BIOLOGY AND BIOCONTROL POTENTIAL OF *TAPHROCERUS SCHAEFFERI* NICOLAY AND WEISS (COLEOPTERA, BUPRESTIDAE), A LEAF MINER ATTACKING YELLOW NUTSEDGE (*CYPERUS ESCULENTUS* L.)

by

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INTRODUCTION

Biological control has proven to be an effective method of weed control. A number of weed species have been successfully controlled through the introduction or augmentation of biotic agents capable of limiting their host's abundance. Biological control has succeeded in some cases where other methods of control have been unsuccessful or impractical. Often the potential of biological control methods are not investigated until other means of control have been found ineffective. This is not a reflection of an inherent weakness of biological control, for there are many economic and environmental advantages to this method of control. Rather, it reflects the lack of a basic knowledge of ecology which makes biological control an unpredictable science.

Perennial rhizomatous weeds such as yellow nutsedge, Cyperus esculentus L. (Cyperaceae) are rapidly becoming serious weed problems throughout the world. The weed currently ranked by some scientists as the worlds worst, purple nutsedge, Cyperus rotundus L., is a perennial rhizomatus weed (Hauser 1971). The mechanization of farming is largely responsible for the increasing severity of these weeds. A drastic decrease in cultural practices, such as the discontinuation of deep plowing, crop rotation, and frequent cultivation, have contributed to the problem. The widespread use of herbicides effective on both annual broadleaf and grass weeds has apparently released many perennials from competion.

Effective herbicide control of perennial rhizomatous weeds is often difficult to achieve. Dormant buds on rhizomes or tubers usually accumulate only sublethal dosages of applied herbicides. The death of apical growth releases lateral buds from apical dominance and new growth often recurs within a few weeks (Bendixen 1970a, Hauser 1968).

Due to the general ineffectiveness of herbicides against perennial rhizomatous weeds the potential of biological control warrants investigation. With the exception of work done on purple nutsedge, this form of control has been largely ignored. A necessary preliminary study of any weed being considered for biological control is a survey of the insect fauna already associated with the plant and an evaluation of their damage. Effective native insects may be present or natural enemies from the target weed's native habitat may have been already imported with the host (Frick and Garcia 1975).

In 1972 the Department of Entomology at Virginia Polytechnic Institute and State University initiated a study of the arthropod fauna of selected weeds in Virginia. A survey of the insect fauna of four Virginia weeds, one of them yellow nutsedge, was conducted by Beisler (1974). With respect to yellow nutsedge, Beisler concluded that three insects warranted an investigation of their biological control potential. The biology of these insects, Taphrocerus schaefferi Nicolay and Weiss (Buprestidae),

Glyphipteryx impigritella Clemens (Glyphiptergidae), and Elliponeura debilis Loew (Chloropidae) was essentially unknown. The present study was undertaken with the objective of investigating the relationship of these insects with yellow nutsedge. Specifically, the objectives of this study were to:

1). Review the literature to obtain available information on yellow nutsedge and the biology and host specificity of these insects;

2). Investigate the biology of the insect judged to possess the greatest potential with the objectives of a). elucidating its life history, b). determining the factors limiting the insects density, c). investigating the synchronization and relationship between host and parasite, and d). evaluating the insect-inflicted damage.

LITERATURE REVIEW

Cyperus esculentus

Cyperus is the second largest genus of Cyperaceae, comprising approximately 700 species world-wide. Cyperaceae, though a large family represented by 83 genera, is of little economic value (Lawrence 1951). *Cyperus* may be distinguished from other Cyperaceae by the presence of strictly 2-ranked scales and terminal umbellate infloresences (Marcks 1974). Kukenthal published a monograph of the genus in 1936. However, Fernald (1950) and others have found many inconsistences in this work. Mohlenbrock (1960) and Marcks (1974) have published treatments of *Cyperus* for the states of Illinois and Wisconsin, respectively. *Cyperus esculentus* and a very closely related species, *Cyperus rotundus*, differ from the remaining species of *Cyperus* in that their rhizomes form tubers. These two species may be differentiated by the infloresence color or specific nature of tuber formation (Hauser 1968).

Yellow nutsedge is the official common name for *Cyperus esculentus* (Weed Society of America 1962). Other common names used include nothern nutgrass (Bell et al. 1962), yellow nutgrass (Justice and Whitehead 1946), and chufa (Killinger and Stokes 1947). Yellow nutsedge is distributed throughout the continental U.S. and southern Canada, and extends south to northern Argentina (Mulligan and Junkins 1976). It is also present in and probably indigenous

to Eurasia (DeBach 1964). Many differences in gross morphological structure have been noted (Costa and Appleby 1976, Mulligan and Junkins 1976). A differential response to herbicides has been obtained with plants from different geographical areas (Boldt et al. 1976, Costa and Appleby 1976, Hauser 1968). In the United States three varieties of yellow nutsedge are sometimes recognized: C. esculentus esculentus L., C. esculentus leptostachyus Boeckl., and C. esculentus sativas Broeckl. (Fernald 1950, Mohlenbrock 1960). The first two varieties are apparently widely distributed and their validity is uncertain. C. esculentus sativas, or chufa, is a cultivated variety indigenous to Europe and North Africa. It is still cultivated in parts of southern United States (Poinar 1964b).

Economic Importance. Yellow nutsedge is a serious weed throughout much of the United States. It infests many agronomic and horticultural crops, lawns, and pastures. The USDA estimated that in 1968 nutsedges as a group infested approximately 7.5 million acres of agronomic crops and were continuing to intensify on 89% of the acreage (USDA 1972). This compares with an estimated 6.7 million acres infested in 1965 with 79% continuing to intensify (USDA 1968).

Yellow nutsedge competes vigorously for nutrients, water, and light, particularly in the early growing season (Keeley et al. 1973). Keeley and Thullen (1975) found that heavy infestations of

yellow nutsedge reduced yields of cotton by 34%. Corn infested with medium and high densities of yellow nutsedge reduced yields 17% and 38%, respectively (Farwell and Hawf 1975). Besides reducing yields and increasing production costs due to increased cultivation and herbicide usage, yellow nutsedge may also lower crop quality and increase harvesting and processing costs. Yellow nutsedge rhizomes pierce the tubers of potatoes, thus reducing their value. In the processing of lima beans, clumps of yellow nutsedge passing through the viners may cause breakdowns. Yellow nutsedge tubers may become mixed with shelled beans and necessitate costly hand sorting (Bell et al. 1962). Bird and Hogger (1973) found two severe nematode pathogens of cotton, Meloidogyne incognita Chitwood and Hoploaimus columbus Sher., in the roots of nutsedge. They suspect nutsedge is serving as a host reservoir and note that the increase in the severity of nematode diseases of cotton have coincided with the recent rise of nutsedge as a weed problem.

Yellow nutsedge is known to be of value to wildlife, and a cultivated variety, chufa, is sometimes grown for swine feed. In its native habitat nutsedge is often utilized by ducks during the winter months (McAtee 1917). As a weed in fields and cultivated land its tubers are dug by rodents and game birds (Martin et al. 1951). There is no quantitive data evaluating the relative importance of yellow nutsedge to wildlife. Martin et al. (1951) ranked the more widely utilized wildlife food plants according to their

importance. Yellow nutsedge is ranked 11th in the Southeast Region of the U.S. for marsh and aquatic plants. It does not appear in the listings of any other region.

Chufa, C. esculentus sativas, is a cultivated variety still grown on small acreages in the United States, Soviet Union, Italy, Hungary, Spain and Egypt (Reid et al. 1972). The plant is primarily used as swine feed, although in southern Europe roasted and ground chufa tubers were sometimes used as a substitute for coffee or cocoa. In Florida, 7,244 acres were planted in 1941 (Killinger and Stokes 1946) and approximately 5,000 acres in 1962 (Poinar 1964b). Most of the chufa acreage in the United States is grown by small farmers in the South. Generally only small fields are cultivated for use as a fall or winter crop in which hogs are released to feed (Killinger and Stokes 1947). Chufa is of little nutritive value. The tubers consist mainly of starch, oil, and sugars with low amounts of protein and high fiber content (MoKady and Dolev 1970, Power and Chesnut 1923).

Biology. Yellow nutsedge occurs in a wide variety of soils ranging from sand to loam to clay, but appears to do best in lighter soils (Hauser 1968, Mulligan and Junkins 1976). This sedge is often restricted to damp areas, for soil moisture has a substantial influence on tuber production and vegetative growth. Tubers are the only vegetative part of the plant to overwinter. Their survival is reduced by soil compaction, dessication, and low tempera-

tures (Bell et al. 1962, Thomas 1969). Overwintering temperatures apparently limit the geographical distribution of yellow nutsedge. Tubers generally do not survive in areas where the minimum air temperature isotherm is below -17.8°C (Stoller 1973).

Yellow nutsedge is a ruderal species usually confined to recently disturbed habitats. Its native habitat is in bogs and marshes and along the margins of rivers, streams, and lakes. This sedge is a poor competitor but does well in its native habitat because spring flooding eliminates most plant competition in the early growing season. In cultivated fields, yellow nutsedge is associated with a variety of colonizing weeds (Mulligan and Junkins 1976).

The principle site of vegetative growth and propagation is the basal bulb. This bulb may be formed from a seedling, but tubers are normally the source of shoots early in the growing season. Tubers themselves are not basal bulbs. A sprouting tuber first produces one or more rhizomes which later terminate in a basal bulb. Apical growth of the basal bulb produces the leafy plant and infloresence. New rhizomes also originate from the basal bulb and grow for some time as indeterminate underground rhizomes. These rhizomes may transform into either tubers or basal bulbs under suitable conditions (Bendixen 1970b, Jansen 1971).

Tumbleson (1960) and Tumbleson and Kommedahl (1962) found that tuber sprouting is inhibited by one or more substances in or

on the epidermis. Apparently both cold temperatures and leaching by water are required to break dormancy. This usually occurs in the next growing season, but some tubers are known to remain dormant for several years. Tubers sprout in the spring in response to warm temperatures. The long photoperiods of spring and early summer induce the transformation of most indeterminate rhizomes into basal bulbs, resulting in the production of many secondary and tertiary plants. As the summer photoperiod declines below 14 hours, few basal bulbs are produced and most rhizomes transform into tubers. Yellow nutsedge flowers in response to an intermediate photoperiod of 12 to 14 hours. Flowering first occurs in early July and may continue through September (Garg et al. 1967, Jansen 1971).

Yellow nutsedge readily reproduces both vegetatively and through the production of seed. Vegetative reproduction may occur through the development of new basal bulbs or indirectly through the formation of tubers. Tumbleson and Kommedahl (1961) found that a single tuber in one growing season produced 1,900 plants and 6,900 tubers in an area with 21 dm diameter.

Yellow nutsedge flowers are perfect, wind pollinated, and self-incompatable. There is a considerable variation in the degree of seed set throughout its range. The amount of seed set is probably correlated with the distance between genetically different plants and the weather conditions at the time of cross-

pollination (Mulligan and Junkins 1976). Hill et al. (1963) planted a single yellow nutsedge seed which developed into a stand yielding 90,000 seeds with a germination rate of 51%. A number of workers have reported germination rates of yellow nutsedge seed ranging from 47% to 96% (Bell et al. 1962, Bell and Larssen 1960, Justice and Whitehead 1946).

Control. Mechanical control techniques such as hand weeding or hoeing are effective at reducing the growth of yellow nutsedge, but impractical on a commercial basis. Cultural control techniques are generally ineffective. Practices such as crop rotation, scheduled fallowing, and regular cultivation or harrowing operations do not in themselves afford economic control (Bell et al. 1962, Orsenigo and Smith 1953).

A large number of herbicides have been evaluated for their efficacy in the control of yellow nutsedge. Apparently the thiocarbamates (EPTC, cycloate, vernolate, and butylate) and triazines (atrizine, cyprazine, cyanize, and ametryne) have been most thoroughly investigated. The herbicides currently used in controlling yellow nutsedge vary with different crops. Soil incorporated butylate is perhaps most often used in corn (Hawf 1974, McLaughlin and Hartwig 1976). EPTC has long been used in potatoes and peanuts although seasonal control is rarely achieved (Parochetti 1974, Selleck and Weber 1976). Bentazon and cyperquat have been found to be fairly effective in turf (Hall and Parochetti 1975,

Jagschitz 1976). Soil incorporated vernolate is widely used in soybeans (Hauser et al. 1972).

A number of new approaches to chemical control of yellow nutsedge have been investigated. Bendixen (1970a) attempted to alter the plant's growth form with growth hormones in such a way that plants might be controlled as annual species. Hauser (1968) reported that the subsurface application of triazine herbicides controlled nutsedge more effectively when soil incorporated. Several devices in the late 1960's were developed for subsurface placement, but apparently none were practical. Another technique involves herbicide crop rotation. In this system both crops and herbicides are rotated with emphasis on maximal chemical pressure on nutsedge (Hauser 1968, Hauser et al. 1974, Hauser et al. 1972).

