was similar for the two populations.

3.4.2 Methods and Materials

B. oleracea capitata (cv Roundup) was direct seeded in 10 cm clay pots on October 7, 1983, in a greenhouse with day and night temperatures of 27°C and 22°C, respectively. The pots were first filled with certain proportions of steamed sandy clay loam soil mixed with soil containing H. schachtii cysts so that the initial population density (P_i) would be 20 eggs and second stage juveniles per cm^3 of soil. The soil was mixed with a cement mixer. Some of the cysts were obtained in Michigan and some from New York. Michigan H. schachtii was cultured in the greenhouse in wooden culture boxes 1.5 m long, 1.0 m wide, and 0.3 m deep. The culture boxes were first filled with sandy-clay loam soil containing H. schachtii cysts and then B. oleracea capitata (cv. King Cole) seedlings were transplanted into the culture box. The culture box was maintained for about 4 months before use. The culture contained about 100 cysts in 100 cm^3 of soil. Each cyst was estimated to have ca 200 eggs and second stage juveniles. New York H. schachtii were posted to Michigan State Univ. in a clay pot of 10 cm diameter. New York H. schachtii were cultured on sandy loam soil in which table beets were seeded. The culture contained about 200 cysts in 100 cm^3 of soil. Each cyst was estimated to have ca 200 eggs and second stage juveniles. New York H. schachtii were stored in a cooler for about 1 month before they were used.

Pots were arranged in a completely randomized block design with 3 treatments and 5 replications for each treatment. The treatments received 20-20-20 fertilizer at 30 kg/ha on the seeding date. The seeds were watered daily until the seedlings were fully established. Emergence occurred as early as 4 days after seeding.

Plants were sampled on week 2, 4, 6, and 8 after seeding. On each sampling date, the following parameters were evaluated:

(1) Fresh weights of shoot and root systems were obtained by direct weighing.

(2) About 0.1 gram of the root system was stained in a solution of lactophenol with 0.01% acid fuchsin, to enumerate second stage juveniles, third and fourth stages juveniles, developing females, adult males, and females with eggs in the root system.

(3) Soil, 100 cm^3, was processed using the centrifugation-flotation technique to determine the number of cysts, second stage juveniles, eggs, and adult males.

3.4.3 Results

Both Michigan H. schachtii and New York H. schachtii reduced (P=0.05) cabbage shoot weight (Figure 34) and root weight (Figure 35). No difference in pathogenicity between Michigan (Hs) and New York (Hs) was observed. At the end of week 8, Michigan (Hs) and New York (Hs) reduced cabbage shoot weight by 38% and 40%, respectively.

The number of cysts in the soil from Michigan (Hs) and New York (Hs) was different (P=0.05) at the end of the growing period. Soil with Michigan (Hs) had 2.6 times more cysts (Figure 36). Eggs in the soil (Figure 37) and second stage juveniles in the soil (Figure 38), had a similar trend to that of cysts in the soil.

Second stage juveniles in the roots had a different trend (Figure 39). There was no significant difference (P=0.05) of second stage juveniles in the roots between Michigan (Hs) and New York (Hs). In both cases, second stage juveniles in the roots peaked in week 2 and 8. Third and fourth stage juveniles in the roots had a similar trend to second stage juveniles in the roots (Figure 40).

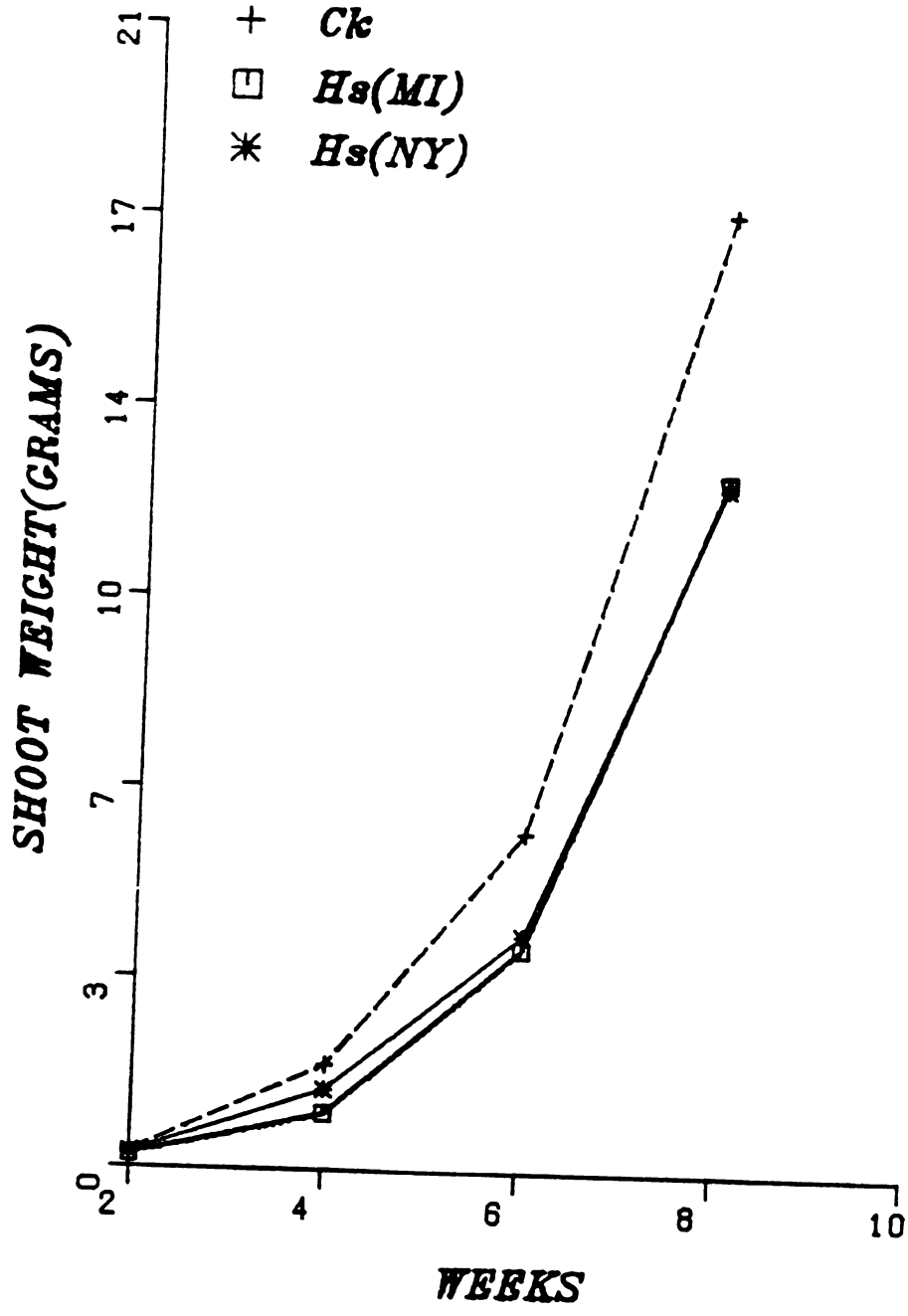

Fig. 34. Fresh shoot weight of cabbage grown in the presence and absence of Michigan H. schachtii (Hs(MI)) and New York H. schachtii (Hs(NY)) for a period of 8 weeks.

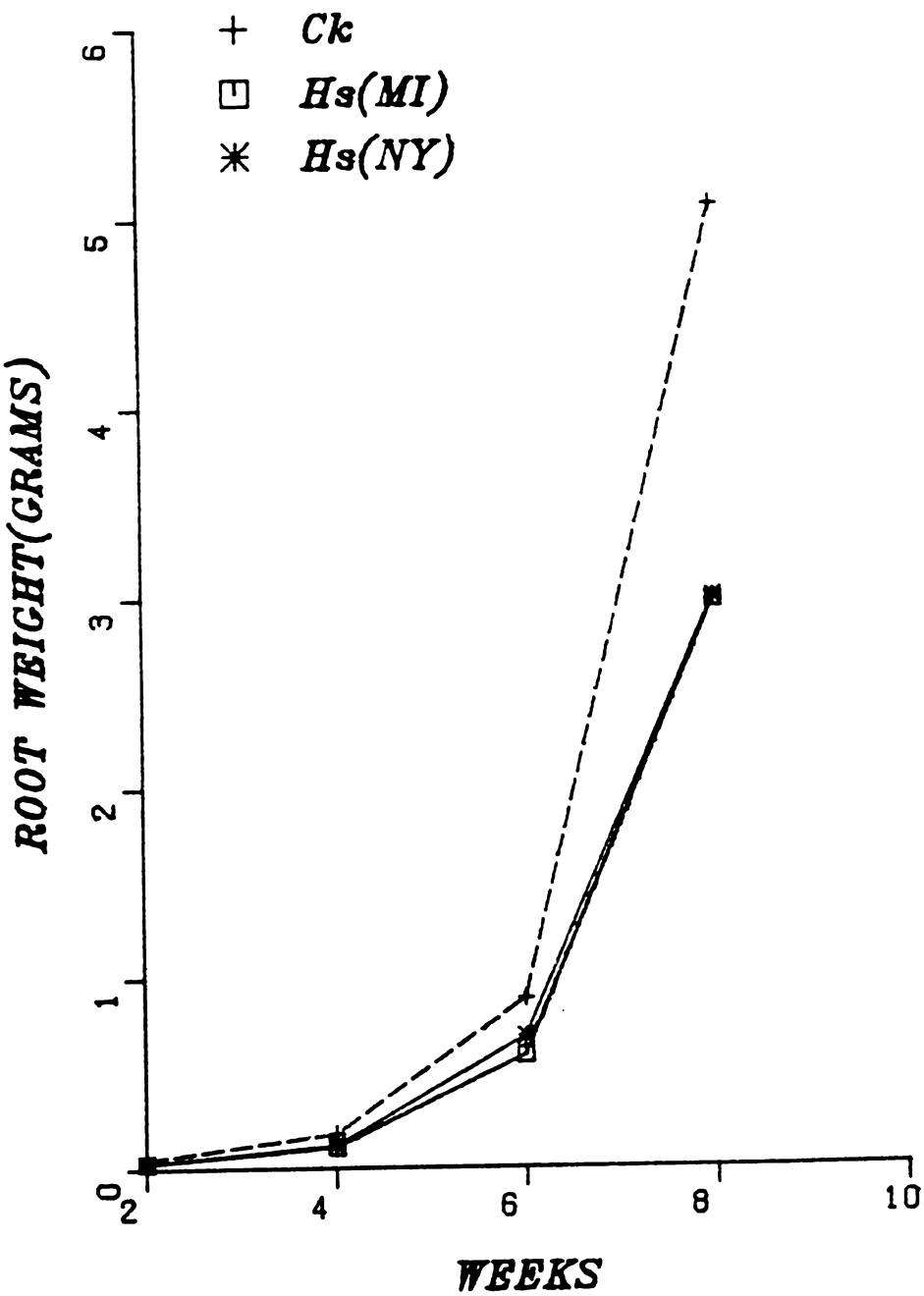

Fig. 35. Fresh root weight of cabbage grown in the presence and absence of Michigan H. schachtii (Hs(MI)) and New York H. schachtii (Hs(NY)) for a period of 8 weeks.

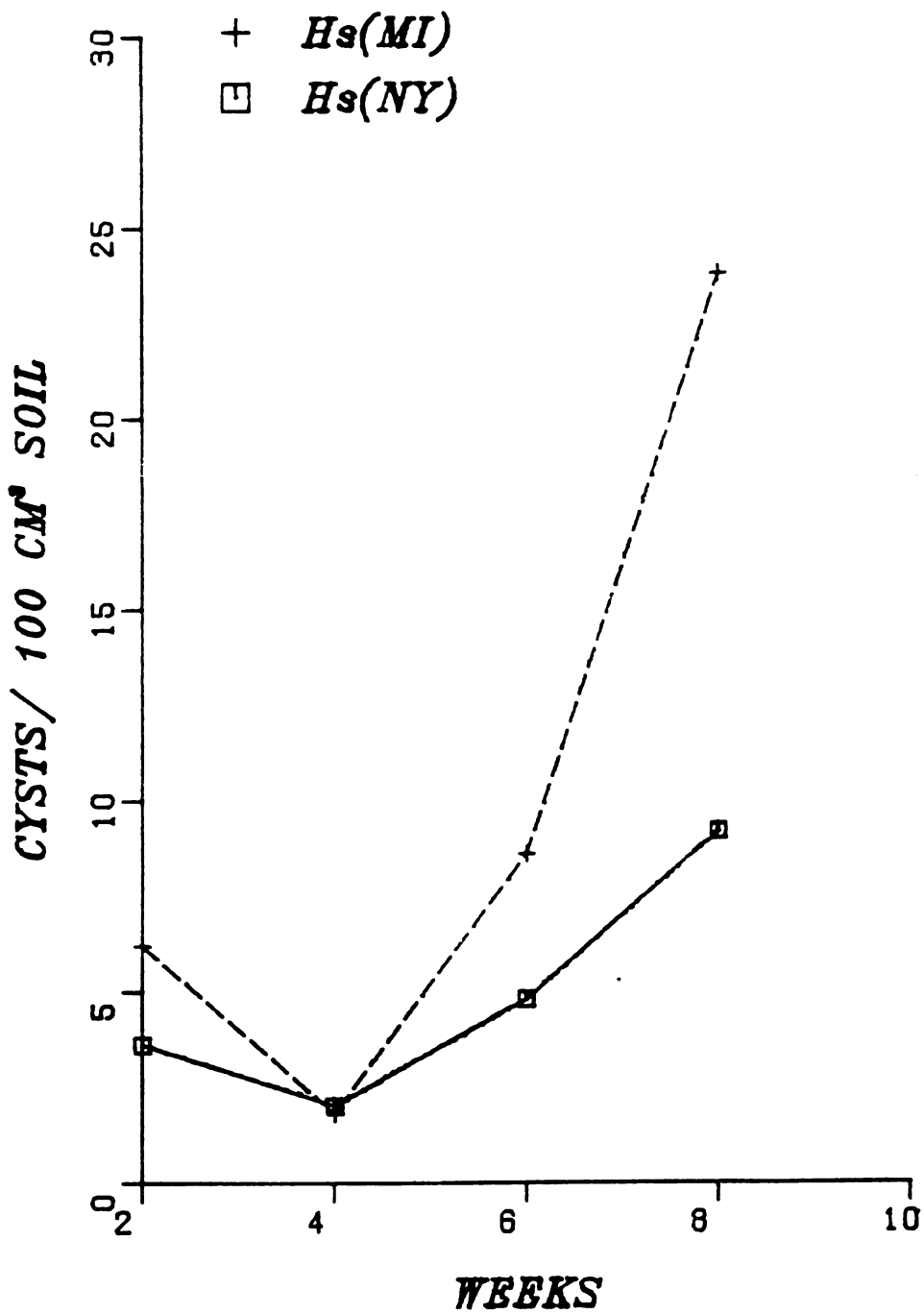

Fig. 36. Number of H. schachtii cysts in 100 cm^3 soil surrounding cabbage grown in the presence of Michigan H. schachtii (Hs(MI)) and New York H. schachtii (Hs(NY)) for a period of 8 weeks.

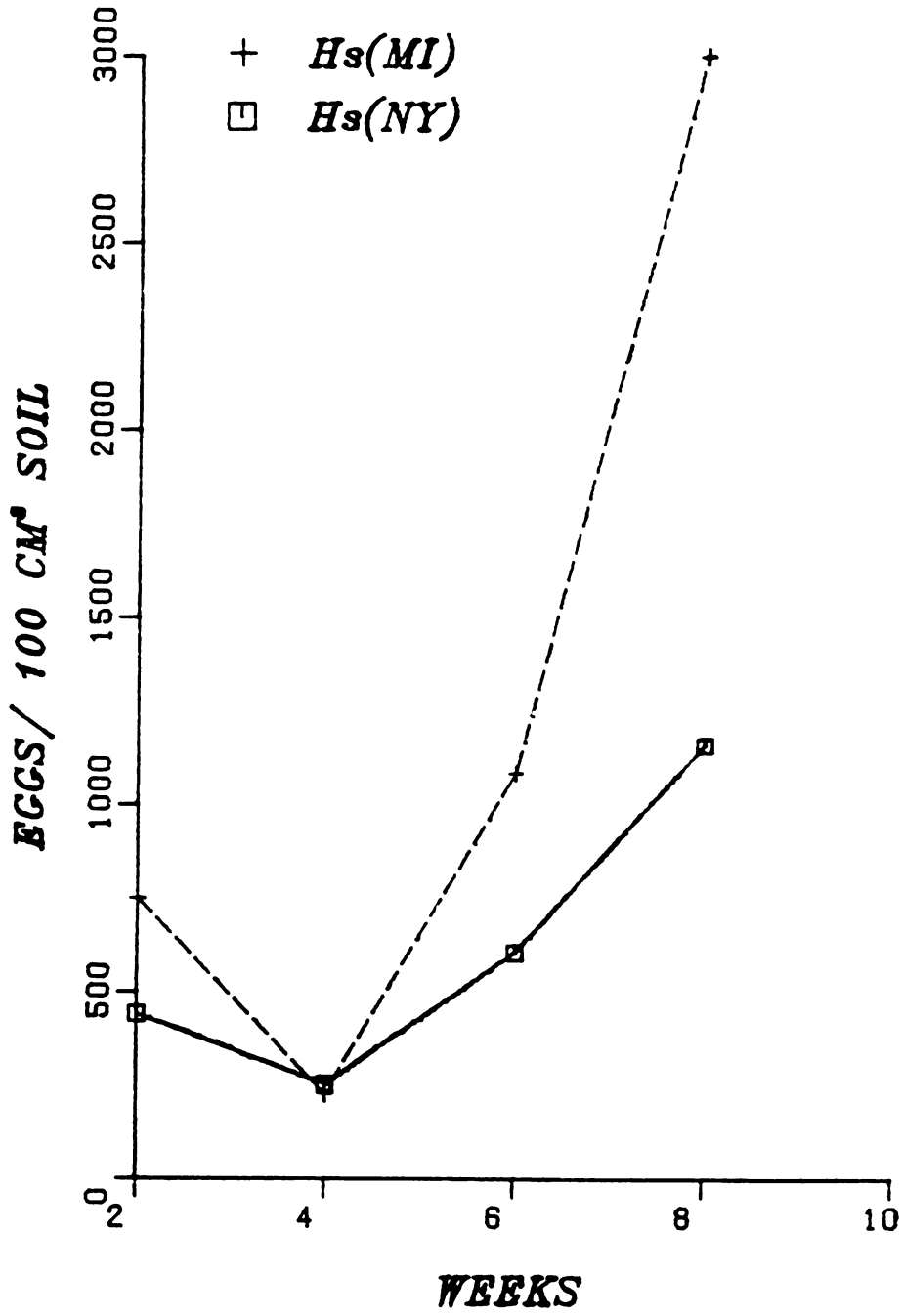

Fig. 37. Number of H. schachtii eggs in 100 cm^3 soil surrounding cabbage grown in the presence of Michigan H. schachtii (Hs(MI)) and New York H. schachtii (Hs(NY)) for a period of 8 weeks.

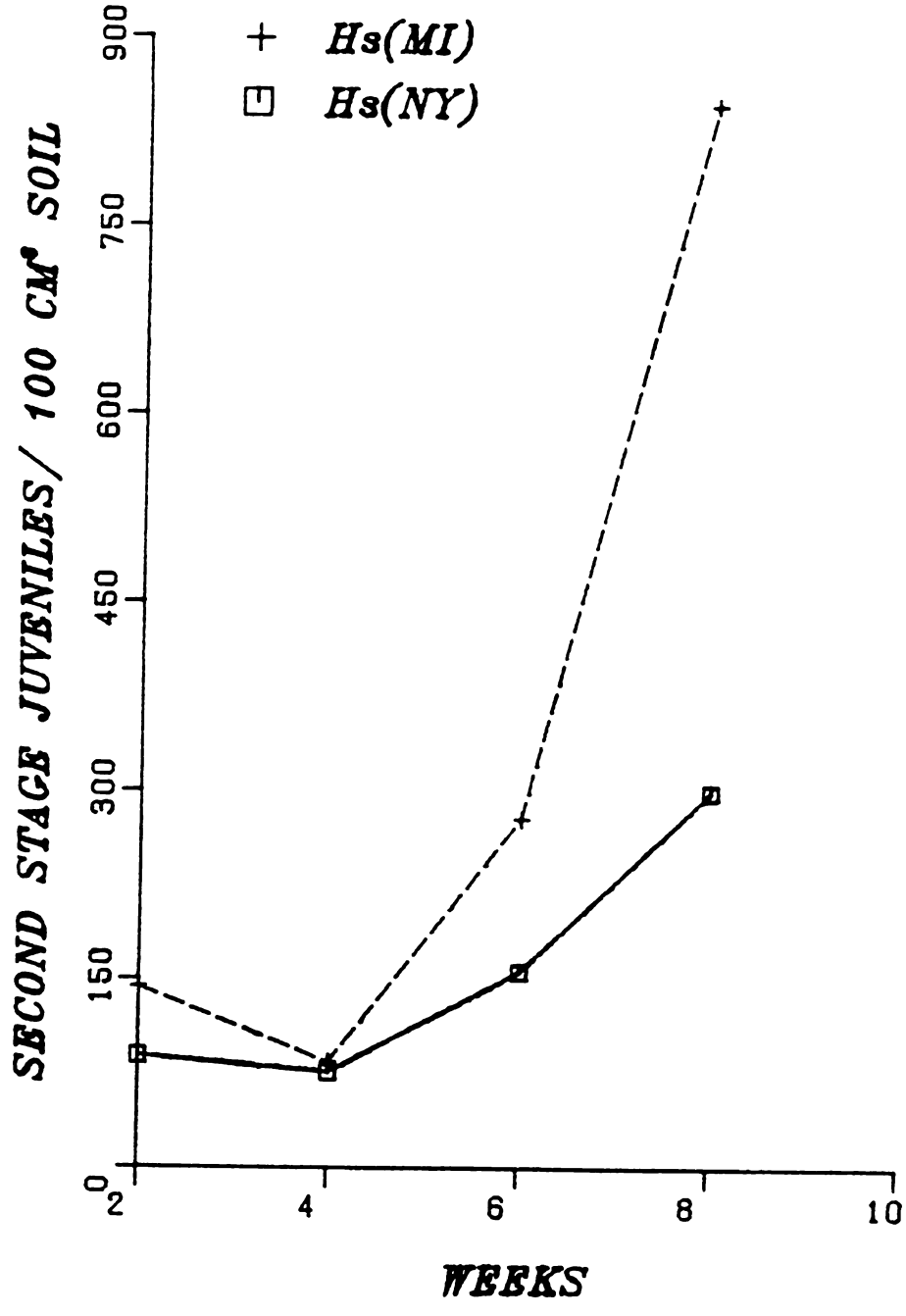

Fig. 38. Number of H. schachtii second stage juveniles in 100 cm^3 soil surrounding cabbage grown in the presence of Michigan H. schachtii (Hs(MI)) and New York H. schachtii (Hs(NY)) for a period of 8 weeks.

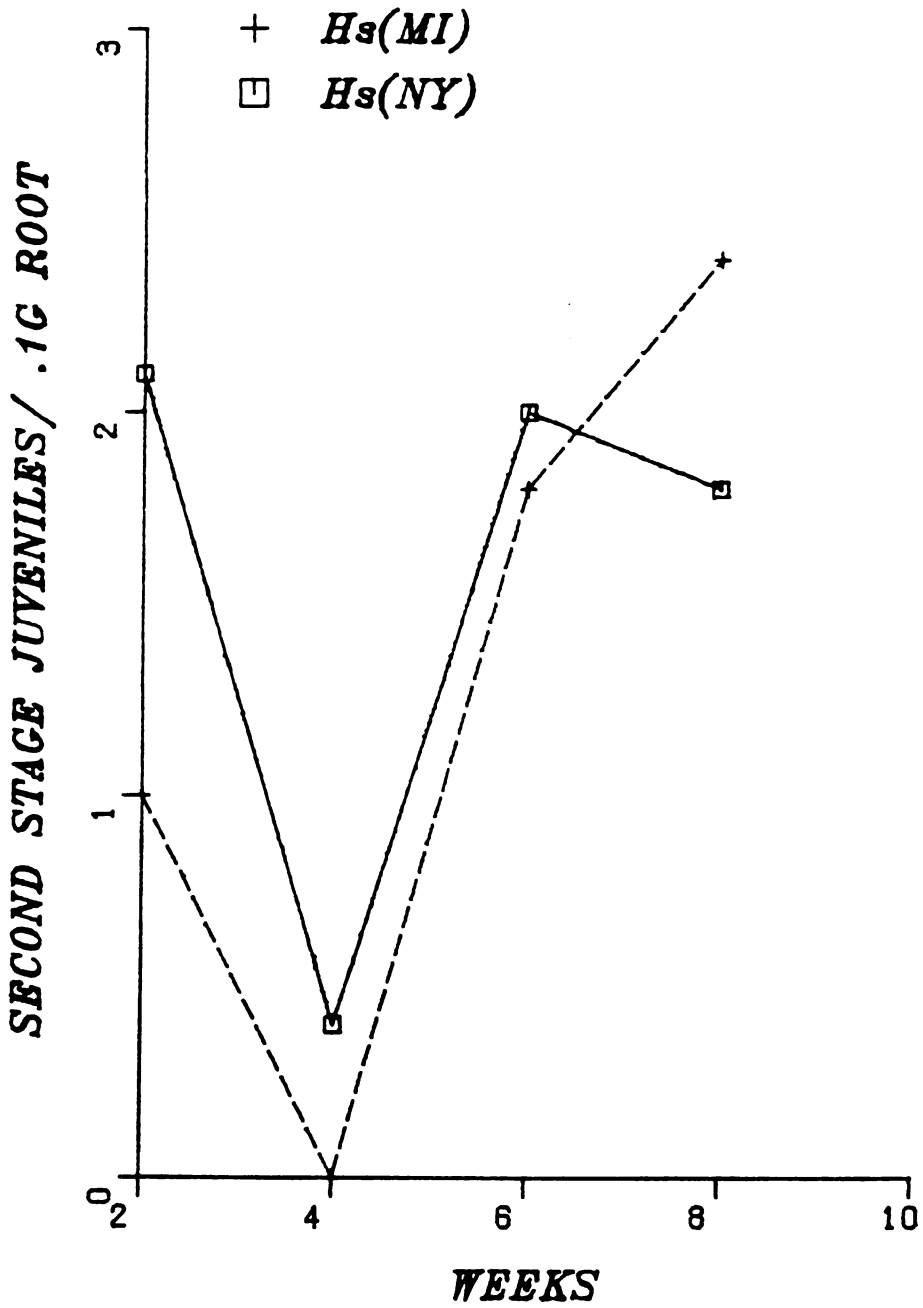

Fig. 39. Number of H. schachtii second stage juveniles in 0.1 gram roots of cabbage grown in the presence of Michigan H. schachtii and New York H. schachtii for a period of 8 weeks.

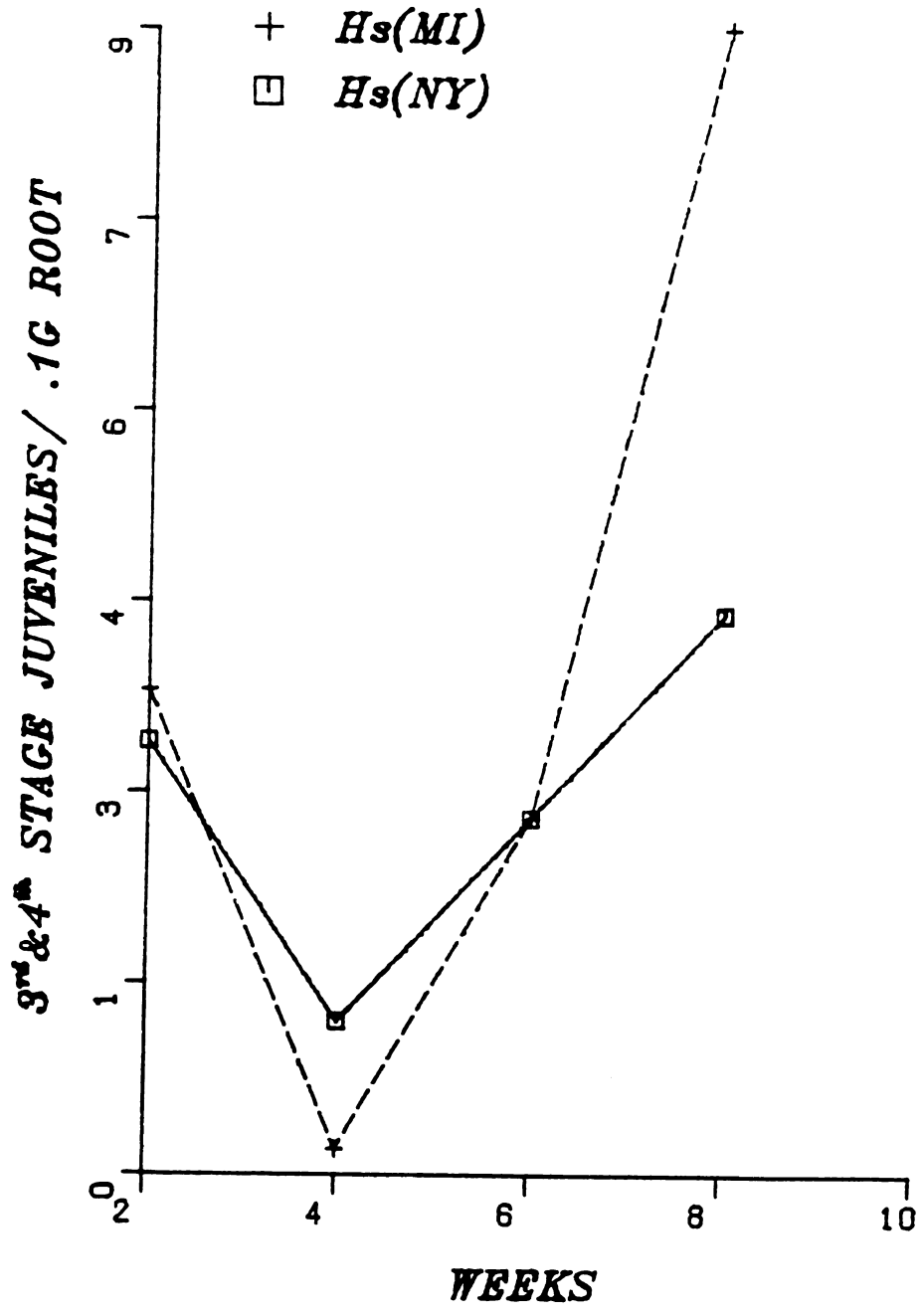

Fig. 40. Number of H. schachtii third and fourth stage juveniles in 0.1 gram roots of cabbage grown in the presence of Michigan H. schachtii and New York H. schachtii for a period of 8 weeks.

Developing females in the roots had a different trend (Figure 41), which only peaked in week 6. There is no significant difference (P=0.05) between Michigan and New York (Hs) developing females in the roots. Adult males in the roots had a completely different trend (Figure 42), with peaks in weeks 4 and 6 for Michigan and New York (Hs), respectively. There is a significant difference (P=0.05) in adult males in the roots between Michigan and New York (Hs). Females with eggs in the roots had a different trend (Figure 43) with only one peak in week 8. Number of females with eggs did not differ significantly (P=0.05) between Michigan and New York (Hs).

3.4.4 Discussion

Pathogenicity of Michigan and New York (Hs) has been reported in the literature (Abawi and Mai, 1980; Mai and Abawi, 1980; Muchena and Bird, 1983). H. schachtii greatly retards cabbage growth by mechanically damaging feeder roots and vascular parenchyma, and directly feeding on the nutrients of the cabbage. Comparisons of H. schachtii pathogenicity data on cabbage obtained in Michigan and New York show no significant difference at P=0.05 (unpublished). The similarity in pathogenicity enables Michigan research on H. schachtii to be replicated or validated by New York researchers.

Michigan H. schachtii appears to have a higher fecundity rate than New York (Hs). Difference in fecundity appears to be a result of different mortality rates of developing juveniles within the root system. Slightly fewer third and fourth stage juveniles, developing females, and females with eggs were in roots with New York (Hs). Probably New York (Hs) requires slightly more living space than Michgian (Hs). Also the difference might be accounted for by the storage

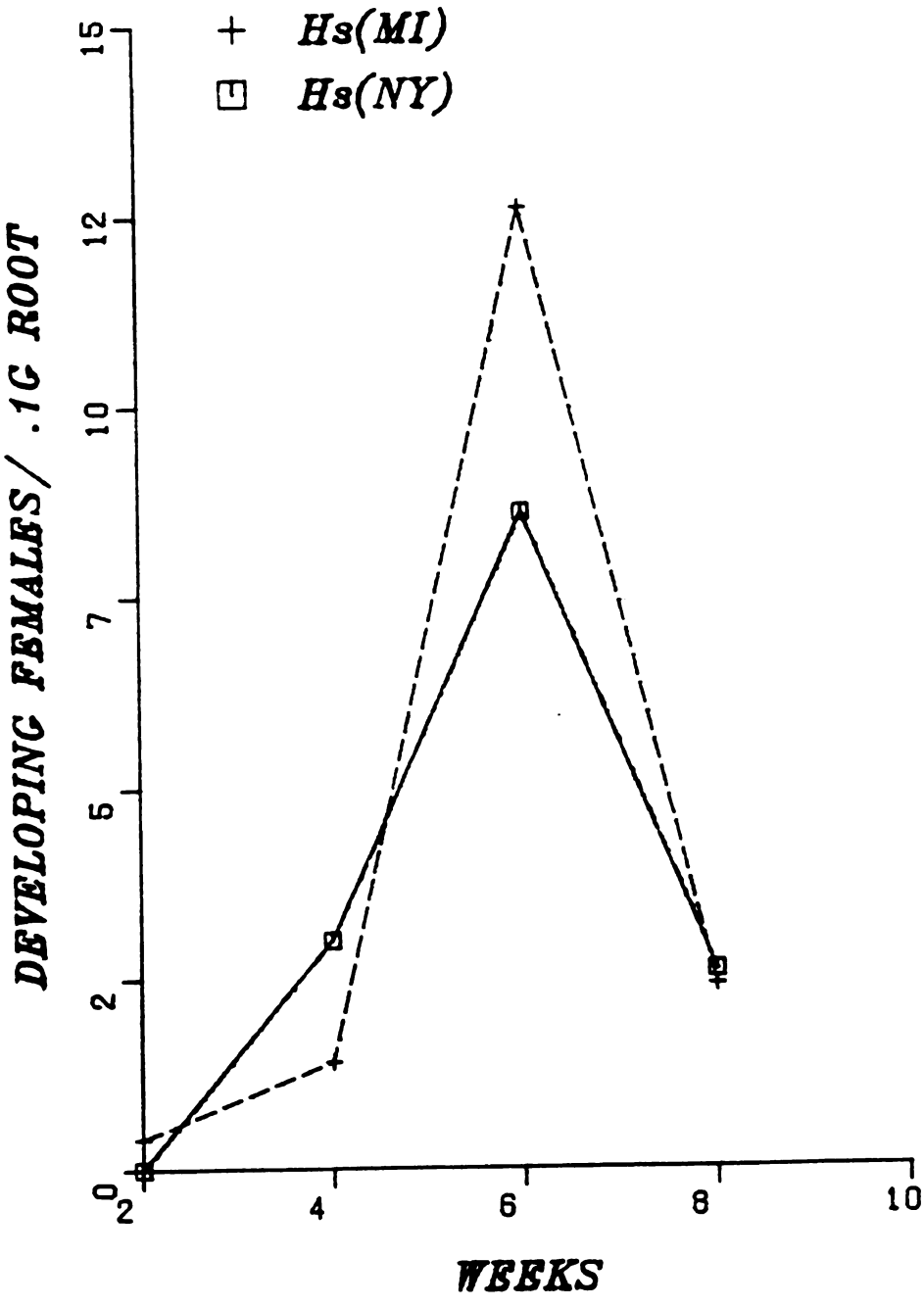

Fig. 41. Number of H. schachtii developing females in 0.1 gram roots of cabbage grown in the presence of Michigan H. schachtii and New York H. schachtii for a period of 8 weeks.

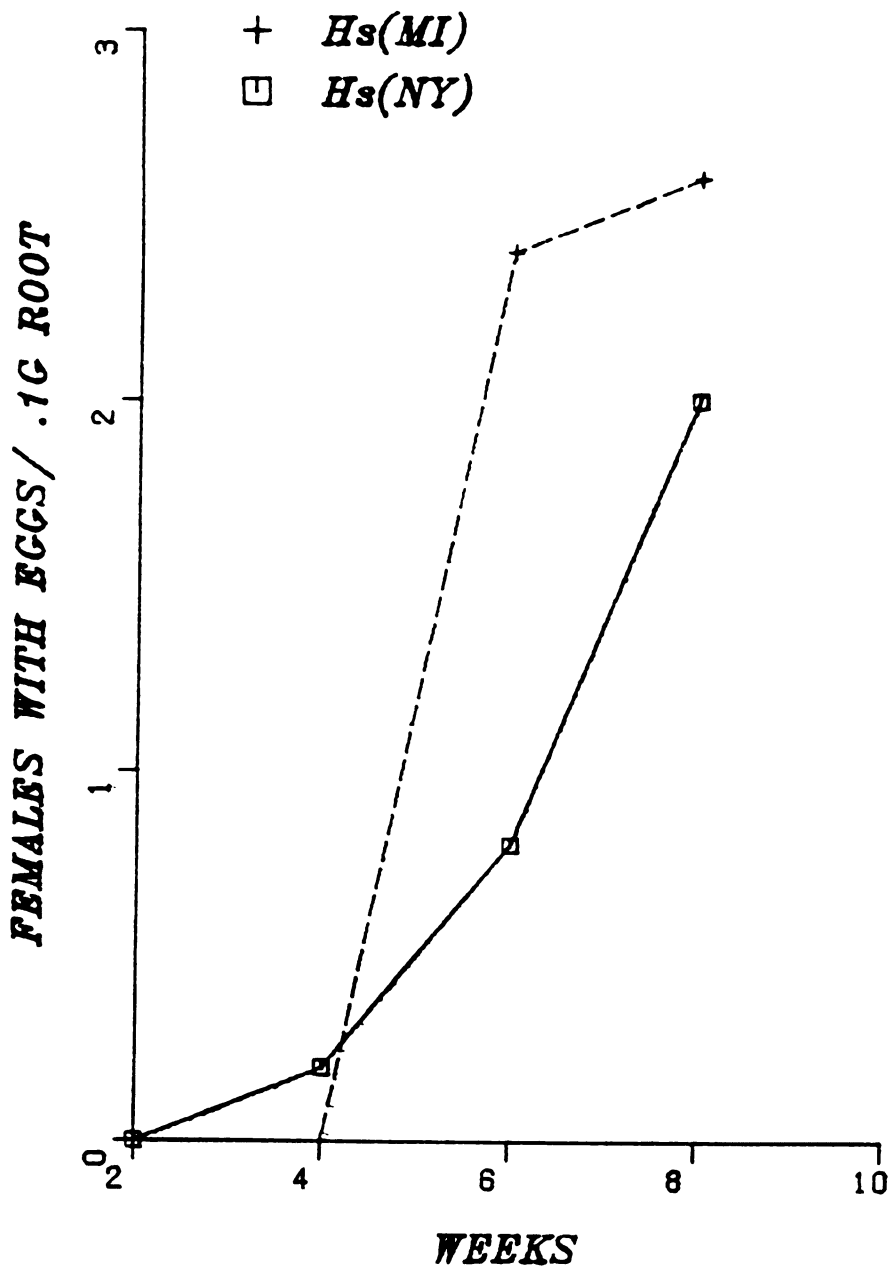

Fig. 43. Number of H. schachtii females with eggs in 0.1 gram roots of cabbage grown in the presence of Michigan H. schachtii and New York H. schachtii for a period of 8 weeks.

of New York (Hs) in a cooler for about a month. The later seem very unlikely because both Michigan (Hs) and New York (Hs) had similar pathogenicity on cabbage.

3.5 INFLUENCE OF PHENAMIPHOS ON CABBAGE SEED EMERGENCE

3.5.1 Introduction

Phenamiphos is generally not phytotoxic when used at low concentrations (Wright, 1981). At high concentrations, phenamiphos is phytotoxic and can inhibit seed emergence (Griffin, 1975). Research of this nature helps in the design of good management tactics and as a guideline for pesticide producers.

The specific objective of this study was to determine the relationships between different rates of phenamiphos application and cabbage seed germination.

3.5.2 Methods

Pre-germinated B. oleracea capitata (cv King Cole) seeds were seeded in 20 cm diameter clay pots on November 1, 1982, in a greenhouse with day and night temperatures of 27°C and 22°C, respectively. The pots were first filled with steamed sandy-clay loam greenhouse soil.

Pots were arranged in a completely randomized block design with 8 treatments and 12 replications. The treatments received 20-20-20 fertilizer at 30 kg/ha on the seeding day. Phenamiphos was applied at a rate of 0, 2.4, 3.6, 4.8, 6.0, 7.2, 9.6, and 14.4 kg ai/ha for treatments 1, 2, 3, 4, 5, 6, 7, and 8, respectively. The seeds were watered daily. Emergence occured as early as 4 days but all the treatments were assessed for emergence after 14 days.

3.5.3 Results

Emergence loss was assessed by noting pots in which the seed did not emerge. The sum of the non-emerged seeds was expressed as a percentage for each treatment. The highest concentration of phenamiphos had the lowest seed emergence (Table 2). Emergence loss ranged from 0% to 50%. There is a high correlation (R^2=.9078) between phenamiphos concentration and cabbage seed loss of emergence (Figure 44).

3.5.4 Discussion

There is a specific relation between the concentration of phenamiphos and cabbage seed loss of emergence. At recommended rates (3-6 kg ai/ha) for H. schachtii control in the fields, phytotoxicity of phenamiphos is minimal. But if higher rates (6-7.2 kg ai/ha) are applied, loss in cabbage seed emergence is up to 33%. A loss of 1/3 of the crop may be unacceptable to most growers. Rates of 9.6 kg ai/ha and 14.4 kg ai/ha were just for experimental purposes because they are above recommended guidelines for phenamiphos application on cabbage.