In spite of a great deal of research conducted in recent years, effective herbicides have not been discovered. The problem, as previously mentioned, is that dormant tubers absorb only sublethal dosages of applied herbicides. Persistant chemicals could perhaps achieve control by remaining in the soil until the new growth recurs. However, the use of such materials is environmentally undesirable. Effective translocation to the tubers is essential for seasonal control with nonpersistant chemicals. Selective herbicides with such an ability have not been developed (Bendixen 1970b, Davis and Dusbabek 1975).

Biological control of yellow nutsedge has not been attempted. Prior to Beisler's survey (1974) little was known about the insect fauna of yellow nutsedge. However, the insects associated with purple nutsedge have been well studied. In the southern United States and other semitropical and tropical areas of the world, yellow and purple nutsedge often grow in mixed stands. It is likely that in these areas they share a similar fauna due to their close relationship. However, purple nutsedge is generally more dominant, and as a consequence studies have concentrated on this species.

Hawaiian scientists were the first to attempt biological control of purple nutsedge. In 1925 they introduced the stem borers Bactra venosana Zeller (Olethreutidae) and Athesapeuta cyperi Marshall (Curculionidae) from the Philippines to Hawaii. The biology of these insects and an evaluation of the factors limiting their effectiveness was studied by Poinar (1964a). The insect fauna of purple and yellow nutsedge was surveyed by Poinar (1964b) in southern California. He concluded that Bactra verutana Zeller appeared to be the most likely agent for the control of both nutsedges. A number of workers have since investigated the biology and biological control potential of this insect (Frick and Garcia 1975, Garcia and Frick 1975, Keeley et al. 1970). The biological control potential of Bactra minima minima Meyrick, indigenous to the Indian subcontinent, has recently been studied in detail (Frick 1976). These insects offer some promise as biological

control agents, but none have proven sufficiently effective in nature. The use of augmentation by mass rearing and inundation early in the growing season is currently being evaluated for Bactra verutana (Frick and Garcia 1975).

Insects Attacking Cyperus esculentus

Taphrocerus schaefferi (Coleoptera, Buprestidae). This species belongs to the tribe Agrilini. The genus Taphrocerus is restricted in distribution to the Americas and is composed of 134 Neotropical and 12 North American species (Obenberger 1937). T. gracilis (Say) is the only member of this genus whose life history has been investigated (Chapman 1923). Nicolay and Weiss (1920), in a treatment of the North American species of Taphrocerus, described T. schaefferi. The known distribution of T. schaefferi is from Texas and Vancouver to eastern United States. Nothing has been published concerning the biology of this species. Beisler (1974) reported that T. schaefferi was a leaf miner of Cyperus esculentus.

Elliponeura debilis (Diptera, Chloropidae). The genus Elliponeura comprises two Neartic species, both of which are widely distributed. Adults of this genus may be distinguished from other chloropids by the absence of a posterior crossvein in the wing. E. debilis was described by Loew in 1869 from specimens collected near Washington D.C. An extensive treatment of the chloropid fauna of Kansas was published by Sabrosky (1935). The known

distribution of E. debilis is from Michigan to New York and south to New Mexico and Florida (Stone et al. 1965).

The biology of E. debilis has not been investigated. One male was swept from red-top grass in Kansas (Sabrosky 1935). Krystowski (1968) collected a number of specimens from Eleocharis obtusa (Willd.) and E. smallii Britt (Cyperaceae). She attempted to rear this species from field collected specimens, but obtained only one female which laid eggs. She determined that larvae are primary invaders of newly formed achenes. Only one larva was usually found present per inflorescence and anywhere from 5 to 25 achenes were destroyed. E. debilis has also been reared from field collected Cyperus esculeutus (Beisler 1974). He obtained adults from July 13 to August 29, 1973.

Glyphipteryx impigritella (Lepidoptera, Glyphipterygidae). The genus Glyphipteryx comprises approximately 220 species worldwide (Chopra 1925). Dyar (1902) lists nine North American species. G. impigritella was described by Clemens in 1862. A synonym, G. exopatella Chambers, was described from specimens collected in Kentucky (Chambers 1875). G. impigritella is known to be distributed from California to Texas, and north to New Hampshire (Forbes 1923). Beisler (1974) obtained 12 specimens from caged Cyperus esculentus plants. These adults were collected in Montgomery Co., Virginia from July 12 to September 13, 1973. Frick observed G.

imprigritella mining the basal portion of the leaves of *Cyperus rotundus* in Stoneville, Mississippi (personal communication, 1976).

MATERIALS AND METHODS

Taphrocerus schaefferi

Host Propagation. Yellow nutsedge was grown in the Entomology Insectary from tubers collected during the fall of 1975 at the VPI & SU Dairy Science (DS) cornfield in Montgomery Co. These plants were used in all subsequent lab studies. Plants were propagated by tubers. Tumbleson and Kummedahl (1962) found that washing tubers in cold water (13°) broke tuber dormancy. This method was successfully used during the present study. Tubers were placed in a half pint mason jar with a screen cover held in place by a band. A nozzle-gun attachment on a garden hose was directed into the jar through the screen, and the tubers were agitated under the full force of the water for about 10 minutes. During the summer and fall it was necessary to place the tubers in ice water for 10-15 minutes after agitation. This was not necessary during the winter and spring because the water used during agitation was cold enough to break tuber dormancy. Tubers were then placed on moist filter paper inside petri dishes until they sprouted. The petri dishes were kept in a slanted position and additional water was added every 4 or 5 days.

All plants were grown in Weblite Soiless Potting Mix ® with osmocote, hydrated lime, and vermiculite added in the following proportions: 40 lbs. Weblite/9 oz. osmocote/9 oz. hydrated lime/40

oz. vermiculite. Miracle Gro was used to fertilize the plants when leaf yellowing occurred.

Life History. Experiments concerning the life history of T. schaefferi were conducted in an environmental chamber (Sherer-Gillett). The controlled environment was set at a 15-hour, 27°C, photophase and 16°C scotophase. A hygro-thermograph was used to record the relative humidity, which ranged between 60 and 80%. The light source of the chamber consisted of ten four-foot florescent light tubes. In the first week of June, 1976, about 200 adult T. schaefferi were collected at the McPherson Farm (MF) in Montgomery Co. These specimens were confined to a 2'x2'x2' plexiglass cage containing potted yellow nutsedge and placed within the environmental chamber. The feeding and mating behavior of the caged beetles was closely observed and recorded. A series of experiments using the eggs obtained from these caged specimens were conducted within the chamber. The egg, larval, and pupal development periods of 20 specimens were determined by observing their stage of development at daily intervals.

Fifteen potted plants were removed from the plexiglass cage and all but one egg per leaf were removed. The hatching date for each of the 90 eggs was recorded by checking the leaves daily. Their fertility was recorded. Twenty of the newly-hatched larvae were used to determine the outline of the mine during development.

Measurements of length and width were taken every day for the first week and thereafter every 3-4 days.

The 70 remaining newly-hatched larvae were used to determine the morphology and duration of each larval instar, and the tissues consumed during larval development. At age intervals of two days, four larvae were removed from their mines and a 1 cm cross section of the mined leaf was taken. This provided a series (at two day intervals) of larvae and mine cross sections throughout the larval developmental period. The larvae were killed in boiling water and preserved in 75% ethanol. Measurements of prothoracic width, body length, and distance between peristomata were recorded for each larva. For a detailed morphologic study, specimens of each instar were cleared in KOH, stained with Essigs (Wilkeys modification), and mounted in balsam (Wilkey 1962). A Zeiss phase-contrast microscope was used to study the slide mounted larvae. The general morphology of preserved larvae was also examined under an American Optical Spencer binocular microscope. Most of the terminology used in the morphologic study was taken from Benoit (1964). The leaf cross sections were temporarily stored in a fixative consisting of FPA with a drop of Polysorbate 80. The tissue was later removed from the fixative, dehydrated with tetrabutyl alcohol, and imbedded in paraffin. An American Optical microtome was used to prepare 18μ cross sections of tissue. The

tissue was stained with safranin and fast green. Standard botanical microtechniques were used (Berlyn and Miksche 1976).

An experiment was designed to determine 1) the maximal number of larvae able to mature on a single leaf, 2) the mass of newly emerged adults, and 3) the leaf mass consumed at each larval density. Six potted plants were confined within the plexiglass cage so as to receive several eggs per leaf. Four replicates of 2, 3, 4, 5, and 6 eggs per leaf and 10 replicates of one egg per leaf were obtained by this method. T. schaefferi development on these leaves was checked at regular intervals and the number of individuals per leaf to reach the third instar, pupal instar, and adult stage was recorded. Ten newly-emerged adults were weighed on a Mettler balance after the beetles had fed for 4-5 days. The mined area and leaf mass consumed at the completion of larval development was determined for each leaf with the following equations:

$$X = A/B$$

$$Y = (C-B)\ X$$

Where X = total mined area in cm^2

Y = total mass consumed

A = mass of total mined area

B = mass of $1cm^2$ mined section

C = mass of $1cm^2$ unmined section

Note: Frass and exuvia were removed before weighing. C was cut just basal to the mine on each leaf and served as a control.

An attempt was made to break the diapause of T. schaefferi. Adults used in this experiment were obtained from lab reared larvae which completed development during July and early August. The beetles were kept in the plexiglass cage with their host plant until September 1, 1976. A total of 17 cages were constructed to hold these specimens inside a growth chamber (Forma Scientific). Fifteen cages consisted of one pint cups (plastic) covered by inverted one quart clear plastic containers. The pint cups were half filled with a mixture of clay, peat moss, and Weblite Soiless Potting Mix®. Two or three yellow nutsedge plants were transplanted into each cup. The mixture was then covered with about 2cm of litter obtained from DS. The bottoms of the clear plastic containers were removed and covered with organdy before being placed on the pint cups. Each cage contained 10 beetles. Two additional cages were constructed in a similar manner from 6"x6" plastic pots and gallon cardboard containers. These cages contained 50 beetles each. All cages were placed in the growth chamber on September 1, 1976. The photoperiod and temperature was gradually reduced from 12 hours, 27°C day, 16°C night to 10 hours, 6°C day, 1°C night by September 29. The cages were watered about once a month, and the relative humidity was kept between 80 and 100%. Cages were removed from the chamber at various intervals to determine mortality and the approximate time of diapause cessation. Diapause was assumed to be broken if mating behavior was initiated.

Field Population. In early June at least 12 nutsedge-infested cornfields in Montgomery, Giles, and Pulaski Counties were examined for the presence of T. schaefferi eggs or adults. In only two of these fields were more than 1 or 2 eggs found to be present. These two sites, located at MF and the VPI & SU Agronomy Field (AF) were selected for a field study. Thirty plants at each site were selected and tagged for periodic sampling. At MF a modified point intercept method was used to randomly select the plants. The sampling device consisted of ten, 2 ft. rods arranged in two vertical, parallel rows 1 ft. apart. It was placed in a randomly selected location within the field three times. At each placement the yellow nutsedge plant closest to each rod tip with at least 1 egg present was tagged for future sampling. At AF the sampling device was impractical due to the sparseness of the T. schaefferi infestation and the restricted distribution of the host. A thorough search of the yellow nutsedge was required to obtain 30 egg-infested plants for tagging.

The leaves on each plant were assigned numbers according to their location on the stem. The lowest leaf received a number one and each successive leaf was numbered accordingly. At each sampling date the leaf condition (dead or alive), number of eggs, larvae, or pupae present were recorded for each leaf of each plant. Plants were first sampled on June 18, 1976. Sampling

was conducted at biweekly intervals during the first month, and thereafter at weekly intervals.

Various methods were used to obtain parasites of the egg, larval, and pupal stages. Egg parasites were sought during June and early July by bringing into the laboratory at weekly intervals egg infested yellow nutsedge. Leaves with eggs present were removed from the plants and placed in plastic bags. The bags were later examined for the presence of parasites.

Two methods were used for obtaining larval and pupal parasites. On July 25, 10 plants with leaf miners present were dug up at MF, brought into the insectary, and potted. Cylindrical organdy sleeves were placed over 30 mined leaves and sealed at each end with duct tape. These sleeves were later checked for the emergence of parasites or adult T. schaefferi. During the first week of August, 80 mined leaves from both sites were brought into the insectary. The mines were examined and the condition of the larvae was noted. Living larvae, pupae, or parasite pupae were placed in petri dishes containing moist cotton. The condition of these insects was checked regularly and any emerged parasites were removed and preserved in 75% ethanol.

A limited study of the density and distribution of T. schaefferi eggs was conducted at MF on June 11. A somewhat homogeneous stand of yellow nutsedge was selected for the study. The point intercept sampling device was placed every 5 paces along randomly selected

lines bisecting the stand. The yellow nutsedge plant closest to each point was examined and the total number of eggs present was recorded.

Damage Evaluation. A cage experiment was designed with the objective of evaluating the effect of high densities of T. schaefferi on yellow nutsedge. During the fall of 1975 a clone of yellow nutsedge was started, and it served as a source of all plants used in this experiment. It has been demonstrated that initial tuber mass is correlated with plant vigor and total vegetative production (Stoller et al. 1972). To ascertain the mass of overwintering yellow nutsedge tubers in the field, 81 tubers at DS were sampled in March 1976. These tubers were brought into the laboratory, cleaned, blotted dry, and weighed.