The phytotoxicity detected using pots might not be detected in the field at equivalent rates. Confinement in the pots might have increased phytotoxicity. Conversely, daily watering might have flushed out most of the pesticide such that the reported phytotoxicity is an underestimate under field conditions. Preliminary research under field conditions favors the latter idea (unpublished). Phytotoxicity was higher when compounded with moisture stress and other unfavorable environmental conditions.

Table 2. Emergence loss of cabbage seeds grown in clay pots in the presence of phenamiphos.

Phenamiphos rate (kg ai/ha)	Number of seeds which did not emerge out of 12	% emergence loss
0	0	0
2.4	1	8.3
3.6	1	8.3
4.8	1	8.3
6.0	2	16.7
7.2	4	33.3
9.6	5	41.7
14.4	6	50.0

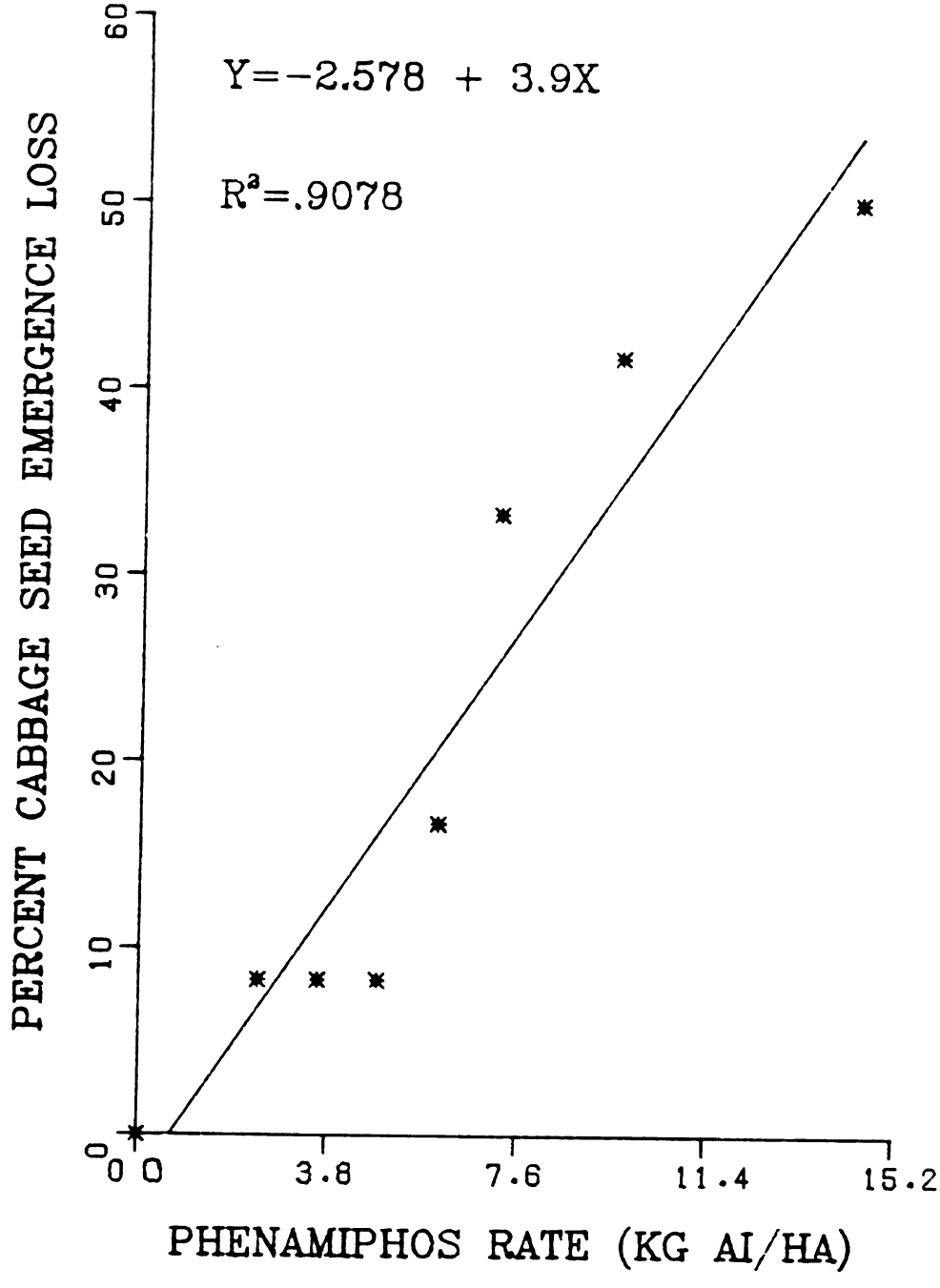

Fig. 44. Relationship between cabbage seeds emergence loss and phenamiphos concentration.

3.6 INFLUENCE OF DIFFERENT RATES OF PHENAMIPHOS ON YIELD OF CABBAGE ASSOCIATED WITH HETERODERA SCHACHTII

3.6.1 Introduction

Control of H. schachtii by various nematicides results in increases in yield. Cabbage yield can be increased six-fold when H. schachtii is controlled with methyl bromide (Radewald et al., 1971) and sugar beet yield can be increased by 20% when H. schachtii is controlled with Carbofuran (Furadan®) at 45 kg/ha (Cooke et al., 1979). Yield increases are greater with fumigant nematicides alone or in combination with granular aldicarb or carbofuran than with the granular compounds used alone (Cooke et al., 1979). In Michigan, H. schachtii on cabbage can be successfully controlled by 1,3-D, 1,3-D with Chloropicrin, 1,3-D with methyl isothiocyanate, or phenamiphos (Grafius et al., 1982). Nematode control should usually be implemented when the marginal revenue derived from the management input is equal to or exceeds the marginal cost (Bird, 1981). For this to be properly determined, it is essential to know the minimum rate of nematicide application that gives optimal yield. This phenomenon is becoming increasingly important with increasing environmental pollution awareness compounded with rigorous EPA regulations.

The objective of this study was to determine yield responses associated with different rates of phenamiphos applications on cabbage associated with H. schachtii.

3.6.2 Methods and Materials

B. oleracea capitata (cv King Cole) was direct seeded in clay drainage tiles (24 cm diameter and 42 cm deep) on November 25, 1982, in a greenhouse with day and night temperatures of 27°C and 22°C, respectively. Tiles were filled with similar proportions of steamed sandy-clay loam soil mixed with soil containing H. schachtii cysts so that the initial population density would be 20 eggs and second stage juveniles per cm^3 of soil. The soil was mixed with a cement mixer. The inoculum was cultured in the greenhouse in wooden culture boxes 1.5 m long, 1.0 m wide, and 0.3 m deep. The culture boxes were first filled with sandy-clay loam soil containing H. schachtii cysts and then B. oleracea capitata (cv. King Cole) seedlings were transplanted into the culture box. The culture was maintained for about 5 months before use. The culture contained about 100 cysts in 100 cm^3 of soil. Each cyst has 200 eggs and second stage juveniles (Mai and Abawi, 1980; Olthof et al., 1974).

Tiles were arranged in a completely randomized block design with 8 treatments and 10 replications for each treatment. Treatments received 15 kg/ha of 20-20-20 fertilizer at seeding. Three additional fertilizer applications at 100 kg/ha of 20-20-20 fertilizer were made at 4 week intervals. Treatments also received phenamiphos application at 1.2, 2.4, 3.6, 4.8, 6.0, 7.2, 8.4, and 9.6 kg ai/ha on the seeding day.

After four weeks the seedlings were sprayed with maneb (fungicide) and orthene (insecticide) at 1.4 kg/ha and 1.6 kg/ha, respectively. The fungicide and insecticide were applied at 4 week intervals throughout the growing season to minimize the effect of pests other than nematodes.

Plants were harvested after 16 weeks. On the harvest date, marketable yield was evaluated by determining head weights of the cabbage.

3.6.3 Results

Phenamiphos application increased (P=0.05) the marketable yield of cabbage (Figure 45). The highest cabbage yields were obtained when the phenamiphos rate was 4.8 and 6.0 kg ai/ha. Rates of 1.2 and 9.6 kg ai resulted in the lowest yields. Intermediate yields were obtained when the rates were 2.4, 3.6, 7.2, and 8.4 kg ai/ha.

3.6.4 Discussion

Yields were generally low in all the treatments. In the field B. oleracea capitata (cv. King Cole) can have marketable yields of 1900 grams but in this experiment the average marketable yield was 700 grams. Greenhouse conditions seem to affect proper growth and development of cabbage. The effect of confinement in a tile can be ruled out because the same cabbage variety grown in equivalent tiles in the field can result in cabbage yield three-fold what was obtained in this experiment.

Cabbage yield was highest at rates which effectively control H. schachtii without any phytotoxic effect on the plant. From the above data, the optimal application rate can be said to be between 4.8 and 6.0 kg ai/ha. Rates below 4.8 kg ai/ha result in loss of cabbage yield because H. schachtii is not fully controlled. The yield loss increased with increase in deviation of the rate from 4.8 kg ai/ha to zero. Yield loss above an application rate of 6.0 kg ai/ha was a result of phytotoxicity. Phytotoxicity, hence yield loss, increased with increase in deviation of the rate from 6.0 kg ai/ha to infinity (very high application rate).

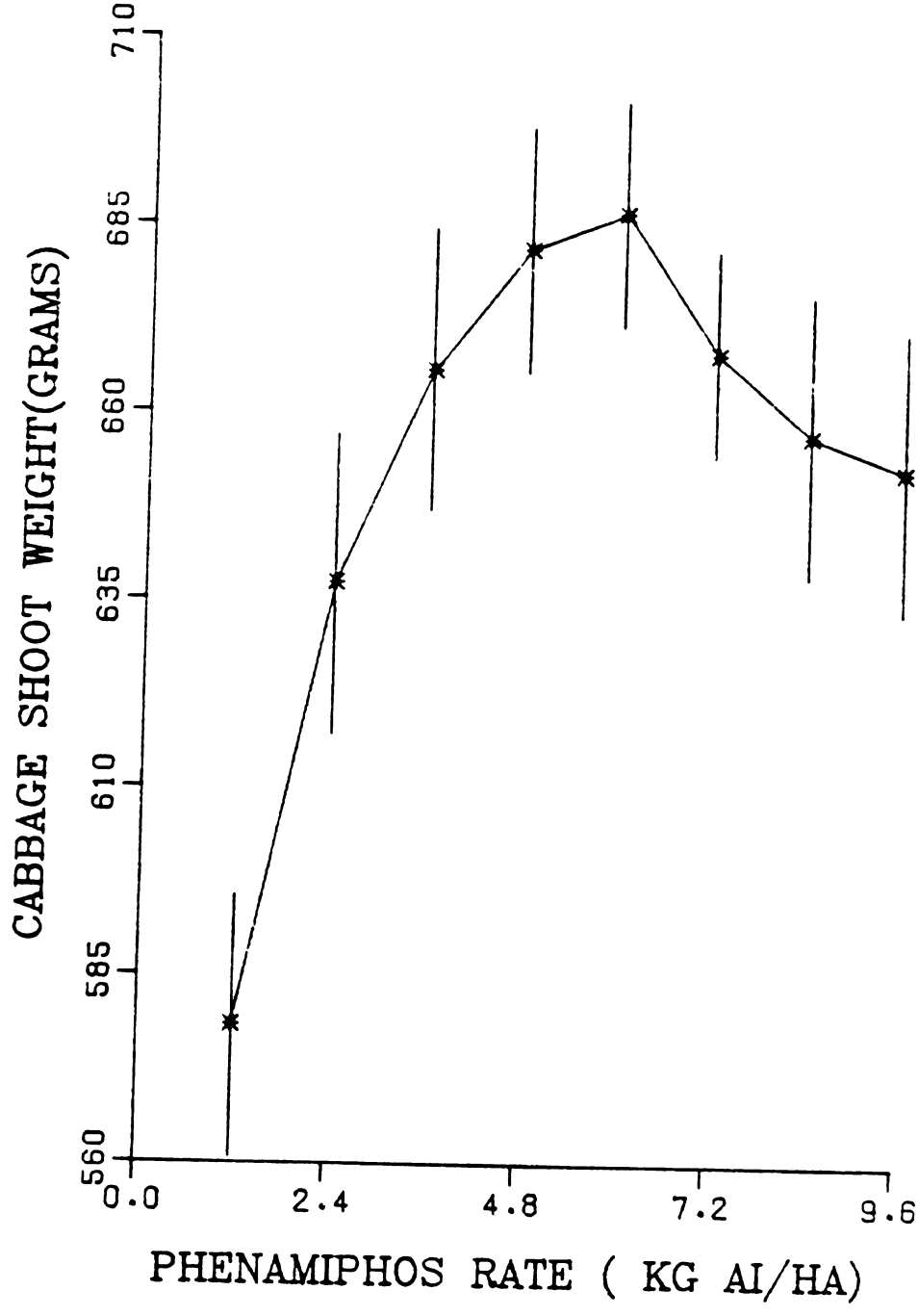

Fig. 45. Shoot weight (± standard error) of cabbage treated with different rates of phenamiphos.

In practice, there are several limitations to the amount of nematicide that can be applied: (a) EPA regulation of highest rates of application, (b) cost of nematicide (it is economically unprofitable to apply high rates of phenamiphos), and (c) it is environmentally unsound to apply high rates. With increasing environmental awareness, this is a very sensitive issue.

3.7 THE ROLE OF PHENAMIPHOS AS A NEMASTAT ON H. SCHACHTII ASSOCIATED WITH CABBAGE PRODUCTION

3.7.1 Introduction

Cabbage yield losses in fields infested by H. schachtii can be reduced by the use of appropriate nematicides. Phenamiphos is fairly effective in controlling H. schachtii associated with cabbage production (Grafius et al., 1982; Greco and Thomason, 1980). At recommended rates of application, phenamiphos is thought to control H. schachtii by depressing hatch of eggs (Greco and Thomason, 1980; Wright, 1981), reducing infectivity of second stage juveniles (Greco and Thomason, 1980; Wright, 1981) and reducing reproduction (Greco and Thomason, 1980; Starr et al., 1978; Wright, 1981). The nemastatic effect that predominates depends on the actual rate of phenamiphos application. Infectivity of second stage juveniles is affected at very low rates of phenamiphos application (Greco and Thomason, 1980). Information on the mode of control is important in assessing the efficacy of the nematicide and in the timing of nematicide application.

The major objective of this study was to assess the efficacy of phenamiphos on H. schachtii associated with cabbage. In addition to this objective, a comparison was made of the effect of single application and split application.

3.7.2 Methods and Materials

B. oleracea capitata (cv Roundup) was direct seeded in clay drainage tiles (24 cm diameter and 42 cm deep) on June 15, 1983, under field conditions. The tiles were first filled with certain proportions of steamed clay loam soil mixed with soil containing H. schachtii cysts so that the initial population dentisy (P_i) would be 20 eggs and second stage juveniles per cm^3 of soil. The soil was mixed with a cement mixer. The inoculum was cultured in the greenhouse in wooden culture boxes 1.5 m long, 1.0 wide, and 0.3 m deep. The culture boxes were first filled with sandy-clay loam soil containing H. schachtii cysts and then B. oleracea capitata (cv. King Cole) seedlings were transplanted into the culture box. The culture was maintained for about 8 months before use. The culture contained about 120 cysts in 100 cm^3 of soil.

Tiles were arranged in a completely randomized block design with 6 treatments and 10 replications for each treatment. The treatments received 15 kg/ha of 20-20-20 fertilizer at seeding. Two additional fertilizer applications at 100 kg/ha of 20-20-20 fertilizer were made at 4 week intervals.

After seeding, some of the treatments received phenamiphos at 3.0 and 6.0 kg ai/ha, respectively. Some of the treatments that received 3.0 kg ai/ha at seeding, received an additional 3.0 kg ai/ha 4 weeks after seeding. After seeding all the treatments were treated with maneb (fungicide) and orthene (insecticide) at 1.4 kg/ha and 1.6 kg/ha, respecitvely. The fungicide and insecticide were applied biweekly throughout the growing season to minimize the effect of pests other than nematodes.

The treatments were watered daily until the seedlings were fully established. Emergence occurred as early as 4 days after seeding and was complete about 8 days after seeding.

Plants were sampled at 4, 8, and 12 weeks after seeding. On each sampling date, the whole plant, including the root system, was dug. Soil was also collected from the tiles. The following parameters were evaluated:

(1) Fresh weights of root and shoot systems were obtained by direct weighing.

(2) About 0.1 gram of the root system was stained in a solutin of lactophenol with 0.01% acid fuchsin, to determine the number of second stage juveniles, third and fourth stage juveniles, developing females, adult males, and females with eggs.

(3) Soil, 100 cm^3, was processed using the centrifugation-flotation technique to determine the number of cysts, eggs, and second stage juveniles.

3.7.3 Results

Phenamiphos application significantly (P-0.05) increased total shoot weight (Figure 46), root weight (Figure 47), and marketable yield. Shoot weight was increased by six-fold, 5-fold, and 3-fold in treatments Hs-Hs + 6 kg ai/ha, Hs-Hs + 3 + 3 kg ai/ha, and Hs-Hs + 3 kg ai/ha, respectively. Root weight was increased by about 3-fold in all the treatments. No marketable yield was derived from treatment Hs-Hs. In treatments where phenamiphos was applied, marketable yield increased with an increase in phenamiphos application rate. The relative marketable yields were 100, 78, 35, and 0% in treatments Hs-Hs + 6 kg ai/ha, Hs-Hs + 3 + 3 kg ai/ha, Hs-Hs + 3 kg ai/ha, and Hs-Hs, respectively.

The number of cysts in the soil fluctuated throughout the growing season (Figure 48). Treatments Hs-Hs, Hs-Hs + 3 kg ai/ha, Hs-Hs + 3 + 3 kg ai/ha, and Hs-Hs + 6 kg ai/ha had P_f/P_i ratios of 11, 8, 3, and 2, respectively. The number of eggs in the soil also followed the same trend (Figure 49). Second stage juveniles in the soil followed a slightly different trend with one peak in week 12 (Figure 50).

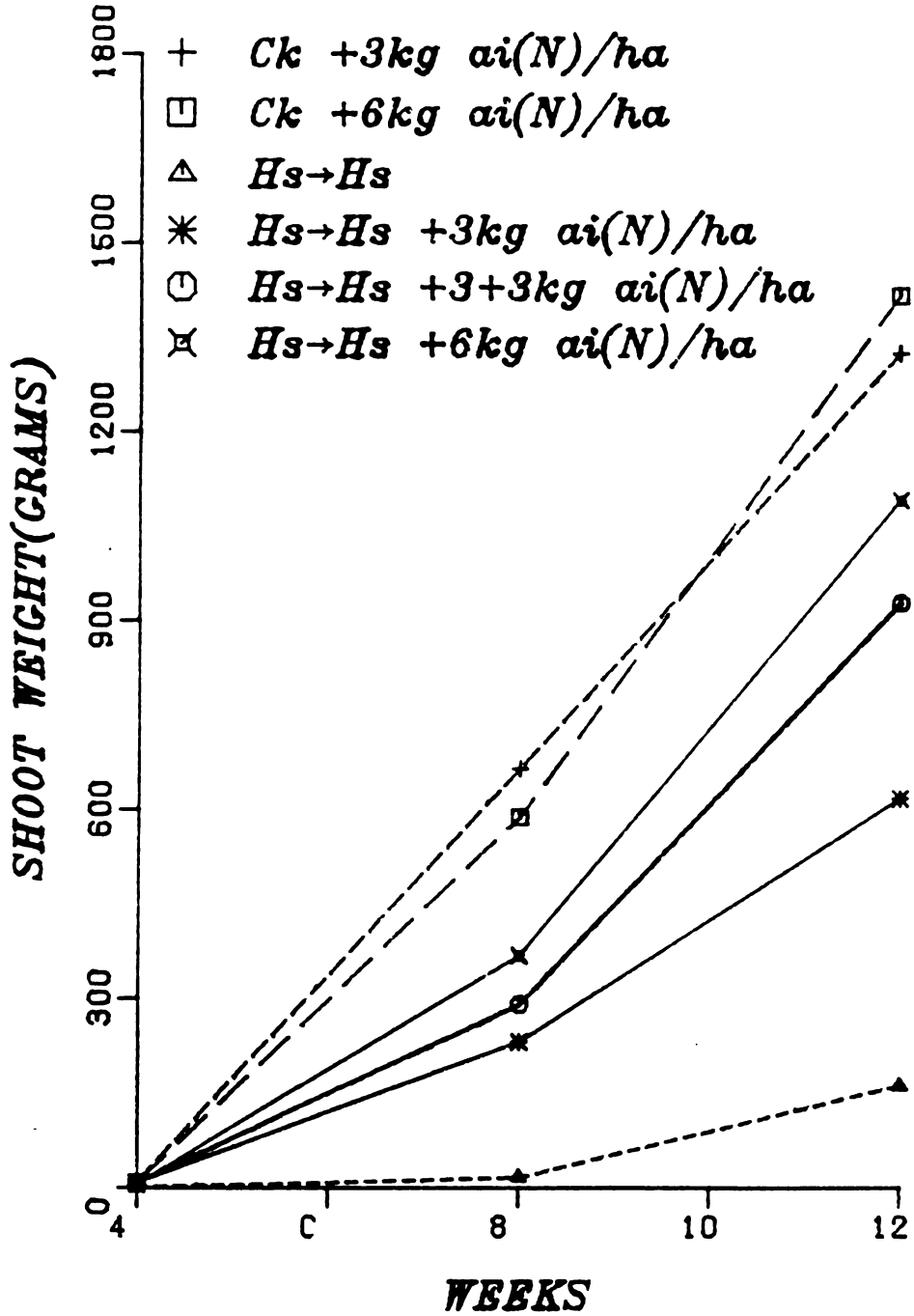

Fig. 46. Fresh shoot weight of cabbage grown in the presence and absence of H. schachtii and phenamiphos of different concentrations for a period of 12 weeks.

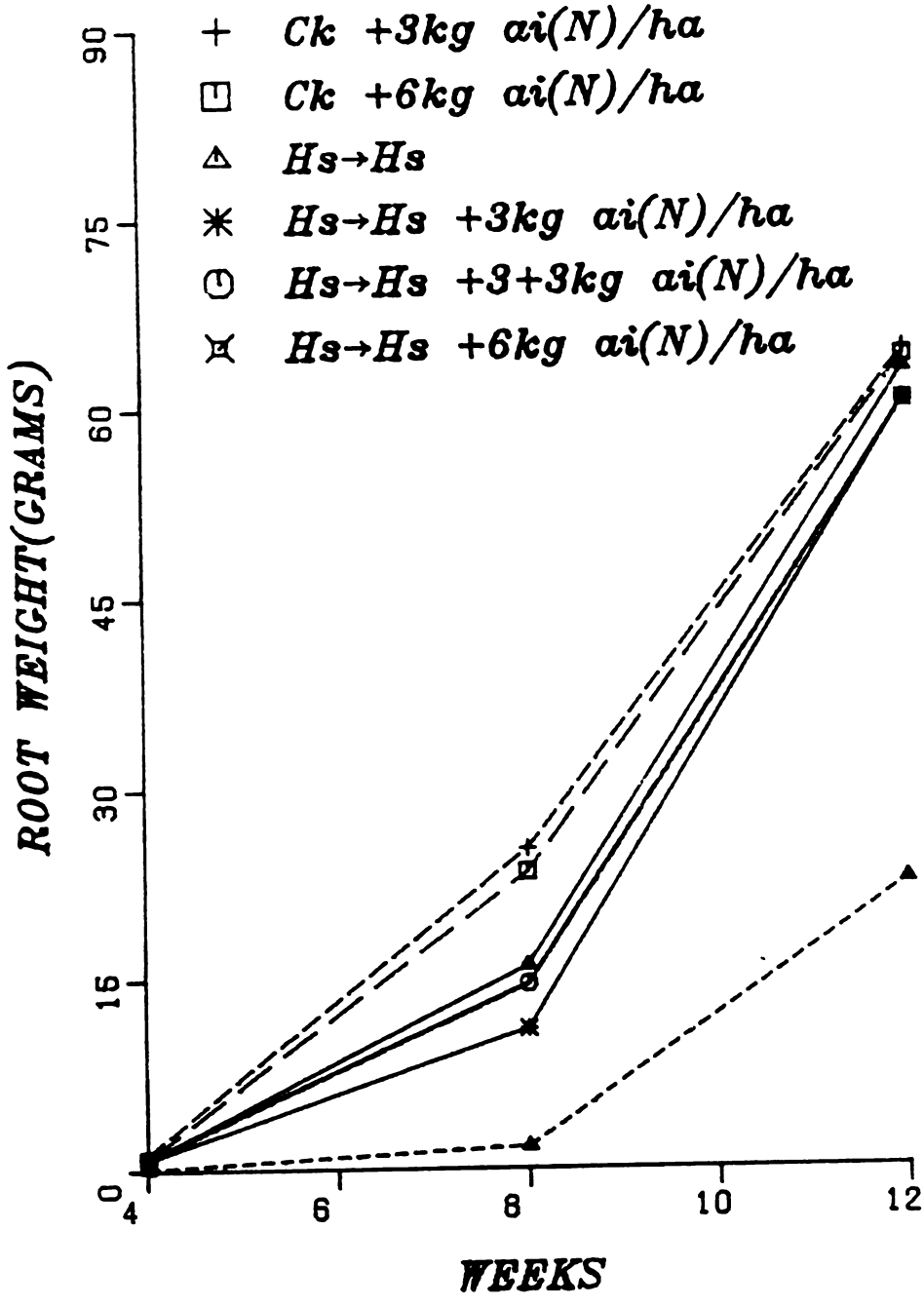

Fig. 47. Fresh root weight of cabbage grown in the presence and absence of H. schachtii and phenamiphos of different concentrations for a period of 12 weeks.

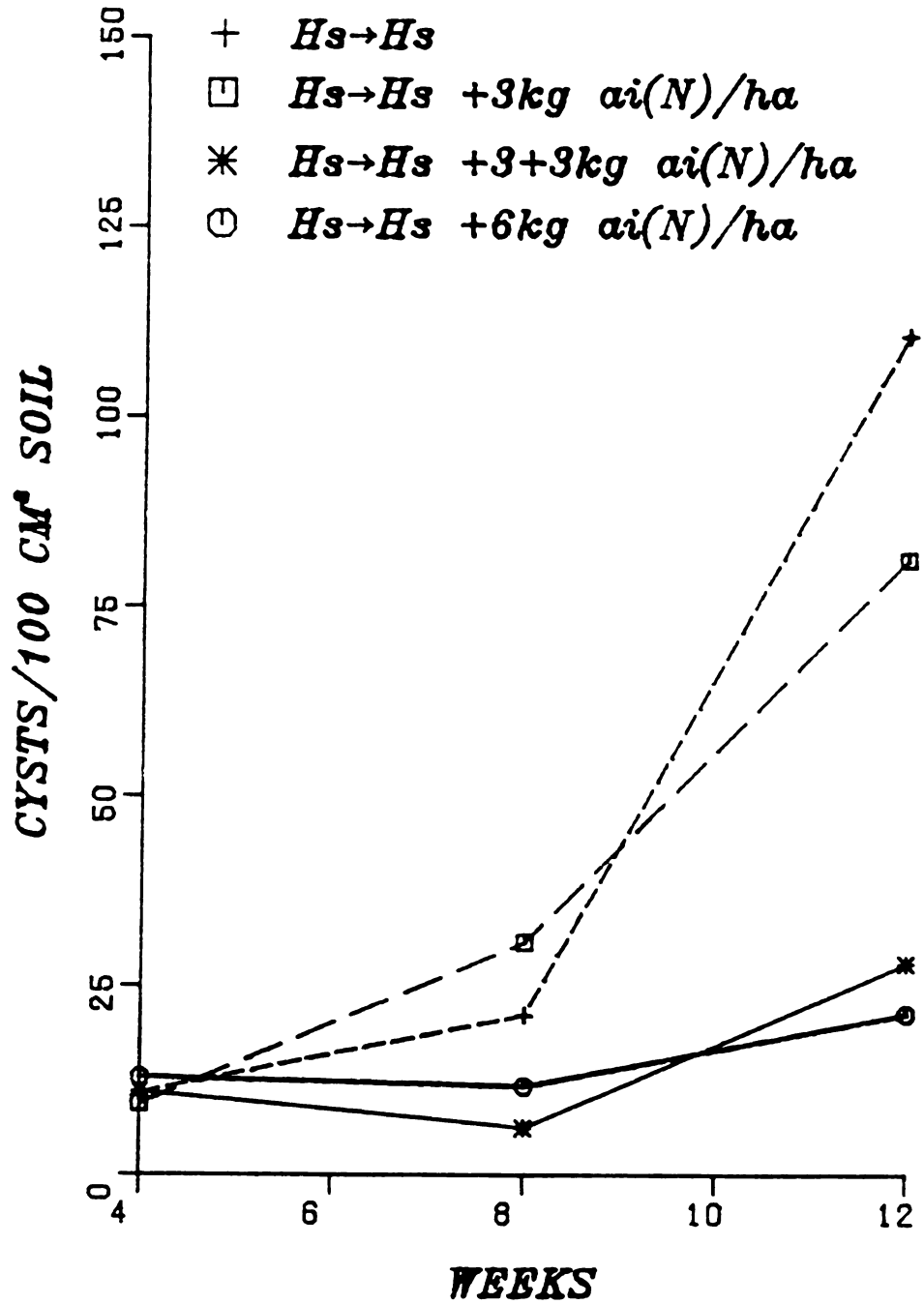

Fig. 48. Number of H. schachtii cysts in 100 cm^3 soil surrounding cabbage grown in the presence of H. schachtii and phenamiphos of different concentrations for a period of 12 weeks.

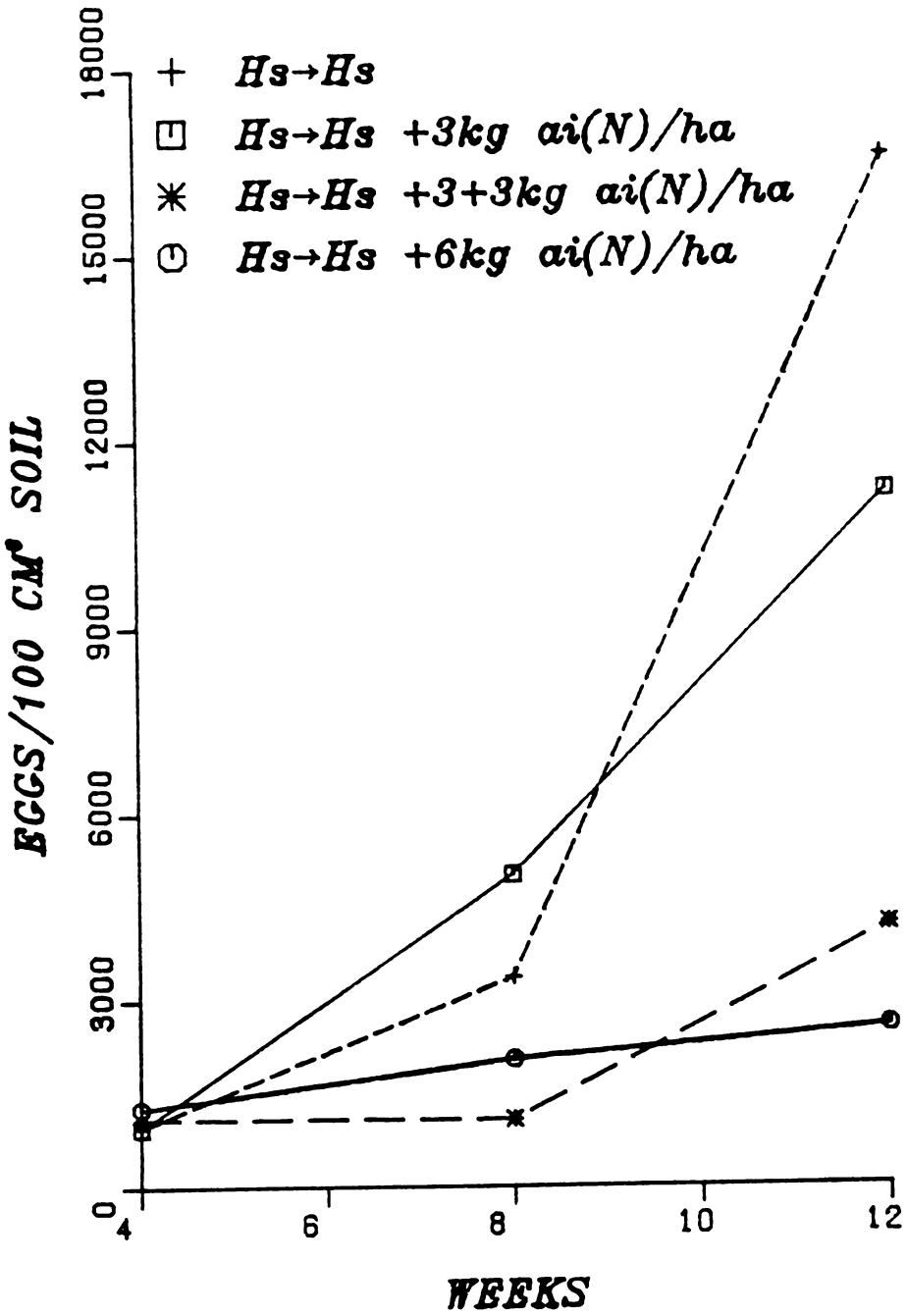

Fig. 49. Number of H. schachtii eggs in 100 cm^3 soil surrounding cabbage grown in the presence of H. schachtii and phenamiphos of different concentrations for a period of 12 weeks.

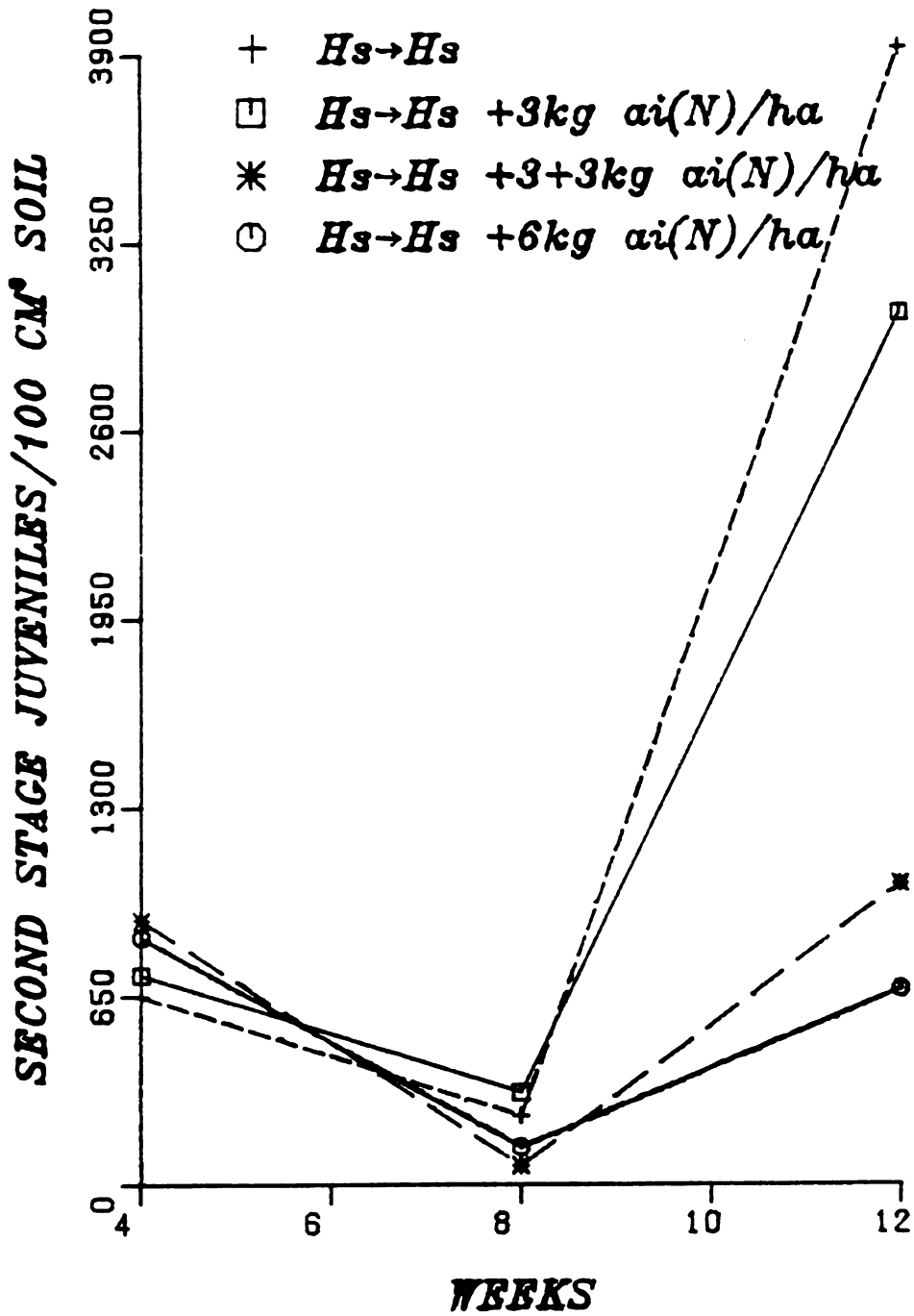

Fig. 50. Number of H. schachtii second stage juveniles in 100 cm^3 soil surrounding cabbage grown in the presence of H. schachtii and phenamiphos of different concentrations for a period of 12 weeks.

Second stage juveniles in roots peaked 2 times (Figure 51). The peaks are on week 4 and 12. Third and fourth stage juveniles followed the same trend (Figure 52). Developing females for treatment Hs-Hs had 2 peaks in week 4 and 12 (Figure 53). Developing females in treatments treated with phenamiphos had only one peak in week 12. Adult males in treatment Hs-Hs had two peaks in week 4 and 8 (Figure 54). Adult males in treatments treated with phenamiphos had one peak in week 4 for treatment Hs-Hs + 3 + 3 kg ai/ha and two peaks for treatment Hs-Hs + 3 kg ai/ha. No adult males were observed in treatment Hs-Hs + 6 kg ai/ha. Females with eggs had two peaks in week 4 and 12 for treatment Hs-Hs (Figure 55). Females with eggs in treatments Hs-Hs + 3 kg ai/ha and Hs-Hs + 3 + 3 kg ai/ha had one peak in week 8. Females with eggs in treatment Hs-Hs + 6 kg ai (N)/ha only peaked in week 12.

3.7.4 Discussion

Phenamiphos application greatly increased cabbage growth by reducing the number of second stage juveniles that penetrated roots and by slowing down the development of those juveniles that might have penetrated the roots. This increased yield by as much as 6-fold. Increased cabbage growth by nematicide application also occurs in New York, Canada, and California (Abawi and Mai, 1980; Potter and Marks, 1976a; Radewald et al., 1971).

The best control of H. schachtii was obtained at an application rate of 6 kg ai/ha. At this rate, phenamiphos was very effective in preventing second stage juveniles from penetrating cabbage roots. At 6 kg ai/ha phenamiphos did not seem to affect the rate of emergence of second stage juveniles. The number of second stage juveniles was the same in treatments with 3 kg ai/ha or 6 kg ai/ha.

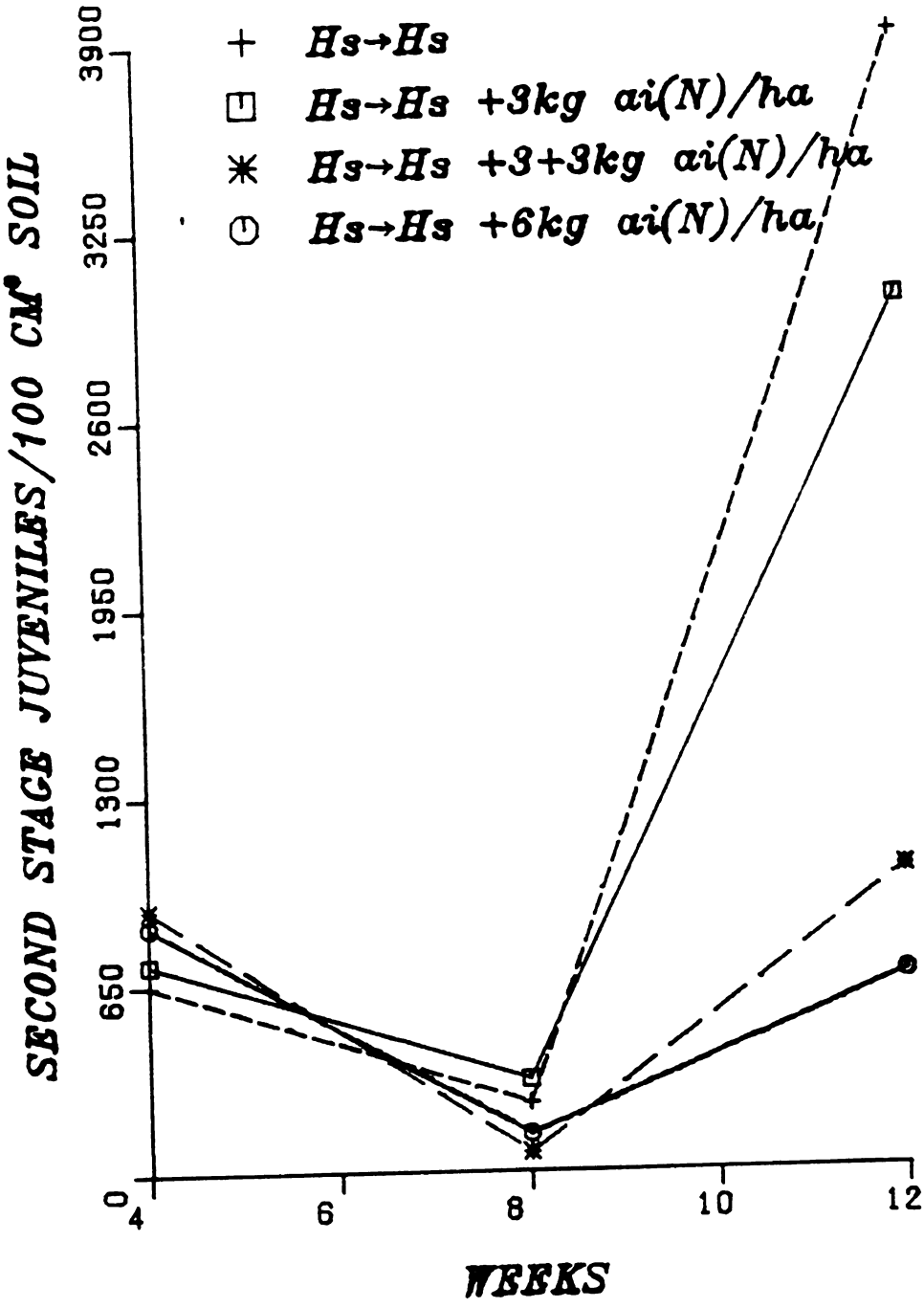

Fig. 51. Number of H. schachtii second stage juveniles in 0.1 gram roots of cabbage grown in the presence of H. schachtii and pehnamiphos of different concentrations for a period of 12 weeks.