In late May 400-500 tubers were removed from the clone and induced to sprout. Tubers used in the cage experiment sprouted between June 5 and June 10. Each day the newly-sprouted tubers were removed from the petri dishes, massed, and placed into peat pots. A total of 80 plants, weighing 100-200 mg were randomly selected for use in the experiment. After 10 days of growth they were placed in the environmental chamber for about 4 days. Half the plants were randomly selected to serve as controls. They were placed in the chamber but not within the plexiglass cage. The remaining plants were placed inside the plexiglass cage so as to receive a heavy infestation of eggs. After another 10 days the

plants were returned to the environmental chamber for the same treatment. When removed from the chamber the plants were transferred to outdoor cages.

Two cages were constructed and served to expose the plants to field conditions without the interference of other organisms. They were set up at the Prices Fork Laboratory in an open meadow. The cages measured 4'x3'x3', were covered on five sides with screen and an inner lining of organdy, and had a hinged door to permit access. The soil at the site was fumigated with methyl bromide one month before the cages were set up. A soil sample was taken and sent to the county Extension Agent for analysis. The Agent evaluated the soil for corn planting and made recommendations for any deficiencies. A pit 18" deep was excavated where the cages were to be located, and the soil placed on a tarp for later use. Plastic bags (12" x 4" and 18" x 10") were used to construct 18" x 4" plastic tubes open at each end. These tubes functioned like pots and isolated each plant's growth from the others. Each tube consisted of four bags, two of each size, positioned so that there would be a thickness of three plastic layers. The excavated soil was used to fill all but the top 10 cm of the plastic tubes. They were placed vertically in the pit and arranged in a 4' x 3' rectangle. The sides of the rectangle were encircled with a sheet of plastic and the rest of the pit was filled in. At this stage of construction the plants were transferred to the plastic tubes. The cage was placed over the plants and the sheet of plastic was taped and stapled

to its base. A total of 32 plants from the environmental chamber were transferred to the cages. Twelve served as controls. Five replicates of plants with 5, 6, 7, and 8 leaves infested with two or more eggs were selected.

Four parameters, total dry weight, fresh weight of tubers, and number of tubers and daughter plants produced, were selected to serve as indicators of plant growth. Keeley et al. (1970) used three of these parameters to quantify the growth of purple nutsedge. The growth of the caged plants was evaluated after nearly all the T. schaefferi had pupated. The soil was removed from their root systems by placing the plants in a sieve and washing away the soil with a nozzle-gun attachment on a garden hose. The tubers fresh weight, number of tubers and daughter plants, and, after two months of drying, total dry weight, was determined.

Elliponeura debils

Yellow nutsedge inflorescences were examined for the presence of E. debilis during the fall of 1975 and 1976. An attempt to rear the insect in the laboratory was made in 1976. Field collected inflorescences were placed in two 1'x2'x2' organdy covered cages within the environmental chamber. Both laboratory grown and field-collected plants were used. Plants obtained from the field were uprotted at the VPI & SU Poultry Science Field (PS) and transferred to pots. Adults emerging in the organdy cages were placed in the

plexiglass cages and supplied with honey water. An attempt was made to induce host flowering in both mature plants and recently sprouted tubers. In one experiment plants of both types were exposed to gradually declining photoperiods, starting at 16 hours. In another experiment sprouting tubers of two clones were exposed to simulated spring and then summer photoperiods and temperatures inside the environmental chamber. The clones were obtained from two different localities, DS and PS, and were presumed to be genetically different.

To detect the presence of eggs and larvae, both stained and unmodified inflorescences were examined under a binocular microscope. Staining was accomplished by emersing the inflorescences in a heated solution of lactophenol and acid fushcin for about an hour. This cleared the inflorescence and stained the insect tissue. The inflorescence was then placed between two plates of glass and examined under the binocular microscope.

Glyphipteryx impigritella

A survey to detect the presence of G. impigritella was conducted during the summer of 1976. On July 12th and 27th about 5 thousand yellow nutsedge plants from MF and DS were collected and returned to the laboratory. They were placed in emergence chambers and checked regularly for the presence of G. impigritella adults. Between August 27 and September 9 MF and PS were examined for the

presence of leaf mining G. impigritella. A total of about 400 plants were examined for larval mines at the base of each leaf.

RESULTS AND DISCUSSION

Taphrocerus schaefferi

Life History. Adult beetles spend most of the day on the lower leaf surfaces, either resting or feeding on the leaf margins (see Fig. 26). When disturbed, they may fly, cling tightly to the leaf surface, or feign death. No premating behavior patterns were detected. Males, upon approaching females, mount from the posteriodorsal side. The beetles usually remain in position for 20-30 minutes, but may stay together for several hours. Females mate several times throughout the oviposition period. They select oviposition sites on the younger leaves emerging from the center whorl. Eggs are laid singly on the upper leaf surface, usually on the midrib (see Fig. 23). The egg is oval in outline and surrounded by a thin transparent chorion which serves as a gluing material.

Observations on the development of T. schaefferi are summarized in Table 1a. Eggs are initially colorless but approximately two days after oviposition they begin to darken. This darkening occurs on the exposed side of the egg in a distinct layer between the chorion and embryo. After 12 hours the egg takes on a shiny black color. The mean incubation period is 16 days. A fertility rate of 95% was obtained with 87 eggs. Eggs persist on the leaves after larval eclosion and are still present at the onset of leaf senescence.

The length of each larval stadium and the mine outline and tissues consumed by each instar are summarized in Figures 1-3 and Table 1b, Plate 1. Upon hatching the larva chews a thin slit through the attached side of the egg and leaf cuticle. As it feed on the upper epidermal and chlorenchyma cells it enters the leaf. Initially the larva may mine in a direction either proximal or distal to the leaf base, but it invariably follows the parallel veination. The larva excavates a mine approximately 0.5 mm wide in one direction for about 10 cm, then turns 180° and retraces the mine. As it travels back toward the egg the mine width is increased to approximately 1.0 mm. The larva continues to mine beyond the egg for a distance of 5 to 10 cm and, once again, turns 180° and mines back toward the egg. As the larva approaches the center of the mine it molts for the first time. The first stadium is approximately four days. Only the upper epidermal layer and some of the chlorenchyma cells are consumed during this stadium. The resulting mine is long and narrow, approximately 1.0 mm wide and 13 cm long.

The second instar larva widens and deepens the central 10 cm portion of the mine. The second stadium is seven days. As in the first instar, only the upper epidermal and chlorenchyma cells are consumed. The outline of this mine is approximately 2.0-2.5 mm wide and 10 cm long.

The third instar continues to widen and deepen the central 10 cm portion of the mine (see Fig. 24). The third stadium is 12 days.

The larva destroys upper epidermal and chlorenchyma cells, bundle sheaths, and vascular bundles. In the mined section of the leaf, all epidermal cells are destroyed and only the semitransparent cuticle remains. The only chlorenchyma cells avoided by the larva are located in a 4-6 mm strip in the V-shaped leaf midsection. Approximately one half, or 35, of the total vascular bundles are consumed. Of the 9 primary vascular bundles in the leaf, 4-6 are destroyed. The resulting mine is somewhat rectangular in outline, about 4 mm wide and 10 cm long. An unmined margin (0.5-1.0 mm wide) is left on each side of the mine.

Larvae always mine in a direction parallel to the leaf veination. When feeding the larva moves its head and thorax horizontally in an arc of about 120°. Leaf tissue is scraped off with the mandibles and manipulated into the mouth. A portion of the removed leaf tissue is never consumed. It accumulates in the center of the mine along with the feces. A single larva destroys an average 0.053g of leaf tissue during its development (see Table 2a). Larvae are cannibalistic and only one larva per leaf survive. In an experiment with four replicates of 2, 3, 4, 5, and 6 eggs per leaf, only one adult emerged from each leaf. Third instar larvae placed in a watchglass were observed to feed on each other. The amount of leaf tissue consumed in mines with more than one egg per leaf is only slightly greater than those with only

one egg. This indicates that cannibalism takes place early in larval development.

Larvae achieve locomotion by moving the body segments in a series of undulations. The venter of the mesothorax and abdominal segments 1-8 possess a pair of fleshy lobes thickly beset with microspines. A single proleg is borne on the 9th abdominal segment. These structures enable the larva to move in any direction, both forward and backward.

Pupation occurs inside the central portion of the mine (see Fig. 25). The pupal stadium is 11 days. Pupae remain motionless on their dorsum for the duration of pupal development. Emerging adults crawl 1-2 cm away from the exuvia and remain motionless within the mine for about three days. After this post-pupal resting period, adults chew a hole in the upper leaf surface and emerge. A mean weight of 0.0019g was obtained for 10 newly-emerged adults.

The results of the diapause study are summarized in Table 2b. A mortality rate of 50% was obtained after about 50 days, although some beetles survived for 140 days. Surviving adults remained alive for several weeks at room temperature and readily fed on yellow nutsedge. However, they never mated and it was assumed that diapause had not been broken. A possible reason for the failure was a lack of subfreezing temperatures. Although this beetle is distributed in southern U.S. where freezing temperatures are rarely encountered, it is conceivable that the more northerly

distributed populations require colder temperatures. Another possibility is that the beetles may have been nutritionally deprived. Adults in the field emerge in July and early August and disperse from the habitat of their host. Alternative food sources, such as pollen, may be required for proper sexual maturation.

Larval instars may be differentiated by the distance between peristomata (see Figure 3). The use of head capsule measurements is not practical because the epicranium is largely withdrawn into the prothorax. Body length and prothorax width are more variable than the peristomata measurements, and cannot be used to differentiate the instars.

Descriptions of Immature Stages. The immature stages of T. schaefferi have not been previously described. Except for T. gracilis, larvae of the Taphrocerus species are unknown. Nicolay and Weiss (1920) described the adult stage. In the following description, the third instar is described in full, while only the structures differing from this instar are present in the first and second instar descriptions. Means of the various measurements occurring through the description are presented with their statistics in Table 3. All larval illustrations are on Plate 2.

EGG. Length: 1.34 mm (range 1.26-1.41); width: 0.47 mm (range 0.37-0.51). Oval in outline, thin and flat; shiny black color, exposed surface smooth. Based on 10 eggs.

FIRST INSTAR (Fig. 14). Body length: 1.68 mm (range 1.28-2.29); peristomata distance: 0.19 mm (range 0.189-0.195); prothorax width: 0.41 mm, (range 0.37-0.44). Similar to third instar, with the following exceptions: head more retracted into prothorax with posterior margin of frons not visible, ratio of head capsule to prothorax width approximately 0.7; prothorax subovoid, slightly wider and 3-4 times longer than other thoracic segments, dorsal and ventral shields scarely distinguishable from membraneous areas, lightly sclerotized, asparate only in most anterior region; mesothorax without microspines in posteriolateral margins; abdominal segments 1-8 with fewer setae (4-8); ninth abdominal segment with dorsal microspines restricted to 2 circular areas; tenth abdominal segment without terminal sclerite, 4-6 setae laterad of anal opening. Based on 3 first-instar larvae.

SECOND INSTAR (Fig. 18). Body length: 3.3 mm (range 2.0-6.2); peristomata distance: 0.23 mm (range 0.21-0.24); prothorax width: 0.61 mm (range 0.40-0.97). Similar to the third instar, with the following exceptions: head retracted into prothorax as in first instar, ratio of head capsule to prothorax width approximately 0.62; prothorax subovoid, about as wide and 3 times longer than other thoracic segments, dorsal and ventral shields as in first instar; tenth abdominal segment without terminal sclerite, 8-10 setae laterad of anal opening. Based on 3 second-instar larvae.

THIRD INSTAR (Fig. 14 and 15). Body length: 5.4 mm (range 3.4-6.7); peristomata distance: 0.29 mm (range 0.27-0.30) prothorax width: 1.0 cm (range 0.69-1.31). Head cordate, largely retracted into prothorax, ratio of head capsule to prothorax width approximately 0.5, weakly sclerotized and light in color with mouthparts heavily sclerotized and yellow brown. Epicranium deeply emarginate posteriorly, occipital foramen defined dorsally by an inverted V-shaped endocarina (a sclerotized, rod-shaped thickening) which tapers posteriorly; parietals (PA) delineated laterally by the frons (FA) and occipital foramen, and anteriorly by the labrum (LB) bearing a peristoma anteriorly, a sulcus extending from the antennal base above the peristoma to the posterior margin of the frons, and an endocarina on the venter extending from the mid-lateral margin of the head capsule to an area mesad of the peristoma. Frons subrectangular, anteriorly with large clypeus, posteriorly reaching the occipital foramen, sharply deliniated laterally and posteriorly by enocarinae; 2 short setae at base of each frontal endocarina, 2 setae on dorsum posterior to peristoma and 2 on peristoma, 1 seta on dorsum of each parietal laterad of frontal endocarina, 3 setae on venter at anterior margin of endocarina. Peristoma (PE, Fig. 17) positioned latero-ventrally, heavily sclerotized and piceous anteriorly, yellowish brown posteriorly with a sulcus limiting it from the parietal; bearing two small setae, ocellus (0) singular, well-developed, positioned anterio-

laterally near base of antenna. Antenna (Fig. 17) situated anterio-dorsally between lateral margin of clypeus and peristoma, relatively large, three segmented with a broad membraneous base; proximal segment (1S) cylindrical, 4-5 times broader than long, slightly sclerotized, yellowish brown, bearing a single large seta ventrally and dorsally; second segment (2S) similar to first except as long as broad, bearing 4 papillae apically mesad to the third segment; apical segment (3S) oblong, constricted basally, and pointed apically. Hypostoma (HY, Fig. 15) (the ventral part of the mouth frame between the ventral mandibular articulations) tan, lightly sclerotized anteriorly, projecting beyond base of maxilla (MX) and labium (LA), divided medialy by a sulcus which extends posteriorly to occipital foramen.