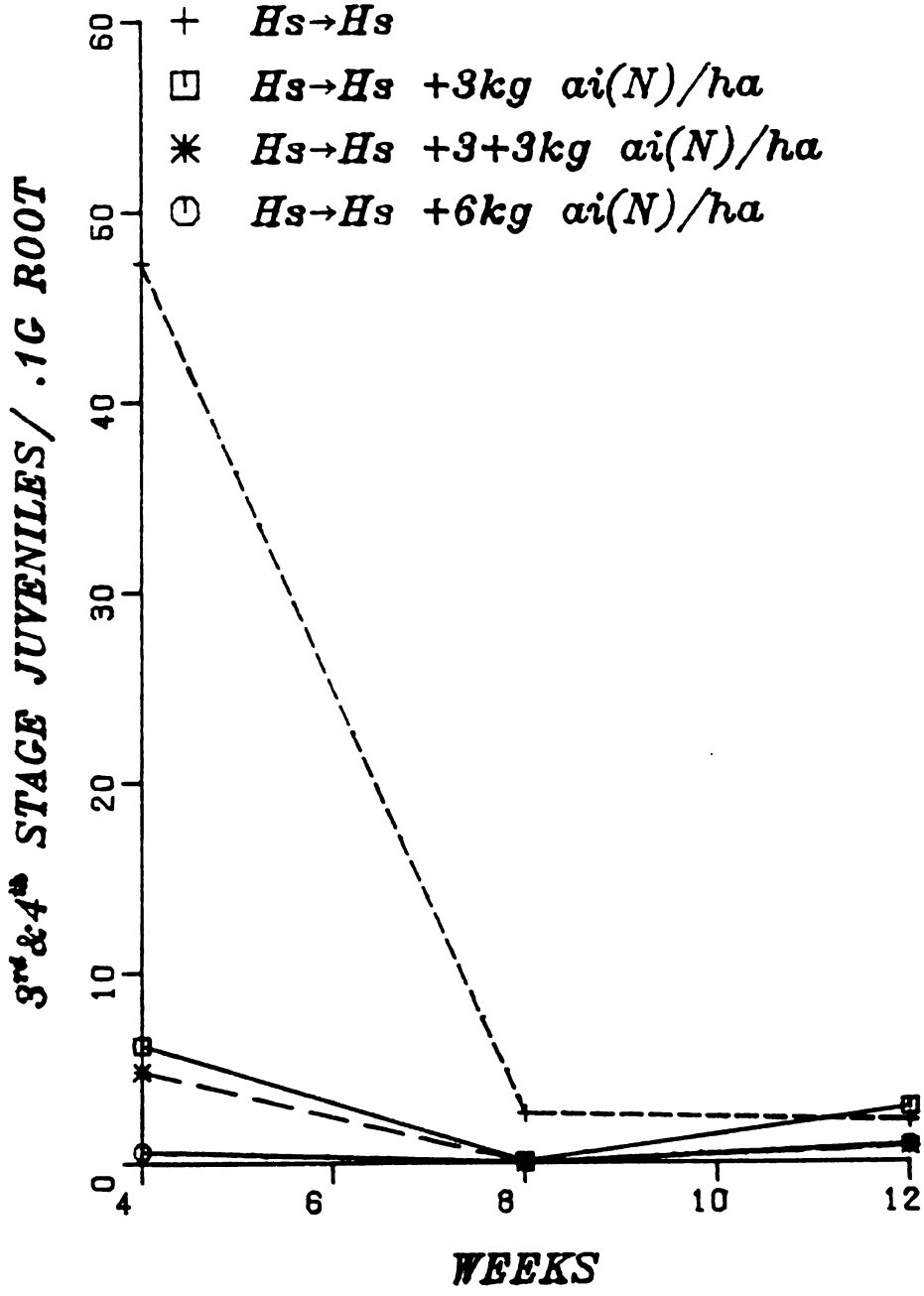

Fig. 52. Number of H. schachtii third and fourth stage juveniles in 0.1 gram roots of cabbage grown in the presence of H. schachtii and phenamiphos of different concentrations for a period of 12 weeks.

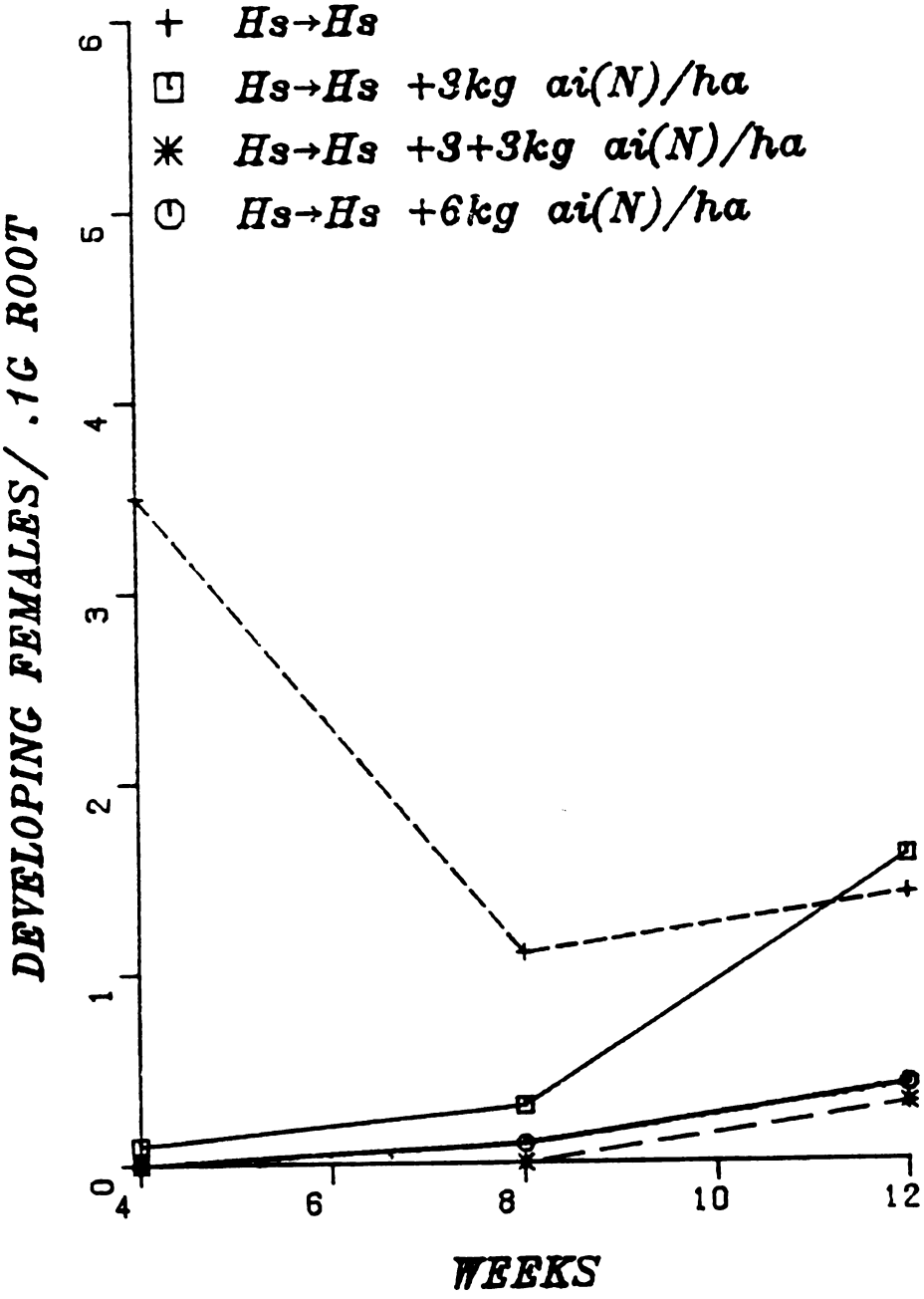

Fig. 53. Number of H. schachtii developing females in 0.1 gram roots of cabbage grown in the presence of H. schachtii and phenamiphos of different concnetrations for a period of 12 weeks.

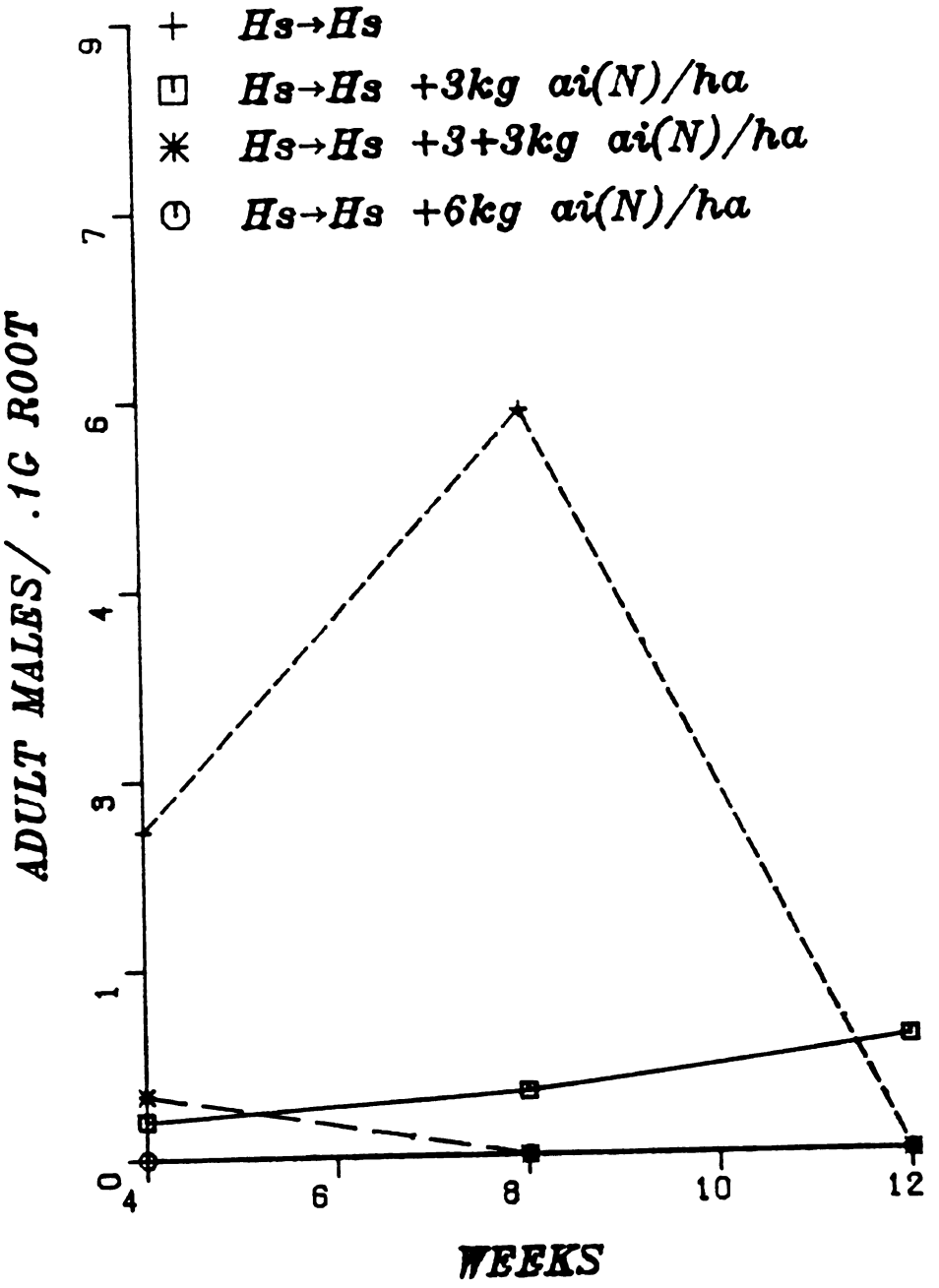

Fig. 54. Number of H. schachtii adult males in 0.1 gram roots of cabbage grown in the presence of H. schachtii and phenamiphos of different concentrations for a period of 12 weeks.

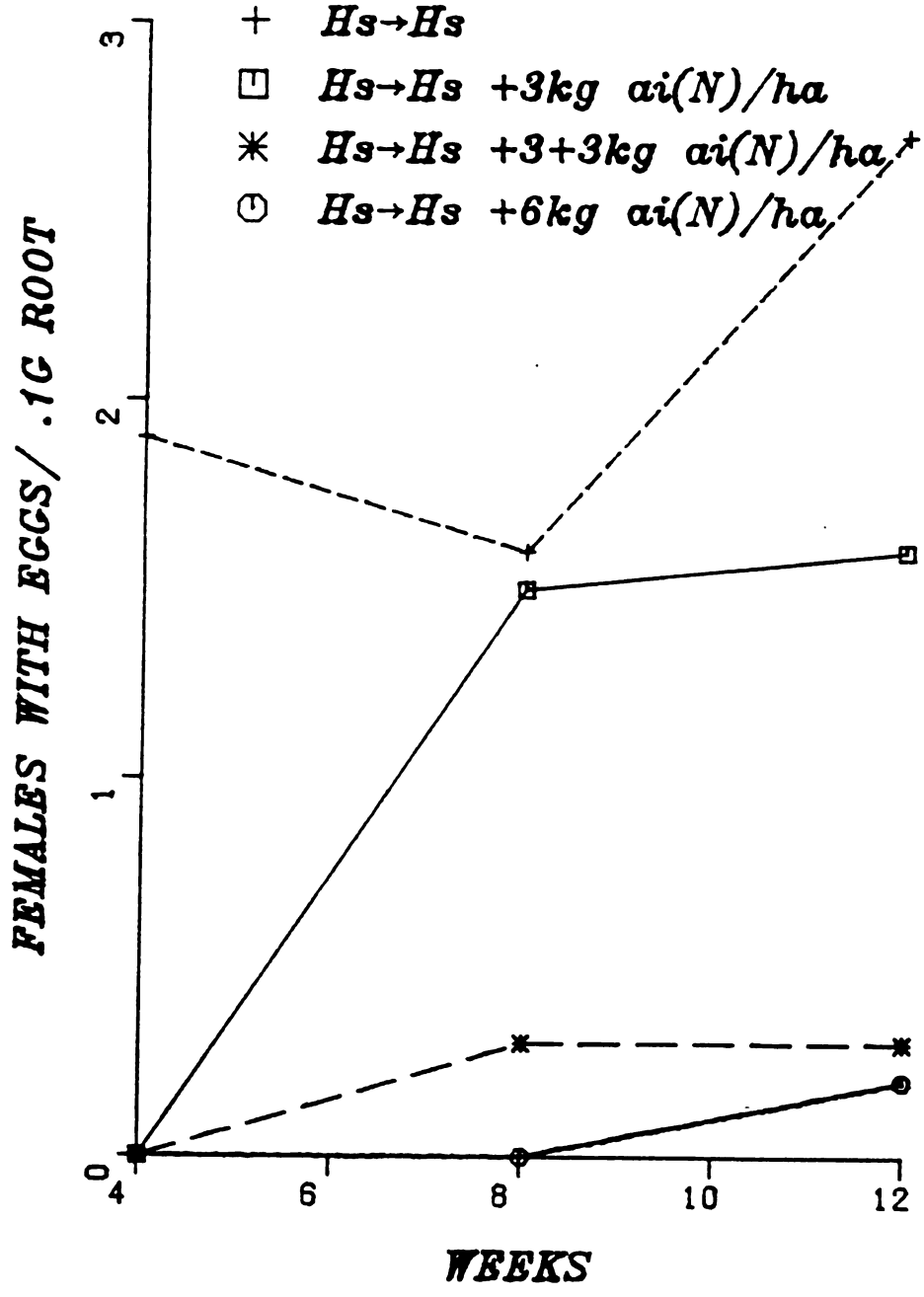

Fig. 55. Number of H. schachtii females with eggs in 0.1 gram roots of cabbage grown in the presence of H. schachtii and phenamiphos of different concentrations for a period of 12 weeks.

The second highest yield was obtained with a split application of 3 kg ai/ha at seeding and 3 kg ai/ha at transplanting. At 3 kg ai/ha at seeding, phenamiphos was not very effective in preventing the penetration of second stage juveniles. But the additional 3 kg ai/ha at transplanting greatly enhanced the nemastatic effect of phenamiphos. This additional 3 kg ai/ha appear to be effective mainly by slowing down the development of juveniles in the root system.

After a period of 8 weeks, a single application of phenamiphos at 3 kg ai/ha appeared to be no longer effective in H. schachtii control. The number of second stage juveniles penetrating roots of treated cabbage increased geometrically after 8 weeks, proportional to the number of remaining second stage juveniles in the soil and amount of root tissue. Plants in soil treated with 3 kg ai/ha had more second stage juveniles per gram root than plants from nontreated soil. This also occurs in New York and California (Abawi and Mai, 1980; Greco and Thomason, 1980). The coefficient of H. schachtii breeding is higher in treated plots (Decker, 1981). The high influx of second stage juveniles in treatment Hs-Hs + 3 kg ai/ha after 8 weeks resulted in a 33% yield loss compared to treatment Hs-Hs + 3 + 3 kg ai/ha. This shows that 4 week old cabbage seedlings transplanted to H. schachtii infested fields are still vulnerable to nematode attack.

H. schachtii had a P_f/P_i ratio of 11, 8, 3, and 2 in treatments Hs-Hs, Hs-Hs + 3 kg ai/ha, Hs-Hs + 3 + 3 kg ai/ha, and Hs=Hs + 6 kg ai/ha, respectively. This shows that when phenamiphos is applied at fairly high rates, it is effective in controlling H. schachtii in cabbage production. Rainfall and/or irrigation can flush out phenamiphos, hence efficacy of the nematicide is reduced (Hough et al., 1975). Therefore, for good H. schachtii control using phenamiphos, the amount of irrigation in treated plots should be reduced.

4. SUMMARY AND CONCLUSIONS

The distribution of Heterodera schachtii cysts, eggs and second stage juveniles in soil surrounding Brassica oleracea capitata roots was aggregated in the upper 20 cm of clay drainage tiles in the greenhouse. The density of H. schachtii was high in the upper 20 cm of clay drainage tiles because H. schachtii in this zone completed about two generations, whereas H. schachtii in deeper layers, only completed one generation. B. oleracea capitata roots were also aggregated in the upper 20 cm of clay drainage tiles. The distribution of B. oleracea capitata roots and age of the root system, dictated the distribution of second stage juveniles, third and fourth stage juveniles, adult males, and females with eggs in roots. Younger life stages were associated with the younger root system and the older life stages were associated with older the root system.

H. schachtii significantly (P=0.05) reduced B. oleracea capitata (cv. Roundup) marketable yield. The pathogenicity of H. schachtii on B. oleracea capitata (cv. Roundup) appeared to be enhanced by optimal H. schachtii developmental conditions. The most important variable to this effect is temperature. Michigan H. schachtii and New York H. schachtii had similar (P=0.05) pathogenicity on B. oleracea capitata (cv. Roundup) grown under greenhouse conditions. Soil with Michigan H. schachtii, had significantly (P=0.05) more cysts, eggs, and second stage juveniles at the end of the growing season than soil with New York H. schachtii. The difference in H. schachtii density, appears to be associated with different mortality rates of developing juveniles in the roots. New York H. schachtii, appear to have a higher mortality rate of developing juveniles in the roots compared to Michigan H. schachtii.

H. schachtii reproduced on B. oleracea capitata under greenhouse and field environments. Three generations of H. schachtii per season were observed on B. oleracea capitata (cv. Roundup) under Michigan field conditions. The number of generation is dictated by temperature or accumulated degree days (base 10°C). For Michigan, H. schachtii requires more DD_{10} to complete a generation than in California because Michigan summer temperatures deviate more from H. schachtii developmental optimal temperature. H. schachtii had a $P_{midseason}$ (P_m)/$P_{inititial}$ (P_i) ratios of 27.0 and 14.0, respectively, in some of the treatments. The high fecundity rate appear to be responsible for the high pathogenicity of this nematode on B. oleracea capitata and Beta vulgaris.

Phenamiphos at 6.0 kg ai/ha or 3.0 kg ai/ha at seeding and an additional 3.0 kg ai/ha at transplanting, significantly (P=0.05) increased B. oleracea capitata (cv. Roundup) marketable yield under field conditions. Phenamiphos mainly controlled H. schachtii by disorienting second stage juveniles from penetrating B. oleracea capitata (cv. Roundup) roots and inhibiting the development of second stage juveniles that had penetrated into the root system. Phenamiphos application reduced the P_f/P_i ratio to 2.0 in some of the treatments.

In the greenhouse, optimum B. oleracea capitata (cv. King Cole) marketable yield was obtained with phenamiphos rates between 4.8 and 6.0 kg ai/ha. Rates below 4.8 kg ai/ha were not effective in controlling H. schachtii. This was confirmed by an independent field experiment where H. schachtii infested soil was treated with phenamiphos at a rate of 3.0 kg ai/ha. Rates above 6.0 kg ai/ha were phytotoxic to B. oleracea capitata. A positive linear relationship between B. oleracea capitata (cv. King Cole) seed emergence and phenamiphos application rate was observed under greenhouse conditions. The

seed emergence loss was increased when equivalent phenamiphos application rates were applied in H. schachtii infested soil. H. schachtii alone can cause considerable seed germination loss and when H. schachtii and phenamiphos are combined, there appear to be an additive effect on seed germination at the lower rates of application.

Greenhouse conditions were not ideal for the proper growth and development of B. oleracea capitata. In the greenhouse, marketable yield was only about one third the normal B. oleracea capitata head weight.

Although the research described int this thesis concerned only the relationship between H. schachtii, B. oleracea capitata, and phenamiphos, it is important not to lose sight of the other factors present in the cabbage agroecosystem that are potentially important as determinants of nematode population growth. Attributes of the host plant, such as the pattern and distribution of root growth and biochemical properties, may influence the increase of H. schachtii. The presence of soil organisms, predaceous nematodes and other phytoparasites may be important in limiting the distribution of H. schachtii. Soil moisture, soil and plant nutrient levels, and other abiotic factors undoubtedly influence the population dynamics of H. schachtii.

System science methodology can be used to study the holistic influence of agroecosystem components associated with H. schachtii and B. oleracea capitata. The conceptual model presented in this thesis increased my understanding of the interaction between H. schachtii and B. oleracea capitata. The modeling process was insightful in identifying research needs concerning the ecology of H. schachtii. The complexity and number of biological components present in the cabbage agroecosystem support the need for further study on the ecology of H. schachtii.

Program Page 1

```
C*****************************************************************
C
C       SUBROUTINE DDAY
C PURPOSE
C CALCULATE NO. OF DEGREE DAYS
C
C DESCRIPTION OF VARIABLES
C TMIN1=FIRST MINIMUM TEMP. FOR HALF THE DAY
C TMIN2=SECOND MINIMUM TEMP. FOR THE OTHER HALF OF THE DAY
C TMAX=MAXIMUM TEMP.
C TLO=LOWER TEMP. THRESHOLD FOR THE SPECIES BEING CONSIDERED
C TUP=UPPER TEMP. THRESHOLD FOR THE SPECIES BEING CONSIDERED
C AHDD=ACTUAL HEATING DEGREE DAYS
C ACDD=ACTUAL COOLING DEGREE DAYS
C
C METHOD
C DESCRIBED BY J.C. ALLEN. "A MODIFIED SINE WAVE METHOD FOR
C CALCULATING DEGREE DAYS". ENVIRON. ENTOMOL. 5:388-396.
```

Program Page 2

```
C
C*****************************************************************
      SUBROUTINE DDAY(TMAX,TMIN1,TMIN2,TLO,TUP,AHDD,ACDD)
      AHDD=0.0
      ACDD=0.0
      DO 1 I=1,2
      IF (I-1)2,2,3
2     TMIN=TMIN1
      GO TO 4
3     TMIN=TMIN2
4     TBAR=(TMAX+TMIN)/2.0
      A=(TMAX-TMIN)/2.0
      IF(TLO-TMAX)5,6,6
6     HDD=0.0
      CDD=0.5*(TLO-TBAR)
      GO TO 15
5     IF(TUP-TMIN)7,7,8
7     HDD=0.5*(TUP-TLO)
      CDD=0.0
      GO TO 15
8     IF (TLO-TMIN)9,9,10
9     IF (TMAX-TUP)11,11,12
11    HDD=0.5*(TBAR-TLO)
      CDD=0.0
      GO TO 15
12    T1=-1.570796
      X2=(TUP-TBAR)/A
      T2=ATAN(X2/SQRT(1.0-X1**2))
      GO TO 16
10    IF(TUP-TMAX)13,14,14
14    T2=1.570796
      X1=(TLO-TBAR)/A
      T1=ATAN(X1/SQRT(1.0-X1**2))
      GO TO 16
13    X1=(TLO-TBAR)/A
      X2=(TUP-TBAR)/A
      T1=ATAN(X1/SQRT(1.0-X1**2))
      T2=ATAN(X2/SQRT(1.0-X2**2))
16    HDD=0.1591549*((TBAR-TLO)*(T2-T1)+A*(COS(T1)-COS(T2))+(TUP-TLO
     +)*(1.1570796-T2))
      CDD=0.1591549*((TLO-TBAR)*(1.578795)+A*COS(T1))
15    AHDD=AHDD+HDD
      ACDD=ACDD+CDD
1     CONTINUE
      RETURN
      END
```

Program Page 3

```
C
C*************************************************************
C
C          SUBROUTINE INIT
C
C PURPOSE
C CALCULATES NO. OF JUVENILES THAT PENETRATE ROOTS AND THEN
C DETERMINE THE OF EACH LIFE STAGE ON THE PLANT
C
C DESCRIPTION OF VARIABLES
C NEMATX=OUTPUT ARRAY 20X12 THAT KEEPS TRACK OF:
C 1. CYSTS HATCHING
C 2. SECOND STAGE JUVS. PENETRATING ROOTS
C 3. DEVELOPMENT OF JUVS. INTO : L2(LATE SECOND STAGE JUVS.);L3
C    (THIRD STAGE JUVS.);L4(FOURTH STAGE JUVS.);ADULT MALES;ADULT
C    FEMALES WITH EGGS;AND CYSTS
C 4. GROWTH OF CABBAGE ROOT VOLUME
C 5. IMPACT OF NEMAS. ON ROOT VOLUME
C 6. NO. OF DD0(DEGREE DAYS BASE 0 C)
C 7. NO. OF DD10(DEGREE DAYS BASE 10 C)
C 8. NO. OF HEATING AND COOLING DEGREE DAYS DEVIATING FROM MDD25
C    (DEGREE DAYS BASE 25 C) TEMP. 25 C TAKEN AS THE OPTIMUM
C CYDENS=INPUT(NO. OF CYSTS PER UINT VOLUME OF SOIL)
C X=TOTAL NUMBER OF ADULT NEMAS./VOLUME : SECOND STAGE JUV=1/10 OF
C ADULT;THIRD STAGE JUV=2/10 OF ADULT,FOURTH STAGE JUV=3/10 OF ADULT
C FAC=NEMA DAMAGE FACTOR TO THE PLANT.DAMAGE FACTOR DEPENDS ON ADULT
C NEMA DENSITY
C PREVOL=PREVIOUS ROOT VOLUME
C CURVOL=CURRENT ROOT VOLUME
C CCNT=CYLINDER COUNT. A NEW CYLINDER IS GENERATED AFTER ACCUMULATING
C 100 DD0
```

Program Page 4

```
C
C*************************************************************************
      SUBROUTINE INIT(NEMATX,CCNT,CDD10,MDD25,CYDENS)
      REAL NEMATX(20,12),CDD10,MDD25,CYDENS,X,FAC,PREVOL,CURVOL,L2
     +,L3,L4,ADULT
      L2=0.0
      L3=0.0
      L4=0.0
      ADULT=0.0
      VOL=0.0
      DO 10 I=1,CCNT
      L2=L2+NEMATX(I,5)
      L3=L3+NEMATX(I,6)
      L4=L4+NEMATX(I,7)
      ADULT=ADULT+NEMATX(I,8)
      VOL=VOL+NEMATX(I,11)
10    CONTINUE
      X=(0.1*L2+0.2*L3+0.3*L4+ADULT)/VOL
      IF(X .GT. 2.0)THEN
      FAC=0.4
      ELSE IF(X .GT. 1.0)THEN
      FAC=0.6
      ELSE IF(X .GT. 0.5)THEN
      FAC=0.775
      ELSE IF(X .GT. 0.3)THEN
      FAC=0.825
      ELSE IF(X .GT. 0.1)THEN
      FAC=0.85
      ELSE IF(X .GT. 0.05)THEN
      FAC=0.875
      ELSE IF(X .GT. 0.001)THEN
      FAC=0.925
      ELSE
      FAC=1.0
      END IF
      NEMATX(CCNT+1,9)=NEMATX(CCNT,9)+9.0*FAC
      NEMATX(CCNT+1,10)=NEMATX(CCNT,10)+7.0*FAC
      CURVOL=((6.28319*(NEMATX(CCNT+1,9)**2))*NEMATX(CCNT+1,10))-
     +NEMATX(CCNT,11)
      NEMATX(CCNT+1,11)=CURVOL
      NEMATX(CCNT+1,4)=CURVOL*CYDENS
      NEMATX(CCNT+1,1)=CDD10
      NEMATX(CCNT+1,2)=MDD25
      NEMATX(CCNT+1,3)=1.0
      NEMATX(CCNT+1,5)=0.0
      NEMATX(CCNT+1,6)=0.0
      NEMATX(CCNT+1,7)=0.0
      NEMATX(CCNT+1,8)=0.0
      NEMATX(CCNT+1,12)=1.0
      RETURN
      END
```

Program Page 5

```
C
C*****************************************************************
C
C           SUBROUTINE UPDATE
C
C PURPOSE
C UPDATES NEMA. DEVELOPMENT DAILY
C
C DESCRIPTION OF VARIABLES
C RATIO=NO. ADULT MALES COMPARED TO NO. OF ADULT FEMALES
C SURFAC=NO. OF L2 THAT SURVIVE TO PENETRATE ROOTS
C ACSURV=ACTUAL NO. OF L2 THAT PENETRATE ROOTS
C L2SURV=NO. OF L2 THAT SURVIVE INSIDE THE ROOTS
C L3SURV=NO. OF L3 THAT SURVIVE INSIDE THE ROOTS
C HATCH=NO. OF EGGS THAT HATCH INTO L2
```

Program Page 6

```
C
C*****************************************************************
C
      SUBROUTINE UPDATE(NEMATX,CCNT,CDD10,MDD25)
      REAL NEMATX(20,12),CDD10,MDD25,RATIO,SURFAC,ACSURV,L2SURV,L3SURV
     +,HATCH
      INTEGER I,CCNT
      DO 10 I=1,CCNT
      NEMATX(I,1)=NEMATX(I,1)+CDD10
      NEMATX(I,2)=NEMATX(I,2)+MDD25
      IF(NEMATX(I,1) .GE. 570.0)THEN
      RATIO=-.00000001*NEMATX(I,8)+0.5
      NEMATX(I,4)=NEMATX(I,4)+RATIO*NEMATX(I,8)
      NEMATX(I,8)=0.0
      NEMATX(I,1)=0.0
      NEMATX(I,2)=0.0
      NEMATX(I,3)=NEMATX(I,3)+1.0
      NEMATX(I,12)=1.0
      ELSE IF((NEMATX(I,1).GE.375.0).AND.(NEMATX(I,12).LT.5.0))THEN
      NEMATX(I,8)=NEMATX(I,7)*ADSURV(NEMATX(I,2))
      NEMATX(I,7)=0.0
      NEMATX(I,12)=5.0
      ELSE IF((NEMATX(I,1).GE.210.0).AND.(NEMATX(I,2).LT.4.0))THEN
      NEMATX(I,7)=NEMATX(I,6)*L3SURV(NEMATX(I,2))
      NEMATX(I,6)=0.0
      NEMATX(I,12)=4.0
      ELSE IF((NEMATX(I,1).GE.180.0).AND.(NEMATX(I,12).LT.3.0))THEN
      NEMATX(I,6)=NEMATX(I,5)*L2SURV(NEMATX(I,2))
      NEMATX(I,5)=0.0
      NEMATX(I,12)=3.0
      ELSE IF((NEMATX(I,1).GE.45.0).AND.(NEMATX(I,12).LT.2.0))THEN
      SURFAC=HATCH(NEMATX(I,2))
      NEMATX(I,5)=NEMATX(I,4)*(1.0-SURFAC)
      NEMATX(I,12)=2.0
      END IF
10    CONTINUE
      RETURN
      END
```

Program Page 7

```
C
C*****************************************************************
C
C          SUBROUTINE DUMPER
C
C PURPOSE
C STORE VALUES FOR ALL THE VARIABLES
C
C DESCRIPTION OF VARIABLES
C DCNT=DAY COUNT. COUNTS THE NO. OF DAYS FOR THE GROWING SEASON
C CYST=NO. OF CYSTS IN EACH CYLINDER
C L2=NO. OF L2 IN EACH CYLINDER
C L3=NO. OF L3 IN EACH CYLINDER
C L4=NO. OF L4 IN EACH CYLINDER
C ADULT=NO. OF FEMALES WITH EGGS IN EACH CYLINDER
C VOL=ROOT VOLUME IN EACH CYLINDER
C PRCNT=PERCENT ROOT VOLUME REDUCTION AT THE END OF THE SEASON
```

Program Page 8

```
C
C*****************************************************************
C
      SUBROUTINE DUMPER(NEMATX,CCNT,DCNT)
      REAL NEMATX(20,12),CYST,L2,L3,L4,ADULT,VOL
      INTEGER PRCNT,CCNT,DCNT
      CYST=0.0
      L2=0.0
      L3=0.0
      L4=0.0
      ADULT=0.0
      VOL=0.0
      PRINT*,'DAY NO. ',DCNT
      WRITE(6,901)
901   FORMAT('0CYLINDER    SUMDD10 SUMDD25',2X,'GEN',9X,'CYST',8X,'L2'
     +,14X,'L3',12X,'L4',12X,'ADULT','R',5X,'O',9X,'VOL')
      DO 10 I=1,CCNT
      WRITE(6,*)I
      WRITE(6,902)(NEMATX(I,J),J=1,11)
902   FORMAT('+',9X,2F9.2,3X,F2.0,5F14.2,2F6.1,F12.1)
      CYST=CYST+NEMATX(I,4)
      L2=L2+NEMATX(I,5)
      L3=L3+NEMATX(I,6)
      L4=L4+NEMATX(I,7)
      ADULT=ADULT+NEMATX(I,8)
      VOL=VOL+NEMATX(I,11)
10    CONTINUE
      PRINT*
      PRINT*
      PRINT*,'TOTAL FOR ALL CYLINDERS'
      PRINT*,'CYST/C.C.      ',CYST/VOL
      PRINT*,'L2/C.C.        ',L2/VOL
      PRINT*,'L3/C.C.        ',L3/VOL
      PRINT*,'L4/C.C.        ',L4/VOL
      PRINT*,'ADULT/C.C.   ',ADULT/VOL
      PRINT*,'ROOT VOLUME  ',VOL
      PRINT*
      PRINT*
      RETURN
      END
```

Program Page 9

```
C
C*****************************************************************
C
C          FUNCTION ADSURV
C
C PURPOSE
C CALCULATES NO. OF ADULT NEMAS. SURVIVING
C
C DESCRIPTION OF VARIABLES
C MORTDD=MORTALITY DEGREE DAYS(NO. OF DEGREE DAYS THAT DEVIATE
C FROM OPTIMUM TEMP. 25 C)
C
C*****************************************************************
C
      FUNCTION ADSURV(MORT DD)
      REAL ADSURV,MORTDD
      ADSURV=1.0-MORTDD/5000.0
      RETURN
      END
C
C*****************************************************************
C
C           FUNCTION L3SURV
C
C PURPOSE
C CALCULATES NO. OF L3 SURVIVING
C
C*****************************************************************
C
      FUNCTION L3SURV(MORTDD)
      REAL L3SURV,MORTDD
      L3SURV=1.0-MORTDD/5000.0
      RETURN
      END
C
C*****************************************************************
C
C           FUNCTION L2SURV
C
C PURPOSE
C CALCULATES NO. OF L2 SURVIVING
C
C*****************************************************************
C
      FUNCTION L2SURV(MORTDD)
      REAL L2SURV,MORTDD
      L2SURV=0.5-MORTDD/1000.0
      RETURN
      END
```

Program Page 10

```
C
C
C*****************************************************************
C
C            FUNCTION HATCH
C
C PURPOSE
C CALCULATES NO. OF EGGS HATCHING
C
C*****************************************************************
C
      FUNCTION HATCH(MORTDD)
      REAL HATCH,MORTDD
      HATCH=0.5-MORTDD/1000.0
      RETURN
      END
C
C*****************************************************************
C
C            MAIN PROGRAM
C
C PURPOSE
C CALLS ALL THE SUBROUTINES IN THE PROGRAM
C
C USAGE
C CALL DDAY(ALSTLO,ACURHI,ACURLO,TLO0,TUP0,CDD0,ACDD)
C CALL DDAY(SLSTTP,SCURTP,SCURTP,TLO10,TUP10,CDD10,ACDD)
C CALL DDAY(SLSTTP,SCURTP,SCURTP,TLO25,TUP25,CDD25,HDD25)
C CALL UPDATE(NEMATX,CCNT,CDD10,MDD25)
C CALL INIT(NEMATX,CCNT,CDD10,MDD25,CYCDENS)
C CALL DUMPER(NEMATX,DCNT,CCNT)
C
C DESCRIPTION OF VARIABLES
C ALSTLO=AIR TEMP. LAST LOW
C ALSTHI=AIR TEMP. LAST HIGH
C SLSTTP=LAST SOIL TEMP.
C ACURLO=AIR TEMP CURRENT LOW
C ACURHI=AIR TEMP CURRENT HIGH
C SCURTP=CURRENT SOIL TEMP
C*****************************************************************
C
      PROGRAM NEMA(INPUT,OUTPUT,TAPE5=INPUT,TAPE6=OUTPUT)
      REAL NEMATX(20,12),CYDENS,SDD0,SDD10,MDD25,TEMPDD,TLO0,TUP0,TLO1C
     +,TUP10,TLO25,SLSTTP,ALSTLO,ALSTHI,CDD0,CDD10,CDD25,
```

Program Page 11

```
C
C*****************************************************************
      INTEGER I,CCNT,J,DCNT,PRCNT
      READ(5,801) CYDENS
801   FORMAT(F5.2)
      READ(5,802)TLO0,TUP0
      READ(5,802)TLO10,TUP10
      READ(5,802)TLO25,TUP25
802   FORMAT(2F5.2)
      TEMPDD=0.0
      SDD0=0.0
      SDD10=0.0
      MDD25=0.0
      DCNT=0
      CCNT=1
      PRCNT=0
      NEMATX(1,4)=(6.283:9*(3.5**2)*15)*CYDENS
      NEMATX(1,1)=0.0
      NEMATX(1,2)=0.0
      NEMATX(1,3)=1.0
      NEMATX(1,5)=0.0
      NEMATX(1,6)=0.0
      NEMATX(1,7)=0.0
      NEMATX(1,8)=0.0
      NEMATX(1,9)=3.5
      NEMATX(1,10)=15.0
      NEMATX(1,11)=1154.536
      NEMATX(1,12)=1.0
      READ(5,803)ASTLO,ALSTHI,SLSTIP
      ALSTLO=TEMP(ALSTLO)
      ALSTHI=TEMP(ALSTHI)
      SLSTIP=TEMP(SLSTIP)
803   FORMAT(3F5.2)
100   IF((DCNT .LE.115) .AND. (SDD0 .LE.2000.0)) THEN
      DCNT=DCNT+1
      PRCNT=PRCNT+1
C WRITE(6,807)DCNT
807   FORMAT('DDAY NO ',I3)
      READ(5,803)ACURLO,ACURHI,SCURTP
      ACURLO=TEMP(ACURLO)
      ACURHI=TEMP(ACURHI)
      SCURTP=TEMP(SCURTP)
C WRITE(6,901)ACURLO,ACURHI,SCURTP
901   FORMAT(' THE AIR TEMP. LO IS ',F5.2,' AIR TEMP. HI IS ',F5.2,
     +' SOIL TEMP IS ',F5.2)
      CALL DDAY(ALSTLO,ACURHI,ACURLO,TLO0,TUO0,CDD0,ACDD)
      SDD0=SDD0+CDD0
      TEMPDD=TEMPDD+CDD0
      CALL DDAY(SLSTTP,SCURTP,SCURTP.TLO10,TUP10,CDD10,ACDD)
      SDD0=SDD0+CDD0
```

Program Page 12

```
      SDD10=SDD10+CDD10
      CALL DDAY(SLSTTP,SCURTP,SCURTP,TLO25,TUP25,CDD25,HDD25)
      MDD25=MDD25+HDD25
      CALL UPDATE(NEMATX,CCNT,CDD10,MDD25)
      IF(TEMPDD .GE. 100.0) THEN
      TEMPDD=0.0
      CALL INTI(NEMATX,CCNT,CDD10,MDD25,CYDENS)
      CCNT=CCNT+1
      END IF
      ALSTLO=ACURLO
      SLSTLO=SCURTP
      IF(PRCNT .EQ. 14) THEN
      CALL DUMPER(NEMATX,DCNT,CCNT)
      PRCNT=0
      END IF
      GO TO 100
      END IF
      PRINT*,'THE CYST DENSITY PER C.C. IS ',CYDENS
      WRITE(6,911)SDDO
  911 FORMAT('ODDO ACUM. FOR SEASON ',F8.2)
      WRITE(6,909)SDD10
  909 FORMAT(' DD10 ACUM. FOR SEASON ',F8.2)
      PRINT*,'TOTAL NUMBER OF DAYS ',DCNT
      FACT=((NEMATX(CCNT,9)**2)*NEMATX(CCNT,10))/(((CCNT*9.0)**2)*
     +(CCNT*7.0))
      FACT=FACT*100.0
      PRINT*,'ROOT VOLUME IS ',FACT,'PERCENT OF OPTIMUM'
      CALL DUMPER(NEMATX,CCNT,DCNT)
      DO 10 I=1,CCNT
      PRINT*, 'CYLINDER NO. ',I
      PRINT*, 'DEPTH TO                  ',NEMATX(I,10)
      PRINT*, 'RADIUS TO                 ',NEMATX(I,9)
      PRINT*, 'VOLUME IS C.C. IS         ',NEMATX(I,11)
      PRINT*, 'THIS CYLINDER IS GEN. NO ',NEMATX(I,3)
      PRINT*, 'DD10 ACCUMULATED FOR GEN. ',NEMATX(I,1)
      PRINT*, 'DD25 ACCUMULATED FOR GEN. ',NEMATX(I,2)
      PRINT*, 'CYST NO./C.C.              ',NEMATX(I,4)/NEMATX(I,11)
      PRINT*, 'L2 NO./C.C.                ',NEMATX(I,5)/NEMATX(I,11)
      PRINT*, 'L3 NO./C.C.                ',NEMATX(I,6)/NEMATX(I,11)
      PRINT*, 'L4 NO./C.C.                ',NEMATX(I,7)/NEMATX(I,11)
      PRINT*, 'ADULT NO./C.C.             ',NEMATX(I,8)/NEMATX(I,11)
      PRINT*
      PRINT*
   10 CONTINUE
      STOP
      END
```

Table B1. Cabbage root weight in grams at different depths of the microtile.