Mouthparts with clypeus (CL, Fig. 14) large, transverse, about 3 times broader than long, extending between antennal bases, without setae, heavily sclerotized, yellow-brown color. Labrum (LB) largely retracted beneath clypeus, cuneiform, widest apically, about twice as long as wide, sclerotized, yellow brown, anterior margin slightly convex, anterio-lateral corners rounded, both corners and lateral margins beset with setae ventrally. Mandible (Fig. 20) broad, yellow brown, inner surface concave; 4 heavily sclerotized and piceous teeth; dorsal tooth bidentate, second tooth longest and largest, third and fourth teeth small and stout; a transverse ridge on the inner mandibular face with two short setae

posteriorly; ventral condyle subconical, heavily sclerotized; a single large seta projecting from lateral side of outer face, molar area bearing numerous papillae dorsally. Maxilla (Fig. 16) well developed, latero-dorsal surface with yellowish-brown sclerites, proximaly with a large subtrapeziform membraneous area; cardo undifferentiated from stipes (ST); stipes subrectangular, elongate, largely withdrawn beneath hypostoma, bearing 3 long setae on venter apical to hypostoma; maxillary palpus (MP) two segmented, first segment subcylindrical, as wide as long, bearing a long anterio-lateral seta, second segment similar to first except slightly smaller, with long seta, and with numerous small apical setae; mala (MA) slightly longer than maxillary palp, subconical, narrowest basally, terminally membraneous, rounded and bearing several long setae. Labium (LA) membraneous, as broad as long, rounded anteriorly, broadly joined to head capsule, no distinction between mentum, prementum, and submentum; ligula fused, bearing short, flat tubercles anteriorly; paraglossa (?) (PG) situated laterad of ligula, elongate, bearing papillae on mesal margin.

Prothorax (P, Fig. 22) cordate, about as wide and twice as long as other thoracic segments, dorsal (DS) and ventral shields yellow brown, coriaceous, asparate, nearly extending length of segment, consisting of 2 subrectangular plates separated by a straight, narrow, membraneous marking (DPM); dorsal shield with 2 broadly rounded lobes projecting laterally, 2 setae near center of

each half-shield, ventral shield without lobes, slightly widest anteriorly, about ¼ wider than dorsal shield, bearing 3 setae near center of each half-shield; on anterior and lateral margins of shield a band of microspines, occasionally in groups of 2 or 3, and a few setae; posterio-lateral corners of segment with a few microspines.

Mesothorax (MS) and metathorax (MT) subrectangular, mesothorax slightly wider than metathorax, both of same length and about one half prothorax length; mesothorax with a sparse medial band of setae, microspines present on anterio- posterio-lateral margins; metathorax with a pair of fleshy lobes on venter and dorsum, lobes covered with microspines and setae except for center, producing a figure-8 pattern, microspines on anterio- and posterio-lateral margins of segment.

Abdominal segments 1-8 subrectangular, almost as wide and slightly longer than meso and metathorax, all of same width; segments 1-8 on dorsum and 1-6 on venter with medial patch of microspines and setae, venter of segments 7 and 8 with microspines and setae restricted to two circular patches; a pair of fleshy lobes medialy located on venter of each segment. Ninth abdominal segment shorter and narrower than abdominal segments 1-8, dorsum with a broad V-shaped band of microspines and setae; venter devoid of microspines, bearing an apparently single proleg with 6-8 lateral setae. Tenth abdominal segment small, tapering posteriorly,

terminating in a lightly sclerotized plate about one third greatest width of segment, anal opening on venter beneath terminal plate, 8-10 setae laterad of anus. Spiracles (Fig. 22) present on mesothorax (TS) and abdominal segment 1-8 (AS) located in anterio-lateral portion of segment, mesothoracic spiracle about one third larger than abdominal spiracles; peritreme (Fig. 21) widest posteriorly with lobed margins, atrial opening subovoid. Based on 12 third-instar larvae.

PUPA. Body length: 5 mm (range 4.6-5.3); head capsule width: 1.0 mm (range 0.96-1.05); prothorax width: 1.4 mm (range 1.3-1.5). Body elongate oval, flattened dorsally, initially translucent white, through most of development red-brown, gradually taking on color of adult; antennae, mouthparts, wings, and elytra appressed against venter, head and mouthparts resting on prosternum; antennae extending latero-posteriorly and appressed against prothorax. Legs with femora and tibiae folded together and extending at right angles from the body midline, fore tarsi resting on the middle coxae and along mesosternum, midtarsi resting along metastarnum, hind tarsi resting on first abdominal segment behind posterior coxal plate near midline; elytra and wings extending almost to posterior margin of second abdominal segment, wing tips approaching midline, elytra obliquely parallel, not extending close to midline. Based on 10 pupae.

Field Population. The precise time of emergence of yellow nutsedge varies considerably in different localities. This sedge appeared in early May at MF and during the middle of May at AF. Overwintering T. schaefferi adults begin to feed on their host soon after it emerges. Mating is initiated at approximately the same time and continues throughout June. Figures 4 and 5 illustrate the occurrence of oviposition, egg eclosion, pupation, and adult emergence at MF and AF, respectively. Because sampling did not begin until June 18, the oviposition date of eggs already present at this time had to be estimated. This was accomplished by assuming an incubation period of 17 days (see Table 1a) and subtracting it from the date of hatching. This data includes all eggs sampled except some of those that were present on leaves with more than 1 egg. The hatching date of an egg could not be determined if a mine was already present beneath it.

The phenology of T. schaefferi is illustrated in Figure 4. Table 1a presents the mean development periods of the immature stages at MF and AF. The mean incubation period of eggs under laboratory and field conditions are very similar, but the larval and pupal developmental periods are quite different. This discrepancy is due to the difficulty in detecting newly pupated T. schaefferi under field conditions. Pupae are at first translucent white and difficult to differentiate from larvae unless examined

with the aid of a light. The total development time of T. schaefferi in both laboratory and field conditions is very similar.

Adults emerging in July continue to feed on yellow nutsedge, but disperse by the middle of August. At MF and AF no adults could be found at the end of August even though host material was still present. It is probable that adults at this time disperse to an overwintering habitat.

Yellow nutsedge has a characteristic growth pattern. New leaves originating from the basal bulb emerge from the stem apex and rapidly expand in length. These leaves photosynthesize for a variable period of time before the onset of senescence. This time period appears to be largely influenced by environmental conditions, particularly soil moisture. However, even the lower leaves of plants grown under optimal conditions in the greenhouse will eventually become senescent. As the plant matures the rate of leaf senesence increases. Figure 7 illustrates the growth pattern of the 60 sampled plants at MF and AF through the summer. At these sites most of the plants had died by September 1. In other localities, such as the fallowing PS and along the border of MF and other cornfields, yellow nutsedge persisted into October. It is likely that the shading effect of the corn was partially responsible for this difference. Yellow nutsedge in its natural habitat occurs in open areas.

The life cycle of T. schaefferi is well synchronized with the growth pattern of yellow nutsedge. Females select only the upper leaves for oviposition sites. This is illustrated in Figure 8, where 80% of the leaves selected for oviposition were in the upper 30% of the available leaves. Females also appear to select the taller and more vigorous plants for oviposition. A survey of the egg distribution in 133 plants revealed a very non-random distribution (see Figure 9). The plants receiving several eggs were among the largest. Although the size of sampled plants was not evaluated quantitatively, the correlation between plant size and egg presence was evident. When egg-infested plants were being collected for the rearing of egg parasites, it was very easy to obtain an abundance of eggs by collecting only the largest plants. It thus appears that females select oviposition sites in the upper level of the nutsedge strata. This would result in a nonrandom distribution of eggs where most eggs are present on the upper leaves of the larger plants.

The ovipositional behavior of females greatly reduces larval mortality resulting from leaf senescence. At MF and AF the mean egg and larval development time was approximately 36 days. The life span of each leaf is variable, usually ranging from 40-55 days. Consequently, it is essential that females oviposit only on younger leaves. The time between egg eclosion and leaf senescence at MF and AF illustrates this synchronization (see

Table 4a). The mean time period between egg eclosion and leaf senescence was 32 days, whereas larvae required an average of 20 days to complete development.

The mortality of the immature stages of T. schaefferi are presented in Table 4b. These figures are estimates, as the actual mortality of each beetle could not be directly ascertained. Larval cannibalism was assumed to occur when more than one larva was present per leaf. The mortality factors leaf senescence and phytophages could be directly observed. However, parasites, predators, or pathogens could actually have been responsible for a number of these mortalities. Consequently, a correction factor had to be calculated to account for parasitism. This factor was determined from only those individuals who were assumed to be parasitized or were known to be survivors. The mortality of an individual was attributed to parasitism (as opposed to leaf senescence or phytophages) if it did not mature after one standard deviation unit beyond the normal mean development time of the field population. Due to the difficulty in detecting newly pupated individuals, the actual mean development time of the larvae was assumed to be equivalent to the mean obtained in the laboratory. The percentage parasitism of these individuals was then calculated and served as a correction factor. A separate correction factor for both eggs and larvae was necessary. The number of individuals whose possible mortality factor was leaf senescence, cannibalism,

or phytophages was then adjusted by this percentage. Egg mortalities at this time were adjusted to account for egg infertility, which was assumed to be 5% of the total egg population (as obtained in a laboratory study).

This data suggests that the primary mortality factor of the immature stages of T. schaefferi is a parasite or parasite complex, a density dependent factor. A sample of the condition of T. schaefferi larvae at MF and AF is summarized in Table 5. Only 29% of all the larvae were in an apparently healthy condition, and approximately 32% of the larvae were already dead when the mine was examined. It is probable that most of these were parasitized, for their bodies were characteristically flattened. Larvae from which parasites were later reared also took on this flattened appearance. Parasites of the egg, larval, and pupal stages of T. schaefferi were obtained. Unidentified mymarid parasites were reared from the eggs. The larvae and pupae were found to be parasitized by two unidentified chalcid species. These two species were reared from 28% of the field collected larvae, as shown in Table 5. They are apparently the primary mortality factor for the immature stages of the beetle.

Damage Evaluation. Overwintering tubers sampled at MF had a mean weight of 89 mg (range 14-260, standard error 6.5). The effect of various T. schaefferi densities on 4 yellow nutsedge parameters is summarized in Table 6 and 7. Plants with leaf

miners present produced slightly more tubers and daughter plants, but less total tuber fresh weight and total dry weight. There are no differences between the plants with 5, 6, 7, and 8 leaves mined. All parameters are highly variable and none are significantly different at the $P < 0.05$ level. In Table 7 the plants with leaf miners present are pooled and compared to the control. A Duncan's multiple range test using Kramer's adjustment (1956) revealed that the total dry weight of the control is significantly larger at the $P < 0.05$ level. None of the other parameters were found to be significant.

Host-Parasite Relationship And Biocontrol Potential. The host-parasite relationship of T. schaefferi and yellow nutsedge appears to be well coevolved. However, yellow nutsedge may actually be a secondary host for the beetle, for the plant is thought to be introduced. Perhaps related Cyperus species serve as a primary host(s) for the beetle.

The host and beetle populations are stablized by 2 density dependent mortality factors: cannibalism and parasitism. Cannibalism would cause substantial larval mortality at high densities and always limit the development to only one larva per leaf. Thus the amount of damage the beetle is capable of inflicting on the host is limited, and the survival of both host and beetle is insured. At low densities T. schaefferi would be largely free of these mortality factors. The significance of larval cannibalism

must be considered from the perspective of the host's natural habitat. Yellow nutsedge is a poor competitor and a ruderal species, and has a very fluctuating population at the local level. This sedge often colonizes recently disturbed habitats and is gradually replaced as succession ensues. Cannibalism has considerable adaptive value because it has a stabalizing effect on both host and beetle and allows T. schaefferi to survive during low host populations. The dispersal behavior of newly-emerged adult beetles is perhaps related to the ruderal nature of the host. These beetles would have an opportunity to locate and colonize newly established yellow nutsedge stands.

The female's behavior of ovipositing on the upper leaves of yellow nutsedge is critical for the survival of the larvae. This behavior is largely responsible for the synchronization between host and beetle. The placement of eggs in the tallest and (perhaps) most vigorous plants is of little adaptive value in the agroecosystem, where the host has very little interspecific plant competition.