Depth (cm)	Weeks			
	2	4	6	8
7	0.086 b[1]	0.93 d	2.59 e	8.91 f
21	0 a	0.25 c	0.84 d	2.78 e
35	0 a	0 a	0.75 d	3.35 e

Table B2. H. schachtii second stage juveniles per 0.1 gram of root tissue from different depths.

Depth (cm)	Weeks			
	2	4	6	8
7	2.9 b[1]	3.4 b	2.4 b	0.1 b
21	0 a	23.3 c	7.4 d	0.5 b
35	0 a	0.3 b	7.1 d	0.1 b

Table B3. H. schachtii third and fourth stage juveniles per 0.1 gram of root tissue from different depths.

Depth (cm)	Weeks			
	2	4	6	8
7	2.6 b[1]	3.3 b	9.4 c	0.5 b
21	0 a	15.1 c	30.0 d	2.0 b
35	0 a	0.3 b	14.9 c	3.3 b

[1]Column means followed by the same letter are not significantly different (P = 0.05) according to the Student-Newman-Keuls multiple range test.

Table B4. H. schachtii developing females per 0.1 gram of root tissue from different depths.

Depth (cm)	Weeks			
	2	4	6	8
7	2.1 b[1]	1.9 b	.9 b	1.0 b
21	0 a	2.1 b	2.2 c	9.5 d
35	0 a	0 a	.6 b	16.7 e

Table B5. H. schachtii adult males per 0.1 gram of root tissue from different depths.

Depth (cm)	Weeks			
	2	4	6	8
7	0.9 b[1]	0.4 b	0.6 b	0.1 b
21	0 a	0.8 b	4.7 c	0.5 b
35	0 a	0 a	0.4 b	0.2 b

Table B6. H. schachtii females with eggs per 0.1 gram of root tissue from different depths.

Depth (cm)	Weeks			
	2	4	6	8
7	0 a[1]	3.2 c	0.1 b	9.3 e
21	0 a	1.1 b	0.5 b	4.6 d
35	0 a	0 b	0 b	1.7 d

[1]Column means followed by the same letter are not significantly different (P = 0.05) according to the Student-Newman-Keuls multiple range test.

Table B7. H. schachtii cysts per 100 cm^3 soil from different depths.

Depth (cm)	Weeks			
	2	4	6	8
7	5.2 a[1]	4.9 a	13.6 d	154.1 e
21	6.3 a	4.5 a	9.0 c	195.6 g
35	8.5 a	4.9 a	0.8 b	43.1 g

Table B8. H. schachtii eggs per 100 cm^3 soil from different depths.

Depth (cm)	Weeks			
	2	4	6	8
5	260.6 b[1]	574 a	778 c	11401 d
21	421.4 a	475 a	407 a	13301 e
35	501.0 a	559 a	43 b	2855 f

Table B9. H. schachtii second stage juveniles per 100 cm^3 soil from different depths.

Depth (cm)	Weeks			
	2	4	6	8
5	114 a[1]	113 a	90 a	16 c
21	132 a	92 a	62 b	13 c
35	183 a	133 a	29 c	14 c

[1]Column means followed by the same letter are not significantly different (P = 0.05) according to the Student-Newman-Keuls multiple range test.

Table B10. Cabbage root weight in grams at different radii and depths

Radii (cm)	Depth (cm) 7				35			
	Weeks				Weeks			
	2	4	6	8	2	4	6	8
2	0.086 b[1]	0.93 d	2.59 e	8.91 f	0 a	0 a	0.75 b	3.35 c
6	0 a	0.14 b	0.29 c	0.65 c	0 a	0 a	0.46 b	1.60 c
10	0 a	0.23 c	0.75 c	2.31 c	0 a	0 a	1.75 c	7.4 d

Table B11. H. schachtii second stage juveniles per 0.1 gram root tissue from different radii and depths.

Radii (cm)	Depth (cm) 7				35			
	Weeks				Weeks			
	2	4	6	8	2	4	6	8
2	2.9 b[1]	3.4 c	2.4 bc	0.1 a	0 a	0.3 a	7.1 c	0.1 c
6	0 a	10.4 c	5.4 c	0.1 a	0 a	0 a	5.4 c	0 a
10	0 a	28.7 d	3.8 c	0 a	0 a	0 a	5.7 c	0 a

[1]Column means followed by the same letter are not significantly different (P = 0.05) according to the Student-Newman-Keuls multiple range test.

Table B12. H. schachtii third and fourth stage juveniles per 0.1 gram root tissue from different radii and depths.

Radii (cm)	Depth (cm) 7				35			
	Weeks				Weeks			
	2	4	6	8	2	4	6	8
2	2.6 b[1]	3.3 b	9.4 c	0.5 a	0 a	0.3 a	14.9 c	3.3 b
6	0 a	7.6 b	9.4 c	0.5 a	0 a	0 a	20.8 c	3.1 b
10	0 a	18.2 c	14.7 c	0.1 a	0 a	0 a	19.5 c	1.2 b

Table B13. H. schachtii developing females per 0.1 gram root tissue from different radii and depths.

Radii (cm)	Depth (cm) 7				35			
	Weeks				Weeks			
	2	4	6	8	2	4	6	8
2	2.1 b[1]	1.9 b	0.9 a	1.0 a	0 a	0 a	0.6 a	16.7 c
6	0 a	0.7 a	0.8 a	0.5 a	0 a	0 a	0.3 a	13.5 c
10	0 a	0.2 a	0.5 a	1.4 a	0 a	0 a	0 a	4.6 b

[1]Column means followed by the same letter are not significantly different (P = 0.05) according to the Student-Newman-Keuls multiple range test.

Table B14. H. schachtii adult males per 0.1 gram root tissue from different radii and depths.

Radii (cm)	Depth (cm) 7				35			
	Weeks				Weeks			
	2	4	6	8	2	4	6	8
2	0.9 b[1]	0.4 a	0.6 a	0.1 a	0 a	0 a	0.4 a	0.2 a
6	0 a	0.2 a	0.4 a	0.2 a	0 a	0 a	0.1 a	0.4 a
10	0 a	0 a	0.5 a	0.1 a	0 a	0 a	0.1 a	0.7 a

Table B15. H. schachtii females with eggs per 0.1 gram root tissue from different radii and depths.

Radii (cm)	Depth (cm) 7				35			
	Weeks				Weeks			
	2	4	6	8	2	4	6	8
2	0 a[1]	3.2 b	0.1 a	9.3 c	0 a	0 a	0 a	1.7 b
6	0 a	0 a	0.2 a	2.1 b	0 a	0 a	0 a	.8 b
10	0 a	0 a	0.2 a	2.7 b	0 a	0 a	0 a	1.6 b

[1]Column means followed by the same letter are not significantly different (P = 0.05) according to the Student-Newman-Keuls multiple range test.

Table B16. H. schachtii cysts per 100 cm^3 soil from different radii and depths.

Radii (cm)	Depth (cm) 7				35			
	Weeks				Weeks			
	2	4	6	8	2	4	6	8
2	5.2 a[1]	4.9 a	13.6 b	154.1 d	8.5 a	4.9 a	0.8 a	43.1 c
6	3.8 a	6.0 a	2.7 a	101.8 c	6.2 a	2.8 a	0.8 a	73.9 c
10	4.4 a	4.9 a	4.7 a	88.9 c	6.0 a	4.3 a	0.7 a	88.9 c

Table B17. H. schachtii eggs per 100 cm^3 soil from different radii and depths.

Radii (cm)	Depth (cm) 7				35			
	Weeks				Weeks			
	2	4	6	8	2	4	6	8
2	260 a[1]	574 b	778 c	11401 e	501 a	603 b	44 a	2856 d
6	241 a	644 b	182 a	7508 d	344 a	445 b	40 a	5529 d
10	372 a	574 b	358 ab	7086 d	382 a	559 b	72 a	6247 d

[1]Column means followed by the same letter are not significantly different (P = 0.05) according to the Student-Newman-Keuls multiple range test.

Table B18. H. schachtii second stage juveniles per 100 cm^3 soil from different radii and depths.

Radii (cm)	Depth (cm)							
	7				35			
	Weeks				Weeks			
	2	4	6	8	2	4	6	8
2	114 a[1]	115 a	90 a	16 b	183 a	133 a	29 b	15 b
6	101 a	136 a	26 b	8 b	160 a	77 a	54 b	10 b
10	102 a	105 a	39 b	8 b	180 a	113 a	53 b	13 b

[1]Column means followed by the same letter are not significantly different (P = 0.05) according to the Student-Newman-Keuls multiple range test.

Table C1. Cabbage shoot weight in grams.

Treatment	Degree Days (Base 10° C)						
	219	542	818	1188	1602	1730	1885
Hs - Hs	0.21 a[1]		0.31 a	13.72 d	152.3 h	438.9 k	742.5 g
Hs - Ck	0.19 b	0.33 a	38.75 f	316.7 j	886.6 l	1364.3 r	3172 u
Ck - Hs	0.23 a	0.46 c	30.61 e	174.8 h	682.4 m	1119.1 s	2330 w
Ck - Ck	0.22 a	0.48 c	53.01 g	362.0 j	1088.9 n	1733.1 t	4117 x

Table C2. Cabbage root weight in grams.

Treatment	Degree Days (Base 10° C)						
	219	542	818	1188	1602	1730	1885
Hs - Hs	0.12 a[1]		0.14 a	1.43 c	10.1 f	24.0 h	83.9 m
Hs - Ck	0.11 a	0.14 a	2.60 d	17.3 g	36.7 j	113.5 n	181.7 t
Ck - Hs	0.12 a	0.19 b	2.12 d	10.1 f	30.9 k	95.4 g	170.9 u
Ck - Ck	0.13 a	0.18 b	3.86 e	18.1 g	44.5 l	132.8 r	191.8 w

[1]Column means followed by the same letter are not significantly different (P = 0.05) according to the Student-Newman-Keuls multiple range test.

Table C3. H. schachtii second stage juveniles per 0.1 gram root tissue.

Treatment	Degree Days (Base 10° C)						
	219	542	818	1188	1602	1730	1885
Hs - Hs	6.2 a[1]	1.7 d	0.9 d	2.2 d	0.4 c	2.4 d	2.2 e
Hs - Ck	4.2 b	1.1 d	0.6 d	1.8 d	0.5 c	0 c	1.5 d
Ck - Hs	0 c	0 c	1.0 d	0.4 c	0.1 c	0.2 c	0.8 d

Table C4. H. schachtii third and fourth stage juveniles per 0.1 gram root tissue.

Treatment	Degree Days (Base 10° C)						
	219	542	818	1188	1602	1730	1885
Hs - Hs	3.6 b[1]	2.8 b	4.7 c	2.2 b	0.2 a	0.8 b	2.9 c
Hs - Ck	5.0 b	2.4 b	1.9 b	0.4 a	0.1 a	0.1 a	1.2 b
Ck - Hs	0 a	0 a	2.1 b	1.8 b	0 a	0 a	1.2 b

[1]Column means followed by the same letter are not significantly different (P = 0.05) according to the Student-Newman-Keuls multiple range test.

Table C5. H. schachtii developing females per 0.1 gram root tissue.

Treatment	Degree Days (Base 10° C)						
	219	542	818	1188	1602	1730	1885
Hs - Hs	3.5 b[1]	5.2 c	2.7 b	1.5 b	0 a	0.2 b	1.5 b
Hs - Ck	4.0 b	6.9 c	2.4 b	1.1 c	0.3 b	0 a	0.9 b
Ck - Hs	0 a	0 a	0.8 a	2.0 b	0 a	0 a	2.1 c

Table C6. H. schachtii adult males per 0.1 gram root tissue.

Treatment	Degree Days (Base 10° C)						
	219	542	818	1188	1602	1730	1885
Hs - Hs	0.7 a[1]	10.9 c	0 a	0.2 b	0.1 a	0.2 b	0 a
Hs - Ck	2.1 b	6.1 c	0.4 b	0 a	0 a	0 a	0 a
Ck - Hs	0 a	0 a	0 a	0.5 b	0 a	0 a	0 a

[1]Column means followed by the same letter are not significantly different (P = 0.05) according to the Student-Newman-Keuls multiple range test.

Table C7. H. schachtii females with eggs per 0.1 gram root tissue.

Treatment	Degree Days (Base 10° C)						
	219	542	818	1188	1602	1730	1885
Hs - Hs	0 a[1]	3.1 b	1.3 b	5.5 c	5.8 c	1.8 b	2.8 b
Hs - Ck	0 a	2.7 b	1.0 b	1.3 b	1.3 b	0.3 a	0.3 a
Ck - Hs	0 a	0 a	0 a	2.4 b	6.5 c	0 a	0.6 a

Table C8. H. schachtii cysts per 100 cm^3 soil.

Treatment	Degree Days (Base 10° C)						
	219	542	818	1188	1602	1730	1885
Hs - Hs	3.4 b[1]	37.2 c	2.9 b	273.9 e	94.9 g	308.0 e	94.6 g
Hs- Ck	4.0 b	39.4 c	0.8 a	31.3 d	6.3 b	36.1 d	7.8 b
Ck - Hs	0 a	0 a	2.1 b	45.2 d	64.2 f	74.2 d	138.2 h

[1]Column means followed by the same letter are not significantly different (P = 0.05) according to the Student-Newman-Keuls multiple range test.

Table C9. H. schachtii eggs per 100 cm^3 soil.

Treatment	Degree Days (Base 10° C)						
	219	542	818	1188	1602	1730	1885
Hs - Hs	538.6 b[1]	2960 c	271.1 e	54780 f	10942 k	61997 l	19582 n
Hs - Ck	608.6 b	3196 c	111.4 d	6260 g	781 h	5135 m	1624 g
Ck - Hs	0 a	0 a	218.9 e	9040 g	8242 k	1504 m	28648 r

Table C10. H. schachtii second stage juveniles per 100 cm^3 soil.

Treatment	Degree Days (Base 10° C)						
	219	542	818	1188	1602	1730	1885
Hs - Hs	117.2 b[1]	516.8 c	118.6 e	42.1 f	5174.7 j	16644 n	4782 n
Hs - Ck	149.4 b	538.4 c	32.6 d	24.3 g	310.9 k	2094 m	416 q
Ck - Hs	0 a	0 a	101.5 e	34.9 h	3040.8 l	3916 m	6736 r

[1]Column means followed by the same letter are not significantly different (P = 0.05) according to the Student-Newman-Keuls multiple range test.

Table D1. Cabbage shoot weight in grams.

Treatment	Weeks			
	2	4	6	8
Ck - Ck	0.3 a[1]	1.92 b	6.22 d	17.6 f
Hs - Hs (MI)	0.23 a	1.02 b	4.08 c	12.7 e
Hs - Hs (NY)	0.27 a	1.46 b	4.33 c	12.6 e

Table D2. Cabbage root weight in grams.

Treatment	Weeks			
	2	4	6	8
Ck - Ck	0.05 a[1]	0.18 b	0.89 c	5.06 f
Hs - Hs (MI)	0.03 a	0.11 a	0.59 d	2.98 e
Hs - Hs (NY)	0.03 a	0.12 a	0.69 d	3.00 e

[1]Column means followed by the same letter are not significantly different (P = 0.05) according to the Student-Newman-Keuls multiple range test.

Table D3. H. schachtii second stage juveniles per 0.1 gram root tissue.

Treatment	Weeks			
	2	4	6	8
Hs - Hs (MI)	1.0 a[1]	0 a	1.8 a	2.4 a
Hs - Hs (NY)	2.1 a	0.4 a	2.0 a	1.8 a

Table D4. H. schachtii third and fourth stage juveniles per 0.1 gram root tissue.

Treatment	Weeks			
	2	4	6	8
Hs - Hs (MI)	3.8 a[1]	0.2 a	2.8 a	9.0 b
Hs - Hs (NY)	3.4 a	1.2 a	2.8 a	4.4 b

Table D5. H. schachtii developing females per 0.1 gram root tissue.

Treatment	Weeks			
	2	4	6	8
Hs - Hs (MI)	0.4 a[1]	1.4 a	12.6 d	2.4 a
Hs - Hs (NY)	0 a	3.0 b	8.6 c	2.6 a

[1]Column means followed by the same letter are not significantly different (P = 0.05) according to the Student-Newman-Keuls multiple range test.

Table D6. H. schachtii adult males per 0.1 gram root tissue.

Treatment	Weeks			
	2	4	6	8
Hs - Hs (MI)	0 a[1]	7.8 b	5.2 b	1.0 a
Hs - Hs (NY)	0 a	0.2 a	6.6 b	3.1 b

Table D7. H. schachtii females with eggs per 0.1 gram root tissue.

Treatment	Weeks			
	2	4	6	8
Hs - Hs (MI)	0 a[1]	0 a	2.4 b	2.6 b
HS - Hs (NY)	0 a	0.2 a	0.8 a	2.0 b

Table D8. H. schachtii cysts per 100 cm^3 soil.

Treatment	Weeks			
	2	4	6	8
Hs - Hs (MI)	6.2 a[1]	1.8 a	8.6 a	23.8 b
Hs - Hs (NY)	3.6 a	2.0 a	4.8 a	9.2 a

[1]Column means followed by the same letter are not significantly different (P = 0.05) according to the Student-Newman-Keuls multiple range test.

Table D9. H. schachtii eggs per 100 cm^3 soil

Treatment	Weeks			
	2	4	6	8
Hs - Hs (MI)	750 a[1]	227 a	1085 b	3001 d
HS - Hs (NY)	441 a	252 a	604 b	1159 c

Table D10. H. schachtii second stage juveniles per 100 cm^3 soil

Treatment	Weeks			
	2	4	6	8
Hs - Hs (MI)	144 a[1]	84 a	278 b	845 d
Hs - Hs (NY)	89 a	76 a	156 b	299 c

[1]Column means followed by the same letter are not significantly different (P = 0.05) according to the Student-Newman-Keuls multiple range test.

Table E1. Shoot weight in grams.

Treatment	Weeks		
	4	8	12
Ck - Ck + 3 kg ai/ha[2]	10.12 c[1]	644.8 f	1323.4 j
Ck - Ck + 6 kg ai/ha	8.27 bc	586.7 f	1414.6 j
Hs - Hs	0.54 a	16.5 d	162.2 e
Hs - Hs + 3 kg ai/ha	8.55 bc	231.3 e	618.2 g
Hs - Hs + 3 + 3 kg ai/ha	8.14 bc	290.7 e	927.8 h
Hs - Hs + 6 kg ai/ha	5.95 b	369.0 e	1090.6 h

Table E2. Root weight in grams.

Treatment	Weeks		
	4	8	12
Ck - Ck + 3 kg ai/ha[2]	1.30 b[1]	25.26 d	64.4 e
Ck - Ck + 6 kg ai/ha	0.93 b	23.43 d	63.9 e
Hs - Hs	0.16 a	1.74 b	22.6 d
Hs - Hs + 3 kg ai/ha	0.84 b	11.03 c	60.1 e
Hs - Hs + 3 + 3 kg ai/ha	0.94 b	14.58 c	60.4 e
Hs - Hs 6 kg ai/ha	0.89 b	16.02 c	69.9 e

[1]Column means followed by the same letter are not significantly different (P = 0.05) according to the Student-Newman-Keuls multiple range test.

[2]Phenamiphos

Table E3. H. schachtii second stage juveniles per 0.1 gram root tissue.

Treatment	Weeks		
	4	8	12
Hs - Hs	2.5 b[1]	2.0 b	3.7 b
Hs - Hs + 3 kg ai/ha[2]	1.1 a	0.8 a	8.5 c
Hs - Hs + 3 + 3 kg ai/ha	0.9 a	0 a	1.7 b
Hs - Hs 6 kg ai/ha	0.2 a	0 a	1.7 b

Table E4. H. schachtii third and fourth stage juveniles per 0.1 gram root tissue.

Treatment	Weeks		
	4	8	12
Hs - Hs	47.3 b[1]	2.9 c	2.2 c
Hs - Hs + 3 kg ai/ha[2]	6.2 a	1.0 a	2.9 c
Hs - Hs + 3 + 3 kg ai/ha	4.8 a	0 a	0.8 a
Hs - Hs + 6 kg ai/ha	0.6 a	0 a	0.9 a

[1]Column means followed by the same letter are not significantly different (P = 0.05) according to the Student-Newman-Keuls multiple range test.

[2]Phenamiphos

Table E5. H. schachtii developing females per 0.1 gram root tissue.

Treatment	Weeks		
	4	8	12
Hs - Hs	3.5 b[1]	1.1 b	1.4 b
Hs - Hs + 3 kg ai/ha[2]	0.1 a	0.3 a	1.6 b
Hs - Hs + 3 + 3 kg ai/ha	0 a	0 a	0.3 a
Hs - Hs + 6 kg ai/ha	0 a	0.1 a	0.4 a

Table E6. H. schachtii adult males per 0.1 gram root tissue.

Treatment	Weeks		
	4	8	12
Hs - Hs	2.6 b[1]	5.9 b	0 a
Hs - Hs + 3 kg ai/ha[2]	0.3 a	0.5 a	0.9 a
Hs - Hs + 3 + 3 kg ai/ha	0.5 a	0 a	0 a
Hs - Hs 6 kg ai/ha	0 a	0 a	0 a

[1]Column means followed by the same letter are not significantly different (P = 0.05) according to the Student-Newman-Keuls multiple range test.

[2]Phenamiphos

Table E7. H. schachtii females with eggs per 0.1 gram root tissue.

Treatment	Weeks		
	4	8	12
Hs - Hs	1.9 b[1]	1.6 b	2.7 b
Hs - Hs + 3 kg ai/ha[2]	0 a	1.5 b	1.6 b
Hs - Hs + 3 + 3 kg ai/ha	0 a	0.3 a	0.3 a
Hs - Hs + 6 kg ai/ha	0 a	0 a	0.2 a

Table E8. H. schachtii cysts per 100 cm^3 soil.

Treatment	Weeks		
	4	8	12
Hs - Hs	10.9 a[1]	21.1 b	110.6 c
Hs - Hs + 3 kg ai/ha[2]	9.4 a	30.7 b	81.1 c
Hs - Hs + 3 + 3 kg ai/ha	11.0 a	6.2 a	27.9 b
Hs - Hs + 6 kg ai/ha	12.9 a	11.7 a	21.3 b

[1]Column means followed by the same letter are not significantly different (P = 0.05) according to the Student-Newman-Keuls multiple range test.

[2]Phenamiphos

Table E9. H. schachtii eggs per 100 cm^3 soil.

Treatment	Weeks		
	4	8	12
Hs - Hs	950.1 a[1]	3370.5 ab	16590 c
Hs - Hs + 3 kg ai/ha[2]	942.0 a	5015.2 b	11165 c
Hs - Hs + 3 + 3 kg ai/ha	1086.3 ab	1072.5 a	4185 b
Hs - Hs + 6 kg ai/ha	1254.0 b	2046.9 ab	2565 b

Table E10. H. schachtii second stage juveniles per 100 cm^3 soil.

Treatment	Weeks		
	4	8	12
Hs - Hs	649.5 a[1]	235.9 cd	3921.7 e
Hs - Hs + 3 kg ai/ha[2]	723.0 ab	316.7 c	3006.0 e
Hs - Hs + 3 + 3 kg ai/ha	910.8 b	64.5 d	1035.0 f
Hs - Hs + 6 kg ai/ha	851.5 ab	129.1 cd	673.4 f

[1]Column means followed by the same letter are not significantly different (P = 0.05) according to the Student-Newman-Keuls multiple range test.

[2]Phenamiphos

LITERATURE CITED

Abawi, G. S., J. Foster, and W. F. Mai. 1973. Differentiation of cysts of Heterodera schachtii and H. trifoli by fenestral length. J. Nematol. 5:74-75.

Abawi, G. S., and W. F. Mai. 1980. Effects of initial population densities of Heterodera schachtii on yield of cabbage and table beets in New York State. Phytopathol. 70:481-485.

Abawi, G. S., and W. F. Mai. 1977. Sugar beet cyst nematode: A threat to the red beet and cabbage industries in New York State. New York's Food and Life Sciences. 10:11-14.

Akratanakul, W., J. R. Bagget, and H. J. Mack. 1977. Effects of plant spacing, fertilizer, and transplanting on axillary heading in cabbage. Hort. Science. 12:56-57.

Allen, J. C. 1976. A modified sine wave method for calculating degree days. Environ. Entomol. 5:388-396.

Ayoub, S. M. 1980. Plant Nematology. An agricultural training aid. Nema. Aid Publication.

Barker, K. R., G. W. Bird, R. A. Chapman, D. W. Dickerson, R. A. Dunn, W. F. Mai, M. Oostenbrink, and I. J. Thomason. 1978. Determining nematode population responses to control agents. In: Methods For Evaluating Plant Fungicides, Nematicides, and Bactericides. R.E. Baldwin, I.F. Brown, R.C. Cetas, and O.L. Coyier (eds.). The American Phytopathological Society. pp. 114-125.

Barker, K. R., and T. H. A. Olthof. 1976. Relationship between nematode population densities and crop responses. Ann. Rev. Phytopathol. 14:327-353.

Becker, R.F. 1978. Cabbage variety update. New York State Processing Veg. Conf.

Bird, G. W. 1981. Integrated nematode management for plant protection. In: Plant Parasitic Nematodes. B.M. Zuckerman and R.A. Rohde (eds.). Academic Press. 3:355-375.

Bird, G. W., and I. J. Thomason. 1980. Integrated pest management: The role of nematology. BioScience. 30:670-674.

Brzeski, M. W. 1975. The effect of pH on Heterodera schachtii Schmidt. International plant protection congress (8th). Moscow. Pracownia Nematologii Inst. pp. 37-44.

Brzeski, M. W. 1969. Nematodes associated with cabbage in Poland. Host-parasite relationships of Heterodera schachtii Schmidt. Komitet Ekologiczny-Polska Akademia Nauk. Kologia Polska-Seria A. 18:227-239.

Caswell, E. P., A. E. MacGuidwin, K. Milne, C. Nelson, and I. J. Thomason. 1981. A simulation model of Heterodera schachtii infecting Beta vulgaris. J. Nematol. 13:434. (Abstract).

Chitwood, B. G. 1953. Plant-parasite nematode problems in Michigan. In: Plant-parasitic Nematodes of Michigan: With Special Reference to the Genera of the Tylenchorhynchinae (Nematoda), 1981. N. Knobloch and G.W. Bird (eds). Michigan Agricultural Experiment Station Research Report. 419:6-10.

Cooke, D. A. and I. J. Thomason. 1979. The relationship between population density of Heterodera schachtii, soil temperature, and sugar beet yields. J. Nematol. 11:125-128.

Cooke, D. A., I. J. Thomason, H. E. McKinney, W. E. Bendixen and R. W. Hagemann. 1979. Chemical control of Heterodera schachtii on sugar beet in California. J. Nematol. 11:205-206.

Davis, H. R., F. M. R. Isenberg and R. B. Furry. 1980. The control of natural-air cabbage storage environment. Plant Sciences. Agricultural Engineering 8. Information Bulletin 137.

Davis, K. A. and J. M. Fisher. 1976. Factors influencing the number of larvae of Heterodera avenae invading barley seedlings in vitro. Nematologica 22:153-162.

Decker, H. 1981. Plant nematodes and their control (Phytonematology). pp 190-248. Amerind Publishing Co. New Delhi.

Drew, R. L. K. 1982. The effects of irrigation and of shelter from wind on emergence of carrot and cabbage seedlings. J. Hort. Sci. 57:215-219.

Dropkin, V. H. 1980. Introduction to plant nematology. p. 206. John Wiley & Sons. New York.

Duggan, J. J. 1963. Relationship between intensity of cereal root eelworm (Heterodera avenae Wollenweber, 1924) infestation and pH value of soil. Irish J. Agric. Res. 2:105-110.

Esser, R. P. and H. L. Rhoades. 1978. Heterodera schachtii A. Schmidt, 1871, (sugar beet nematode) a severe pest of cabbage in Florida. Nematology circular. Division of Plant Industry. Florida Department of Agricultural and Consumer Services. No. 38.

Evans. G. C. 1972. The quantitative analysis of plant growth studies ecology. Vol. I, p. 736. Univ. Calif. Press. Berkeley.

Federva, O. J. and S. J. Pscodna. 1983. Michigan Agricultural Statistics. Michigan Department of Agriculture. p. 34.

Ferris, H. 1981. Dynamic action thresholds for diseases induced by nematodes. Ann. Rev. Phytopathol. 19:427-436.

Ferris, H. 1978. Nematode economic thresholds: derivation, requirements, and theoretical considerations. J. Nematol. 10:341-349.

Franklin, M. T. 1972. C. I. H. Descriptions of plant-parasitic nematodes. Set 1, No. 1.

Furry, R. B., F. M. R. Isenberg and M. C. Jorgensen. 1981. Postharvest controlled atmosphere storage of cabbage. Search: Agriculture No. 19.

Geeson, J. D. and K. M. Browne. 1980. Controlled atmosphere storage of winter white cabbage. Ann. Appl. Biol. 95:267-272.

Goodey, J. B. 1963. Laboratory methods for work with plant and soil nematodes. Tech. Bull. 1. Ministry of Agriculture, Fisheries, and Food. Her Majesty's Stationery Office, London. p. 26.

Grafius, E., A. Wells, H. S. Potter, C. T. Stephens and G. W.Bird. 1982. Control of insects, diseases and nematodes on commercial vegetables. Cooperative Extension Services. Michigan State Univ. Ext. Bull. 312:20-22.

Greco, N. and I. J. Thomason. 1980. Effect of phenamiphos on Heterodera schachtii and Meloidogyne hapla. J. Nematol. 12:91-96.

Green, C. D. and D. N. Greet. 1972. The location of the secretions that attract male Heterodera schachtii and H. rostochiensis to their females. Nematologica 18:347-352.

Griffin, G. D. 1980. Effect of nonhost cultivars on Heterodera schachtii population dynamics. J. Nematol. 12:53-57.

Griffin, G. D. 1977. Effects of soil moisture on control of Heterodera schachtii with aldicarb. J. Nematol. 9:211-215.

Griffin, G. D. 1975. Control of Heterodera schachtii with foliar application of nematicides. J. Nematol. 7:347-351.

Graney, L. 1983. There is a significant morphological difference between New York H. schachtii and Michigan H. schachtii. Personal Communication.

Hamblen, M. L. and D. A. Slack. 1959. Factors influencing the emergence of larvae from cysts of Heterodera glycines. Ichinole. Cyst development, conditions, and variability. Phytopathol. 49:317. (Abstract)

Hara, T. and Y. Sonada. 1979. The role of macronutrients for cabbage head formation. Soil Science Plant Nutr. 25:103-111.

Holt, H. E. 1971. Hybrid cabbage varieties. The Vegetable Growers News 25:3.

Hough, A. and I. J. Thomason. 1975. Effects of aldicarb on the behavior of Heterodera schachtii and Meloidogyne javanica. J. Nematol. 7:221-229.

Hough, A., I. J. Thomason and W. F. Farmer. 1975. Behavior of aldicarb in soil relative to control of Heterodera schachtii. J. Nematol. 7:215-221.

Jatala, P. and H. J. Jensen. 1976a. Self-interactions of Meloidogyne hapla and Heterodera schachtii on Beta vulgaris. J. Nematol. 8:43-48.

Jatala, P. and H. J. Jensen. 1976b. Parasitism of Beta vulgaris by Meloidogyne hapla and Heterodera schachtii alone and in combination. J. Nematol. 8:200-205.

Jatala, P. and H. J. Jensen. 1976c. Histopathology of Beta vulgaris to individual and concommitant infections by Meloidogyne hapla and Heterodera schachtii. J. Nematol. 8:336-341.

Jenkins, W. R. 1963. A rapid centrifugation-flotation technique for separating nematodes from soil. Plant Disease Reporter. 48:692

Jenkins, W. R. and D. P. Taylor. 1967. Plant Nematology. p. 96. Reinhold Publishing Corp. New York.

Johnson, R. W. and D. R. Viglierchio. 1969. Sugar beet cyst nematode (Heterodera schachtii) reared on axenic Beta vulgaris root explants. Selected environmental factors affecting penetration. Nematologica 15:129-143.

Jones, F. G. W. 1957. Soil populations of beet eelworm (Heterodera schachtii) in relation to cropping. Further experiments with microplots and with pots. Nematologica 2:257-272.

Jorgenson, E. C. 1970. Antagonistic interaction of Heterodera schachtii (Schmidt) and Fusarium oxysporum (Wall) on sugar beets. J. Nematol. 2:393-397.

Kerstan, W. 1969. Die Becinflussung Des breschlechterverhaltnisses in Der Gattung Heterodera. Nematologica 15:210-228.

Kretchman, D. W. and M. A. Jameson. 1978. Cabbage cultivar evaluation trials. Department of Horticulture. Ohio Agricultural Research and Development Center. Horticulture Series, No. 453.

Maggenti, A. 1981. General Nematology. p. 6. Springer-Verlag. New York.

Mai, W. F. 1971. Controlling nematodes. pp. 4-6. (In) Plant Parasitic Nematodes I. B. M. Zuckerman, W. F. Mai and R. A. Rohde (eds.). Academic Press. New York.

Mai, W. F. and G. S. Abawi. 1980. Influence of crop rotation on spread and density of Heterodera schachtii on a commercial vegetable farm in New York. Plant Disease 64:302-305.

Mai, W. F., G. S. Abawi and R. F. Becker. 1972. Population levels of Heterodera schachtii in New York and damage on red table beet and cabbage under greenhouse conditions. Plant Disease Reporter 56:434-437.

Miller, J. P. 1972. Growers guide for vegetable crops. Cooperative Extension Service. College of Agriculture. Washington State University E. M. 2925.

Muchena, P. K. and G. W. Bird. 1983. The role of phenamiphos as a nemastat for Heterodera schachtii control in cabbage production. J. Nematol. 15:485. (Abstract)

Mulvey, R. H. 1960. The value of cone top and underbridge structures in the separation of some cyst-forming nematodes. pp. 212-215. (In) Nematology. Fundamentals and Recent Advances With Emphasis on Plant Parasitic and Soil Forms. J. N. Sasser and W. R.Jenkins (eds.). The Univ. of North Carolina Press.

Mulvey, R. H. and M. Golden. 1983. An illustrated key to the cyst-forming genera and species of Heteroderidae in the western hemisphere with species morphometrics and distribution. J. Nematol. 15:1-70.

Norton, D. C. 1979. Relationships of the physical and chemical factors to populations of plant parasitic nematodes. Ann. Rev. Phytopathol. 17:279-299.

Pendergrass, A., F. M. R. Isenberg, L. L. Howell and J. E. Carrol. 1975. Ethylene-induced changes in appearance and hormone content of Florida grown cabbage. Can. J. Plant Sci. 56:319-324.

Potter, J. W. and C. F. Marks. 1976a. Efficacy of oxamyl against Heterodera schachtii on cabbage. J. Nematol. 8:38-42.

Potter, J. W. and C. F. Marks. 1976b. Persistence of activity of oxamyl against Heterodera schachtii on sugar beets grown in microplots. J. Nematol. 8:35-37.

Olthof, H. A. 1978. Influence of population densities of Heterodera schachtii on sugar beets grown in microplots. J. Nematol. 10: 255-258.

Olthof, H. W., J. W. Potter and E. A. Peterson. 1974. Relationship between population densities of Heterodera schachtii and losses in vegetable crops in Ontario. Phytopathol. 64:549-554.

Oyer, E. B. 1961. Growing cabbage in New York. New York State College of Agriculture. Cornell Extension Bulletin 1042.

Radewald, R. D., B. J. Hall, F. Shibuya and J. Nelson. 1971. Results of preplant fumigation trial for the control of sugar beet nematode on cabbage. Plant Disease Reporter 55:841-846.

Ryder, E. J. 1979. Leafy salad vegetables. pp. 127-169. The AVI Publishing Company, Inc. New York.

Santo, G. S. and W. J. Bolander. 1979. Interacting effects of soil temperature and type on reproduction and pathogenicity of Heterodera schachtii and Meloidogyne hapla on sugar beets. J. Nematol. 11:289-291.

Schmitt, D. P. and D. C. Norton. 1972. Relationships of plant parasitic nematodes to sites in native Iowa prairies. J. Nematol. 4:200-206.

Starr, J. W., W. F. Mai and G. S. Abawi. 1978. Effects of oxamyl on the reproduction of Meloidogyne hapla and Heterodera schachtii. J. Nematol. 10:378-379.

Steele, A. E. 1977. Effects of selected carbamate and organophosphate nematicides on hatching and emergence of Heterodera schachtii on sugar beet. J. Nematol. 9:149-154.

Steele, A. E. 1976a. Effects of oxime carbamate nematicides on development of Heterodera schachtii on sugar beet. J. Nematol. 8:137-141.

Steele, A. E. 1976b. Improved methods of hatching Heterodera schachtii larvae for screening chemicals. J. Nematol. 8:23-25.

Steele, A. E. 1975. Population dynamics of Heterodera schachtii on tomato and sugar beet. J. Nematol. 7:105-111.

Steele, A. E. 1973. The effects of hot water treatment on survival of Heterodera schachtii. J. Nematol. 5:81-84.

Steele, A. E. 1972. Development of Heterodera schachtii on large rooted crop plants and the significance of root debris as substratum for increasing field infestations. J. Nematol. 4:250-255.

Steele, A. E. 1971. Orientation and development of Heterodera schachtii larvae on tomato and sugar beet roots. J. Nematol. 3:424-426.

Steele, A. E. and J. M. Fife. 1969. Effect of liquid nutrient culture, vacuum distillation and dialysis on hatching activity of sugar beet root diffusate of Heterodera schachtii. J. Nematol. 1:223-226.

Steele, A. E. and L. R. Hodges. 1975. In vitro and in vivo effects of aldicarb on survival and development of Heterodera schachtii. J. Nematol. 7:305-312.

Strandberg, J. O. 1979. Growth and phenology of cabbage in a winter production area. Proc. Florida State Hort. Soc. 92:93-96.

Thomason, I. J. and D. Fife. 1962. The effects of temperature on development and survival of Heterodera schachtii Schmidt. Nematologica 7:139-145.

Thompson, H. C. and W. C. Kelly. 1957. Vegetable crops. pp 275-295. McGraw-Hill Book Co. Inc. New York.

Thorne, G. 1961. Principles of Nematology. pp. 270-293. McGraw-Hill Book Co., Inc. New York.

Triantaphyllou, A. C. 1973. Environmental sex differentiation of nematodes in relation to pest management. Ann. Rev. Phytopathol. 11:441-462.

Van Gundy, S. D., L. H. Stolzy, T. E. Szuskiewicz and R. L. Rackham. 1962. Influence of oxygen supply on survival of plant parasitic nematodes in soil. Phytopathol. 52:628-632.

Volk, G. M., C. E. Bell and E. N. McCubbin. 1947. The significance and maintenance of nitrate nitrogen in Bladen pine sandy loam in the production of cabbage. Agricultural Extension Service. Gainsville, Florida. Bulletin 430.

Wallace, H. R. 1963. The Biology of Plant Parasitic Nematodes. 290 p. Edward Arnold. London.

Wallace, H. R. 1959. Further observations on some factors influencing the emergence of larvae from cysts of the beet eelworm, Heterodera schachtii Schmidt. Nematologica 4:245-252.

Wallace, H. R. 1958. Observations on the emergence of cysts and the orientation of larvae of three species of the genus Heterodera in the presence of host plant roots. Nematologica 3:236-243.

Wallace, H. R. 1956. The effect of soil structure on the emergence of larvae from cysts of the beet eelworm. Nematologica 1:145-146.

Ware, G. W. 1978. The Pesticides Book. pp. 35-40. Freeman and Co. San Francisco.

Weaver, J. E. and W. E. Brunner. 1927. Root development of vegetable crops. (First Edition). McGraw-Hill Book Co., Inc. New York.

Webster, J. M. 1972. Economic Nematology. pp. 49-52. Academic Press. London.

Webster, J. L. 1953. Cabbage seed. Seed production series. No. 1. British Columbia Department of Agriculture.

Wood, W. B. 1914. Cabbage Production in Ohio. Ohio Agricultural Extension Service. The Ohio State Univ. Bulletin 391.

Wright, S. J. 1981. Nematicides: Mode of action and new approaches to chemical control. pp. 426-433. (In) Plant Parasitic Nematodes. V III. B. M. Zuckerman and R. A. Rohde (eds.).

Wright, G. P. 1950. Sugar beet nematode in the Salinas district. Spreckels Sugar Beet Bull. 114:35-40.