However, in the native habitat of the host, selection of the most vigorous plants in the early growing season would be of definite advantage. The less vigorous host plants would likely be outcompeted during the summer months. Host vigor is inversly related to the rate of leaf senescence, which in turn influences the survival of the beetle.

The development of T. schaefferi causes only minimal damage to the host. Mining occurs only in mature leaves as a result of the long egg incubation. The mine formed by the first and second instar is superficial. Third instar larvae destroy a substantial amount of tissue, but this feeding occurs near the onset of leaf senescence. The cage experiment indicates that the growth of the host is somewhat limited by high densities of T. schaefferi. However, these densities would not occur under natural conditions because the larger plants would receive a greater proportion of the eggs. As a result, larval mortality due to cannibalism would be substantial and the population would decline. Many of the smaller plants would be largely unaffected, as they would receive few eggs. As a consequence, the biological control potential of T. schaefferi is limited.

Elliponeura debilis

E. debilis was found infesting yellow nutsedge inflorescences at DS and PS. The host initiates flowering in late July and peaks in mid-August, but it continues to produce new inflorescences until frost. It is likely that this fly has alternate cyperaceous hosts during the earlier part of the summer. E. debilis adults first emerge from the inflorescences in mid-August. An average of 1 to 2 individuals per inflorescence were found throughout the summer

and fall. Adults were obtained from field collected inflorescences as late as mid-October.

Attempts to induce yellow nutsedge flowering for rearing purposes were largely unsucessful. Plants exposed to declining photoperiods did not flower. Of the 2 clones exposed to simulated spring and summer conditions, only 1 flowered. Seed set did not occur because of the self-incompatibility of the plant. An attempt to rear E. debilis in the laboratory failed. Adult flies were easily obtained in abundance from field collected inflorescences. In the plexiglass cage they fed on the sugar solution and readily mated, but apparently never oviposited on the host. All greenhouse plants flowered in early August and were probably too mature and not acceptable to the adult flies. However, flowering plants from the field in all stages of development were placed in the cage with them. No eggs or larvae were ever dected on these plants, and adults never emerged from them.

Glyphipteryx impigritella

The presence of G. impigritella was not detected by either of the two sampling methods. Apparently the population in the surveyed fields was too low for detection with the limited survey effort.

Table 1a. Developmental periods of T. schaefferi under laboratory and field conditions.

Stage	No. obs.	Mean No. days	Standard error	Range
Laboratory*				
Egg	21	16.1	0.33	14-20
Larval	16	20.0	0.30	18-22
Pupal	16	11.4	0.34	10-15
Post-pupal	16	3.3	0.28	1-5
Field				
Egg	35	16.8	0.97	8-32
Larval	11	27.4	1.25	22-32
Pupal	9	6.8	0.68	5-12

*Photoperiod 15 hours, 27°C, 16°C night.

Table 1b. Cumulative area of mine outline formed by each larval instar of T. schaefferi.

Instar	No. obs.	Mean cm^2 area	Standard error	Range
First	51	1.21	0.07	0.40-2.75
Second	9	2.64	0.35	1.40-4.58
Third	15	4.65	0.41	2.00-7.70

Table 2a. Area of mine outline and total leaf mass destroyed on leaves with 1 and 2-6 T. schaefferi eggs present.

Variable	No. obs.	Mean	Standard error	Range
Total area (cm^2)				
Single egg per leaf	11	4.75	0.19	3.71-5.90
2-6 eggs per leaf	10	5.16	0.24	4.06-6.49
Mass consumed (g)				
Single egg per leaf	11	0.053	0.003	0.035-0.067
2-6 eggs per leaf	10	0.059	0.006	0.032-0.089

Table 2b. Diapause mortality of T. schaefferi.

Days of exposure to winter conditions*	No. adults	Percent mortality
30	10	0
60	20	60
105	20	80
130	20	100
140	180	97

* Photoperiod 10 hours, 6°C, 1°C night.

Table 3. Measurements of the immature stages of T. schaefferi.

Variable	No. obs.	Mean (mm)	Standard error	Range
Egg				
Length	10	1.34	0.023	1.26-1.41
Width	10	0.47	0.056	0.37-0.51
First instar				
Peristomata distance	8	0.19	0.001	0.19-0.20
Prothorax width	8	0.41	0.009	0.37-0.44
Body length	8	1.68	0.142	1.28-2.29
Second instar				
Peristomata distance	11	0.23	0.003	0.21-0.24
Prothorax width	11	0.61	0.046	0.40-0.97
Body length	11	3.29	0.351	2.03-6.24
Third instar				
Peristomata distance	23	0.29	0.002	0.27-0.30
Prothorax width	23	1.00	0.037	0.70-1.31
Body length	23	5.39	0.229	3.43-6.71
Pupa				
Head capsule width	10	1.02	0.012	0.96-1.05
Prothorax width	10	1.41	0.017	1.32-1.47
Body length	10	5.06	0.007	4.56-5.31

Table 4a. Time between larval eclosion of T. schaefferi and senescence of mined leaf.

Site	No. obs.	Mean No. days	Standard error	Range
McPherson Farm	86	32.1	1.33	7-62
VPI & SU Agronomy Field	43	33.6	1.58	18-64

Table 4b. Egg, larval, and pupal mortality of T. schaefferi.

Mortality factor	Eggs No.	Eggs %	Larvae No.	Larvae %	Pupae No.	Pupae %
PPP*	31	38	133	74	7	100
Leaf senescence	34	42	11	6		
Phytophages	2	3	1	0.5		
Cannibalism			35	19		
Infertility	14	17				
Total mortality	81	29	180	90	7	37
Total survivorship	199	71	19	10	12	63

*Parasites, predators, or pathogens.

Table 5. Condition of T. schaefferi larvae sampled at MF and AF on August 4-6.

Site	Healthy No.	Healthy %	Parasitized No.	Parasitized %	Dead No.	Dead %	Not Present No.	Not Present %
McPherson Farm	14	35	9	23	14	35	3	7
VPI & SU Agr. Field	7	20	13	37	10	29	5	14
Total	21	28	22	29	24	32	8	11

Table 6. Effect of various T. schaefferi densities on 4 yellow nutsedge* growth parameters.

Variable	No. obs.	Mean	Standard error	Range
Number of tubers				
Control	12	32.0	2.54	22-47
5 leaves mined	5	29.2	3.28	20-37
6 leaves mined	5	32.4	3.01	27-44
7 leaves mined	5	36.0	4.59	27-51
8 leaves mined	5	33.8	4.75	19-46
Number of daughter plants				
Control	12	4.9	0.58	3-10
5 leaves mined	5	4.4	1.60	1-9
6 leaves mined	5	5.8	0.66	4-8
7 leaves mined	5	5.0	0.95	2-8
8 leaves mined	5	6.0	1.27	2-8
Tuber weight (g)				
Control	12	5.2	0.51	2.3-7.2
5 leaves mined	5	4.2	0.54	2.1-5.3
6 leaves mined	5	4.7	0.80	3.1-7.2
7 leaves mined	5	5.3	0.89	2.9-7.8
8 leaves mined	5	5.0	0.63	3.6-6.9
Total dry weight (g)				
Control	12	7.3	0.59	4.1-10.0
5 leaves mined	5	5.6	0.67	4.3-8.2
6 leaves mined	5	6.1	0.66	3.6-7.4
7 leaves mined	5	6.1	0.65	4.5-7.5
8 leaves mined	5	5.5	0.53	4.3-7.4

* Initial tuber mass 100-200 mg.

Table 7. Pooled effect of various T. schaefferi densities on 4 yellow nutsedge growth parameters.

Variable	No. obs.	Mean*	Standard error	Range
Number of tubers				
Control	12	32.0a	2.54	22-47
5-8 leaves mined	20	32.8a	1.91	19-51
Number of daughter plants				
Control	12	4.9a	0.58	3-10
5-8 leaves mined	20	5.3a	0.56	1-9
Tuber weight (g)				
Control	12	5.2a	0.51	2.3-7.2
5-8 leaves mined	20	4.8a	0.35	2.1-7.8
Total dry weight (g)				
Control	12	7.3a	0.59	4.1-10.0
5-8 leaves mined	20	5.8b	0.30	3.6-8.2

*Means followed by the same letter do not differ significantly ($P \leq 0.05$) as determined by Duncans multiple range test.

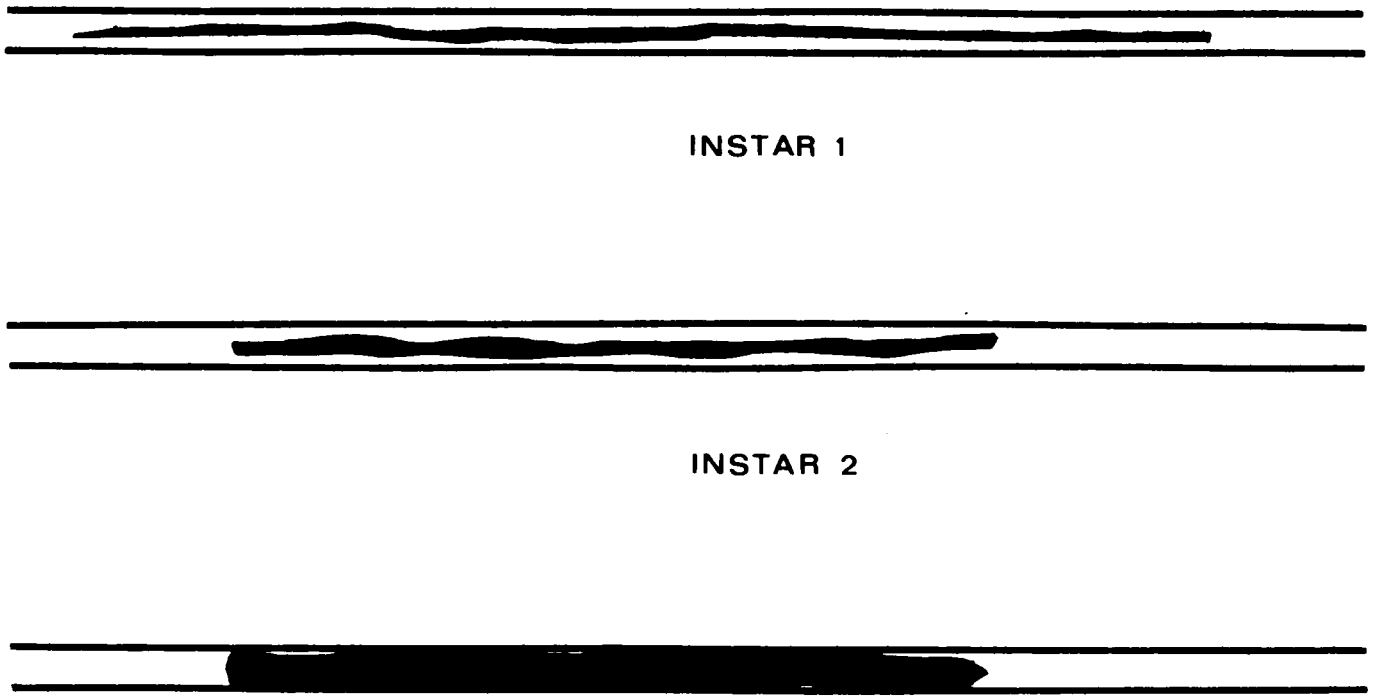


FIG 1. MINE OUTLINE FORMED BY EACH LARVAL INSTAR OF T. SCHAEFFERI.

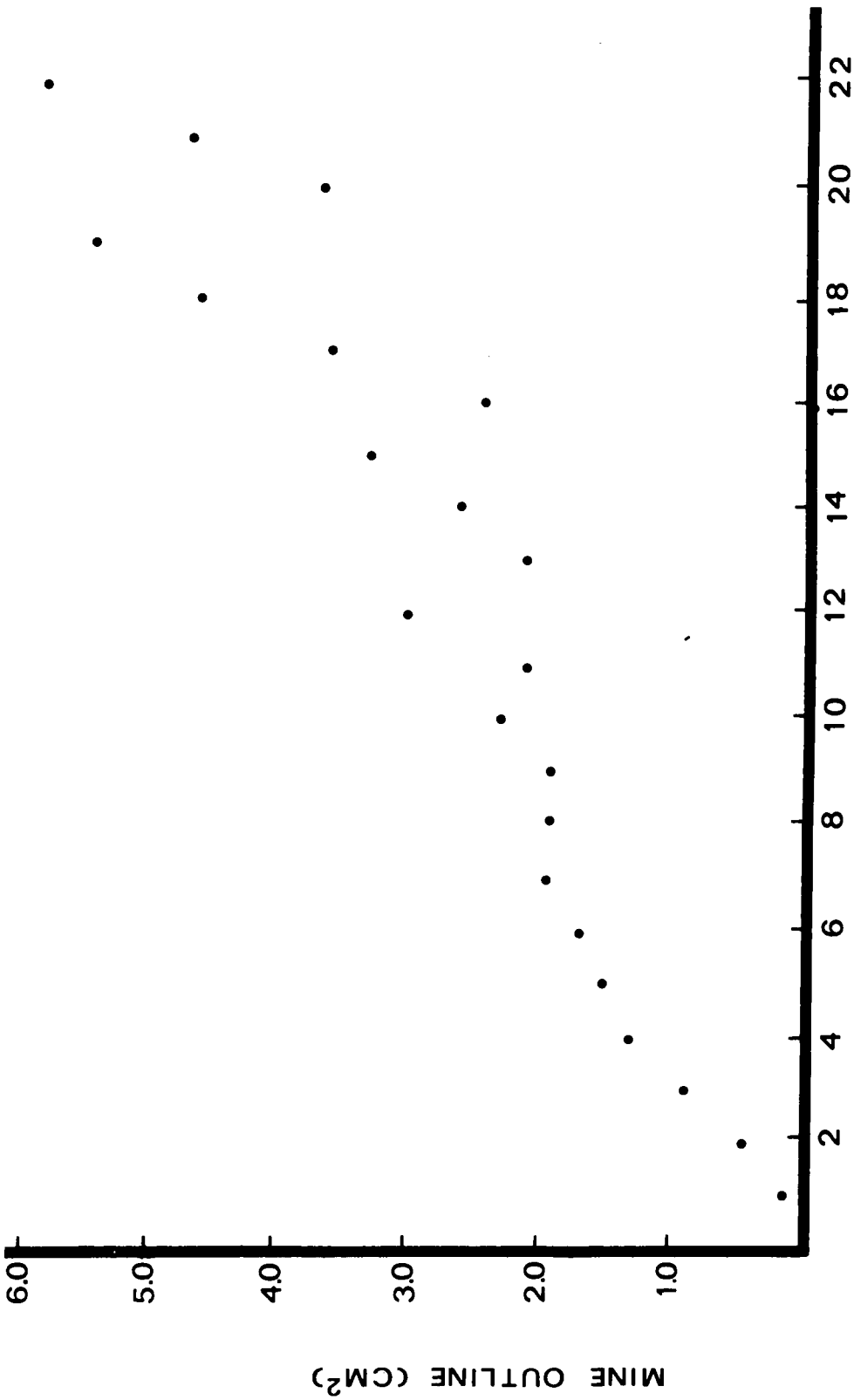


FIG 2. AREA OF MINE OUTLINE DURING LARVAL DEVELOPMENT OF I. SCHAEFFERI.

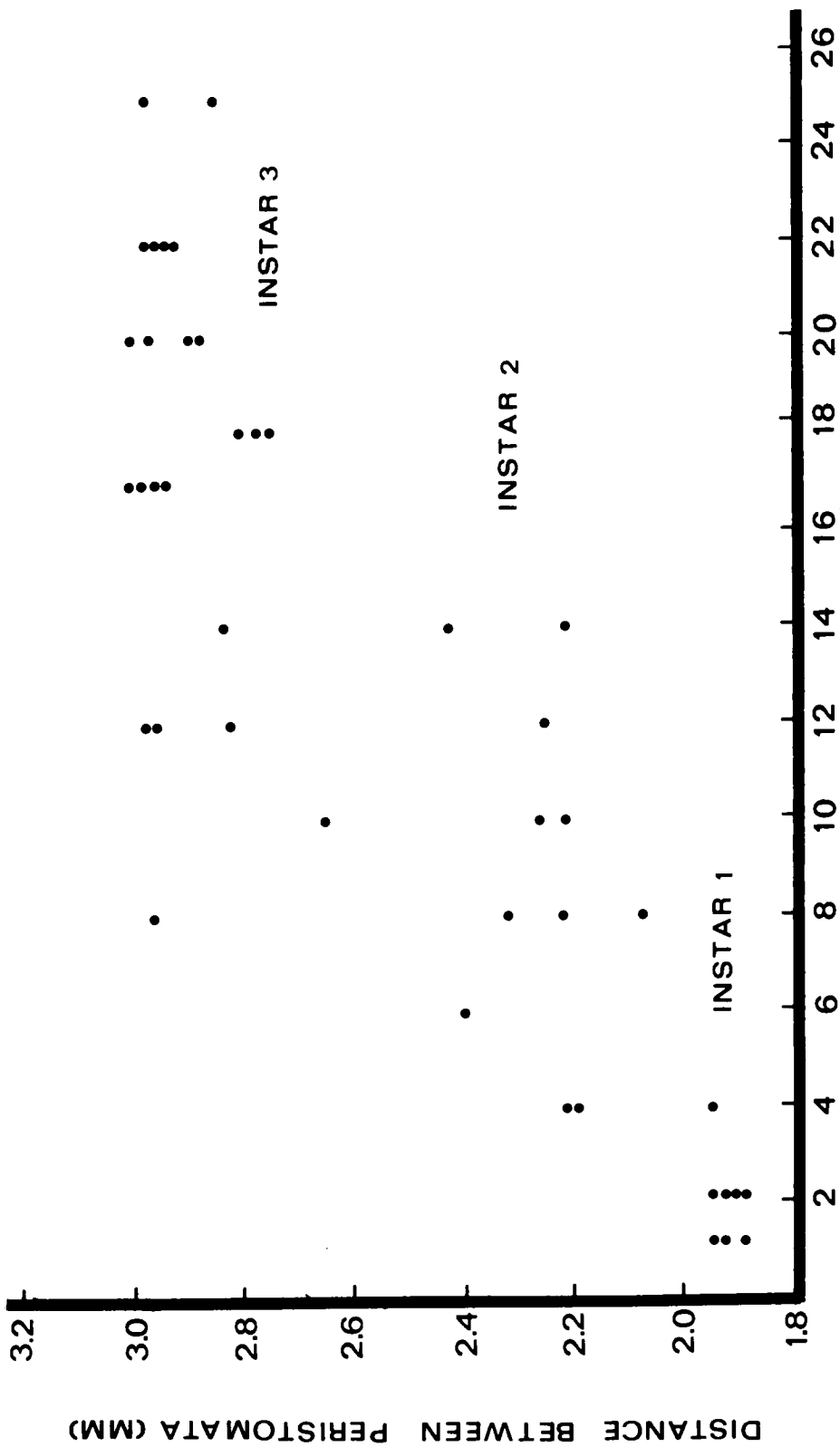


FIG 3. DISTANCE BETWEEN PERISTOMATA DURING LARVAL DEVELOPMENT OF I. SCHAEFFERI.

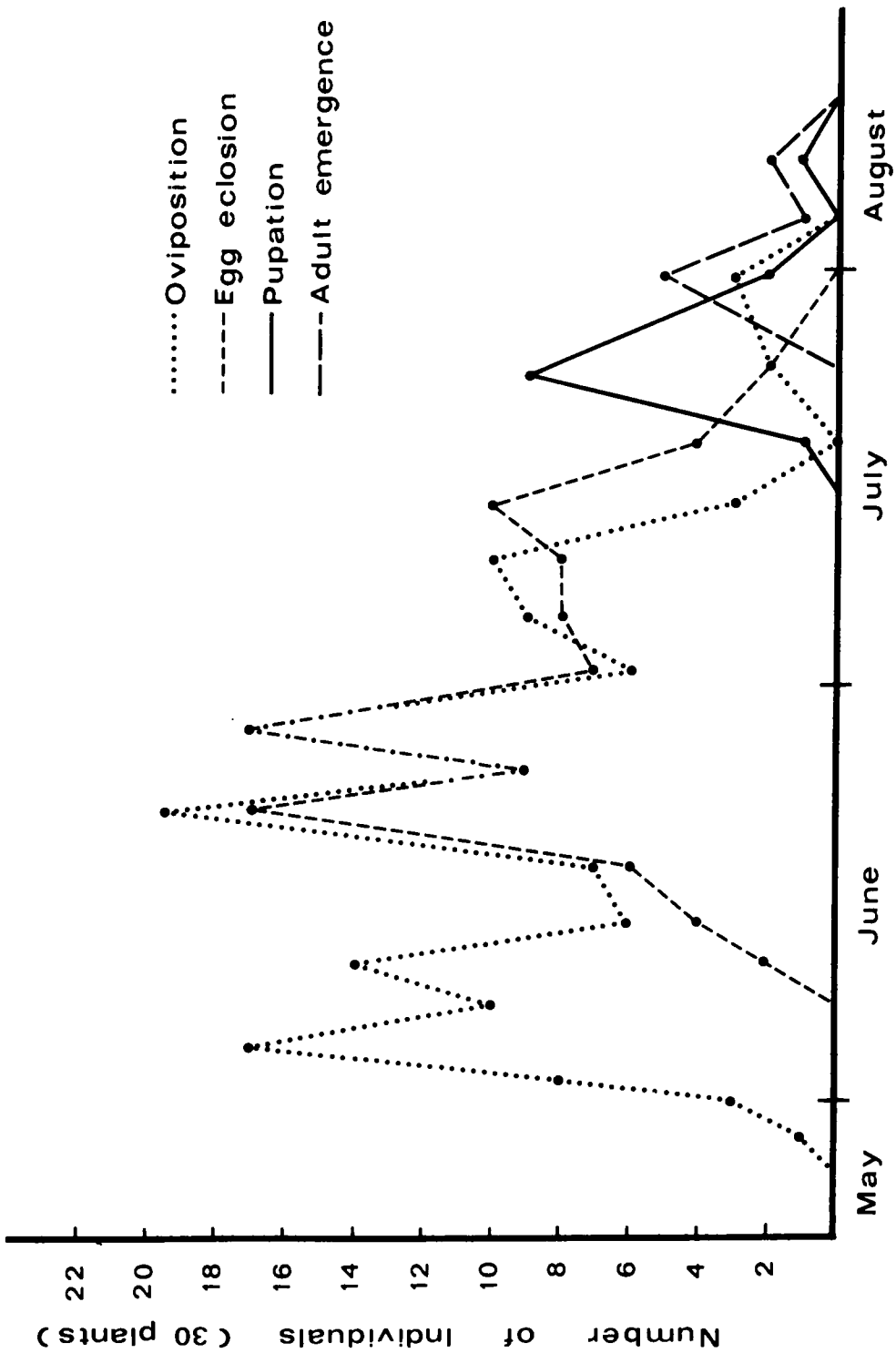


Fig 4. T. schaefferi oviposition, egg eclosion, pupation, and adult emergence at MF.

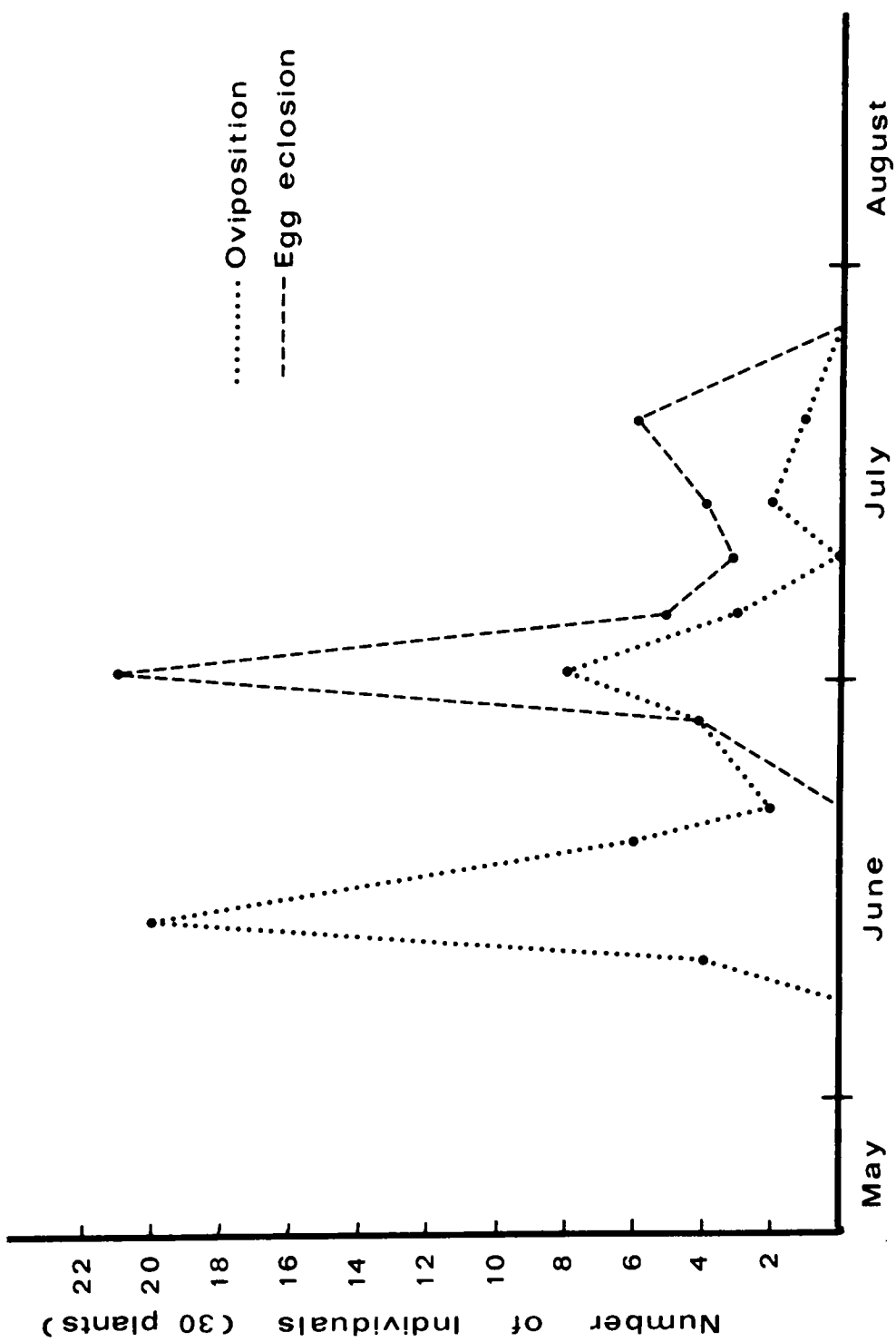


Fig 5. I. schaefferi oviposition, egg eclosion, pupation, and adult emergence at AF.

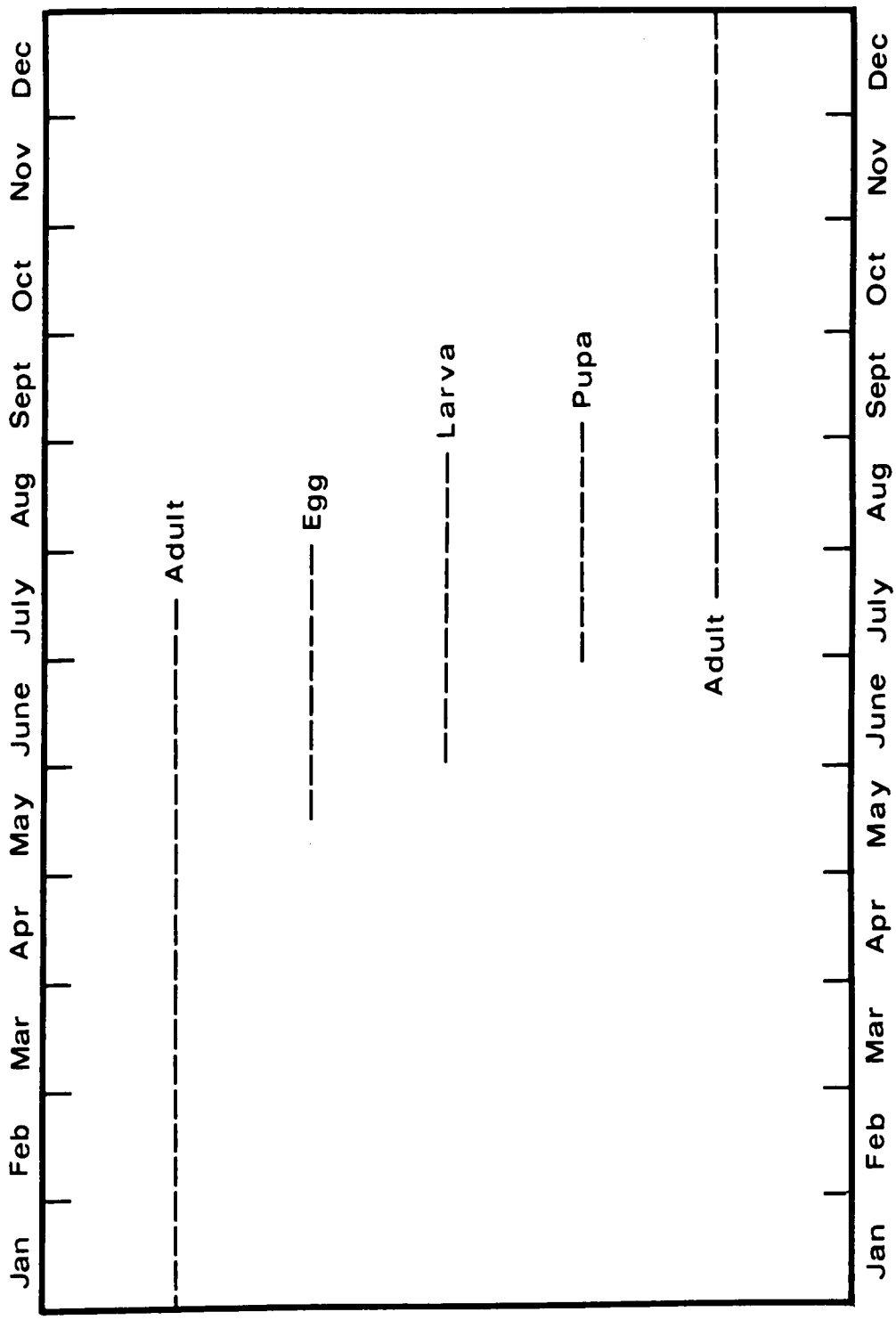


Fig 6. Phenology of I. schaefferi.

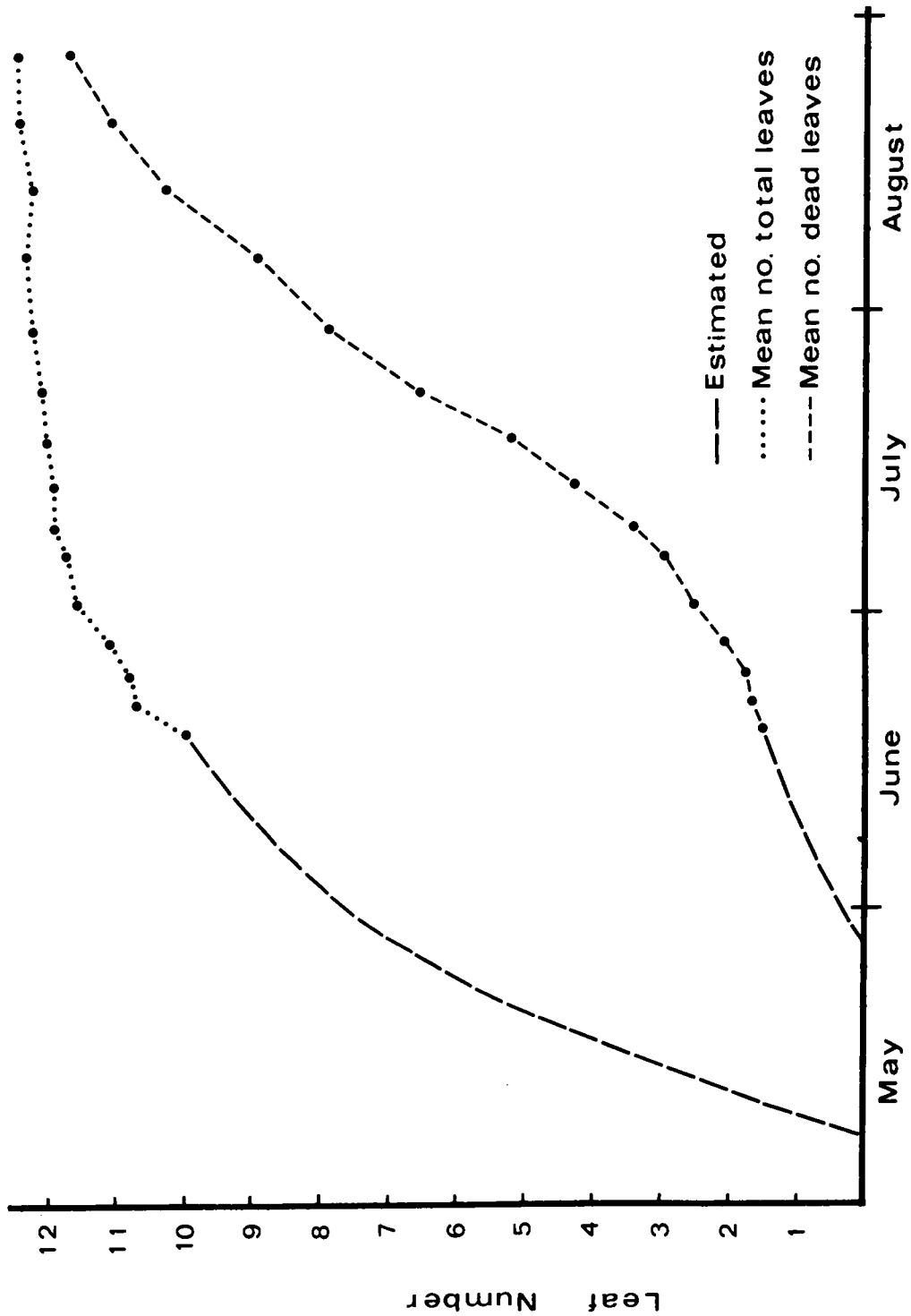


Fig 7. Growth pattern of yellow nutsedge at MF and AF.

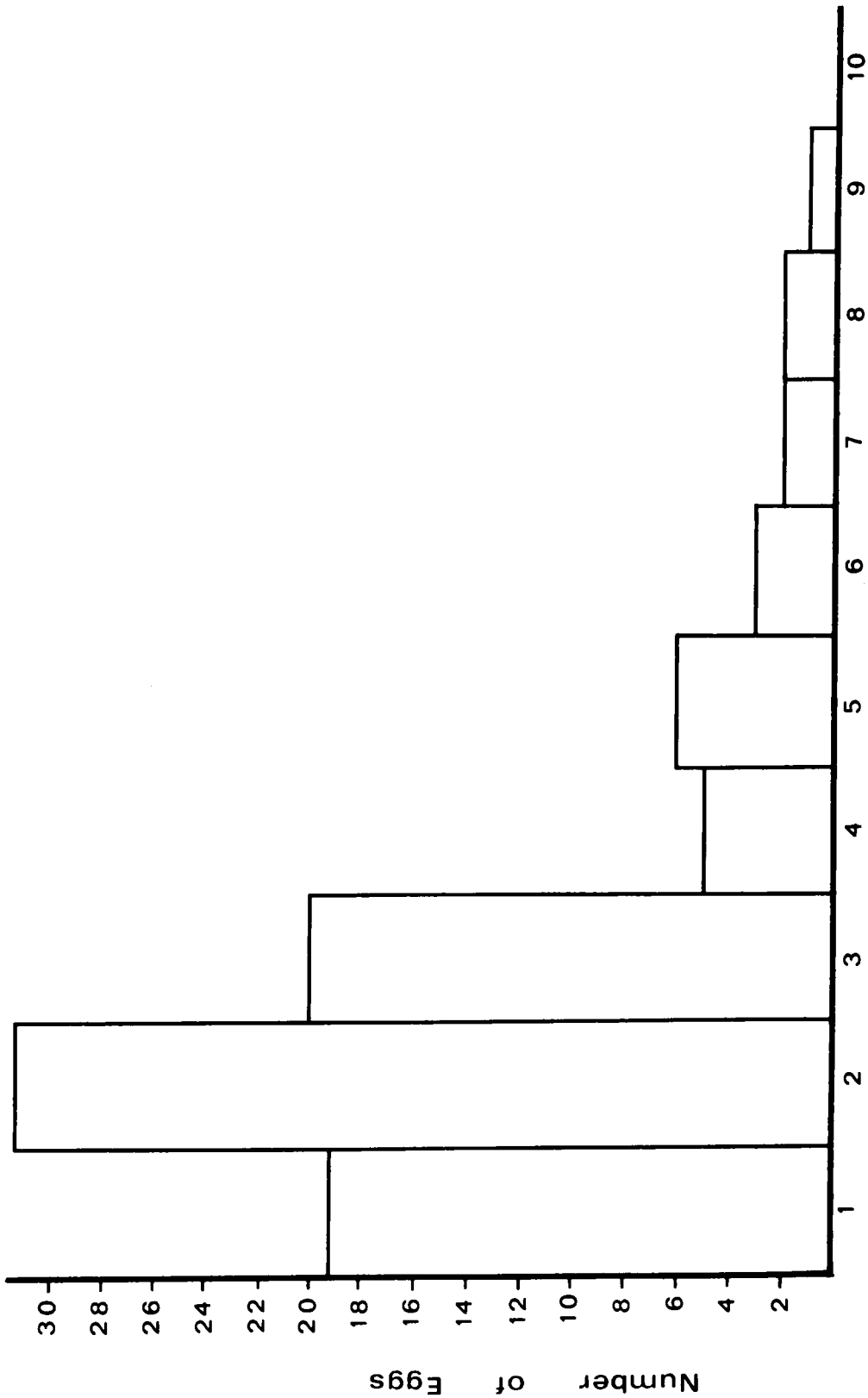


Fig 8. Distribution of T. schaefferi oviposition sites on host strata levels.

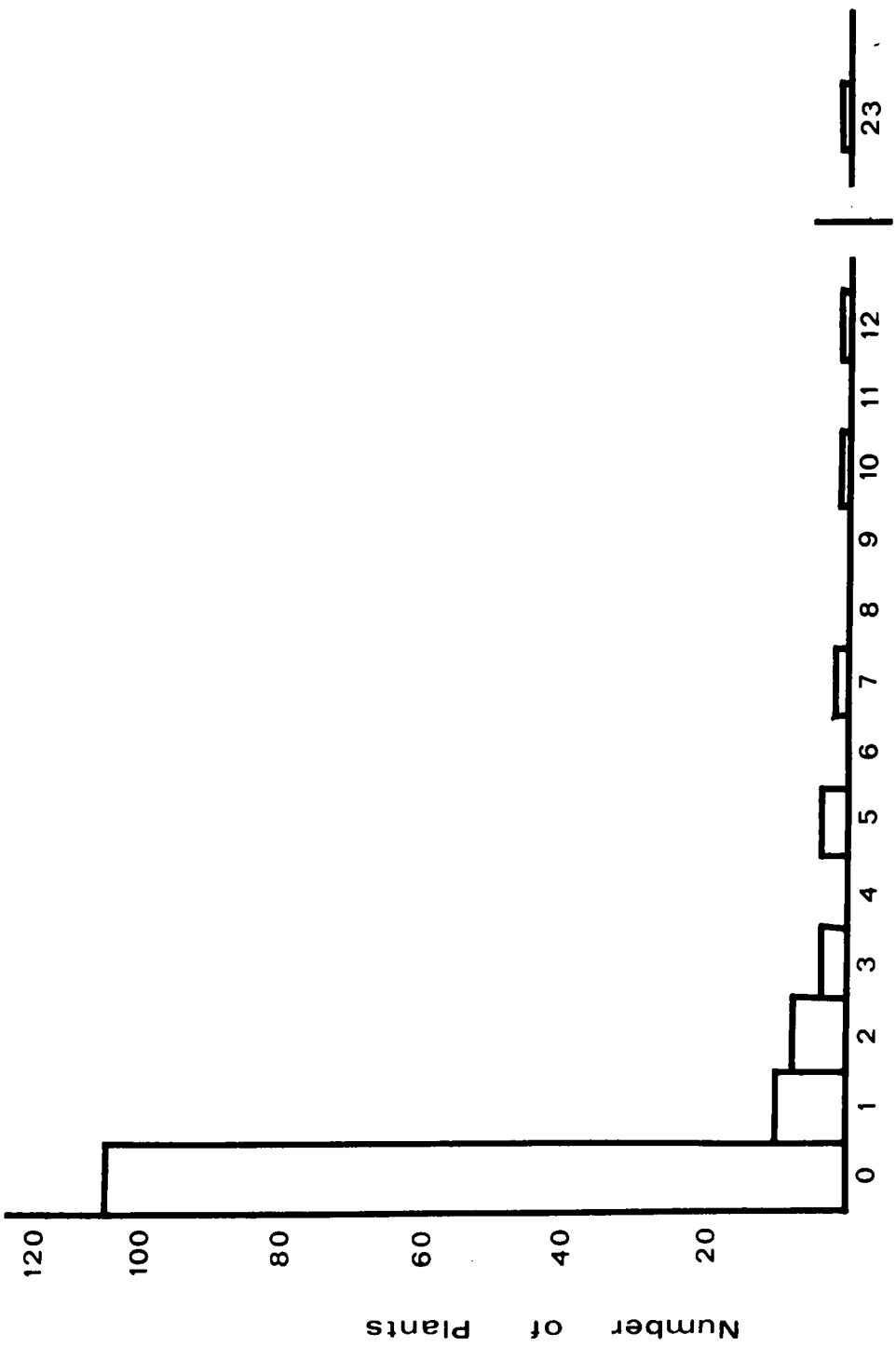


Fig 9. Distribution of T. schaeferi eggs on yellow nutsedge.

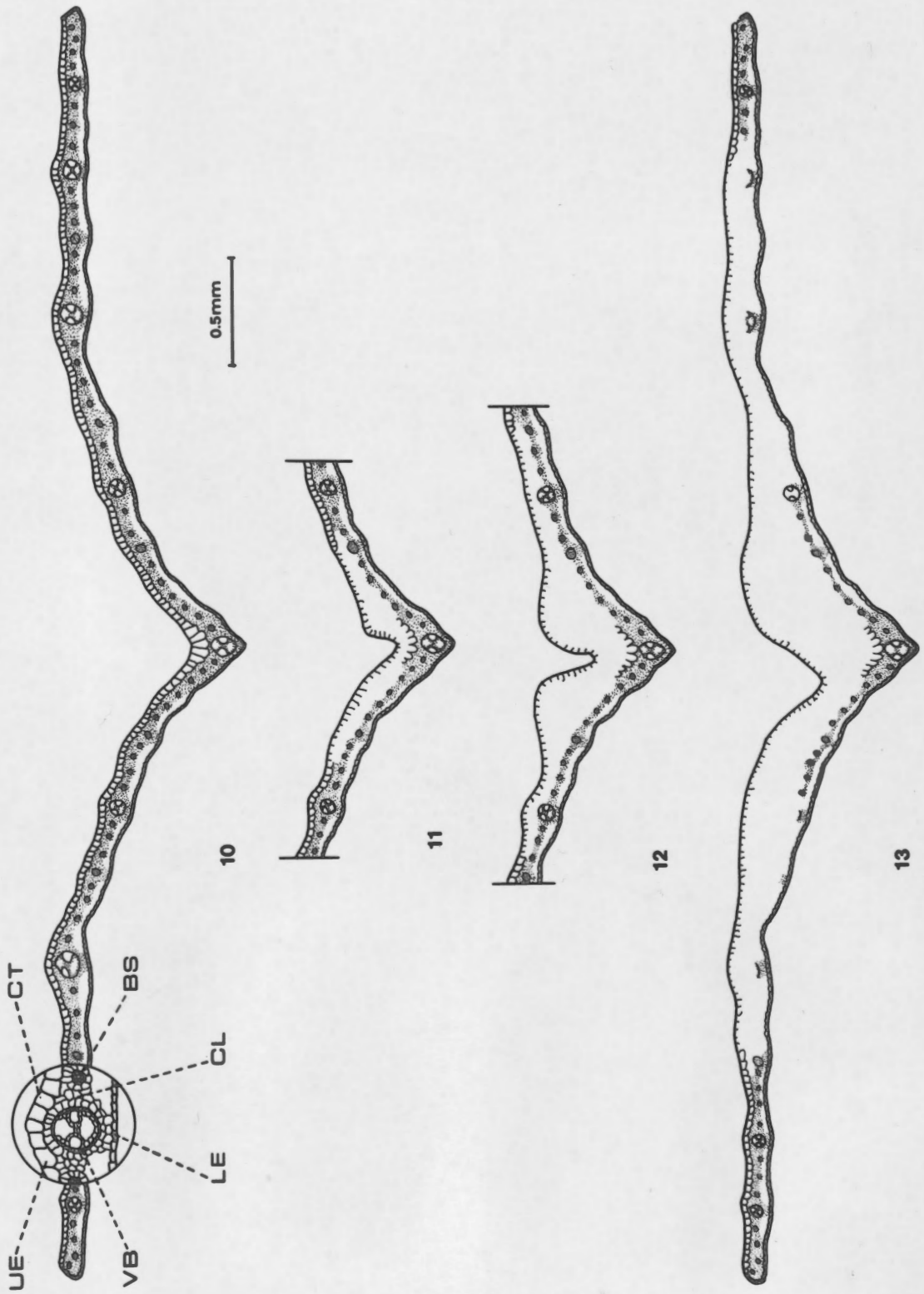
PLATE 1. Cross sections of Cyperus esculentus.

Fig. 10. Leaf cross section. UE, upper epidermal layer; CT, cuticle; VB, vascular bundle; CL, chlorenchyma; BS, bundle sheath; LE, lower epidermal layer.

Fig. 11. Leaf cross section of first instar mine.

Fig. 12. Leaf cross section of second instar mine.

Fig. 13. Leaf cross section of third instar mine.


UE
VB
LE
CL
BS
CT
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10
11
12
13

PLATE 2. Larval illustrations of Taphrocerus schaefferi.

Fig. 14. Head capsule, dorsal view. LB, labrum; CL, clypus; FA, frons; PE, peristoma; PA, parietal.

Fig. 15. Anterior aspect of head capsule, ventral view. MD, mandible; LA, labium; MX, maxilla; HY, hypostome.

Fig. 16. Mouthparts, ventral view. PG, paraglossa; MA, mala; MP, maxillary palp; ST, stipes.

Fig. 17. Right peristoma and antenna, ventral view. 1S, first antennal segment; 2S, second antennal segment; 3S, third antennal segment; O, ocellus.

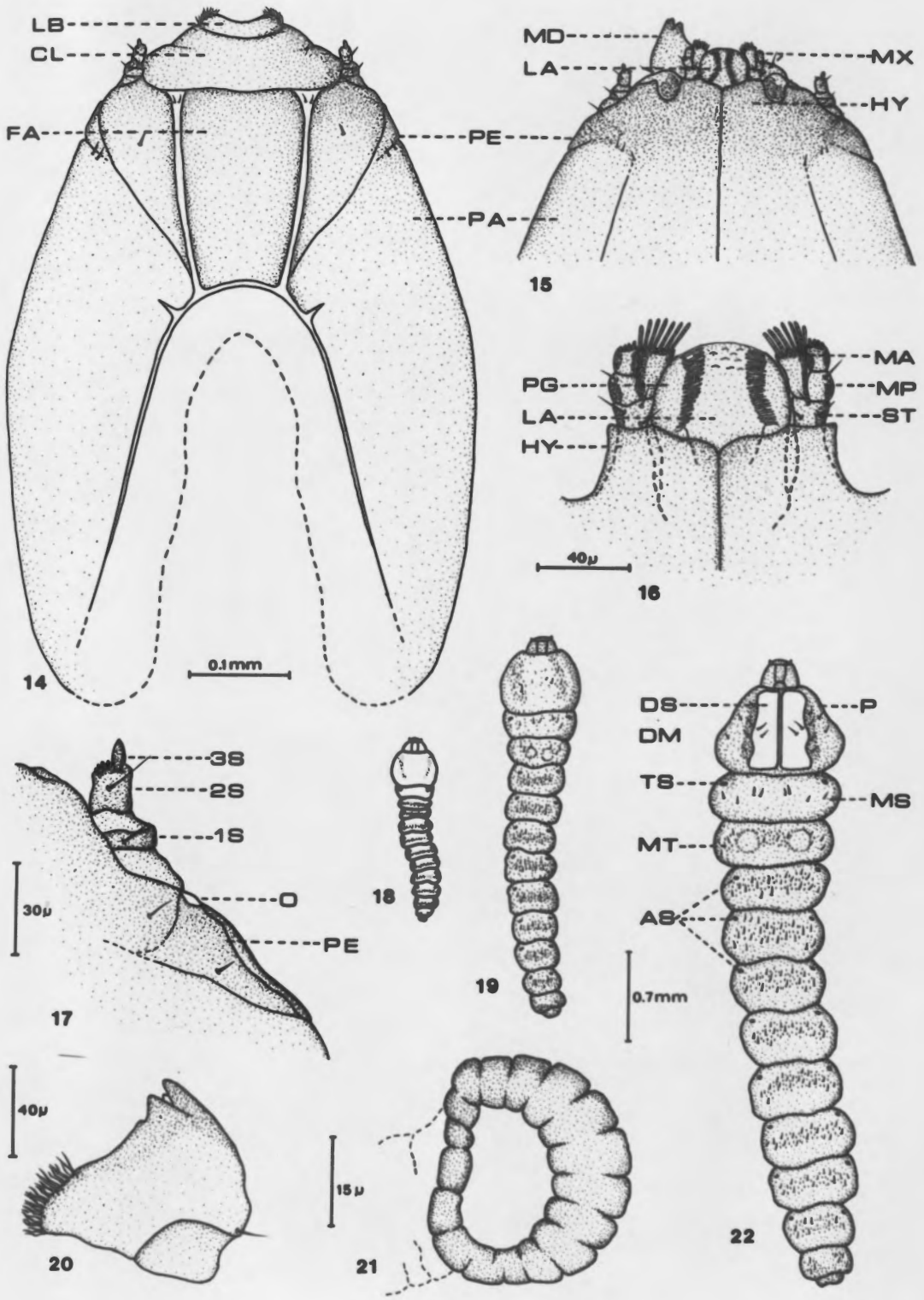
Fig. 18. First instar larva, dorsal view.

Fig. 19. Second instar larva, dorsal view.

Fig. 20. Right mandible, dorsal view.

Fig. 21. Right mesothoracic spiracle.

Fig. 22. Third instar larva, dorsal view. DS, dorsal shield; P, prothorax; DM, dorsal shield marking; TS, thoracic spiracle; MS, mesothorax; MT, metathorax; AS, abdominal spiracle.


LB
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PG
LA
HY
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3S
2S
1S
O
PE
30µ
17
18
19
DS
DM
TS
MT
AS
P
MS
0.7mm
22
40µ
20
15µ
21

Fig. 23. Egg of T. schaefferi on leaf midrib of yellow nutsedge.

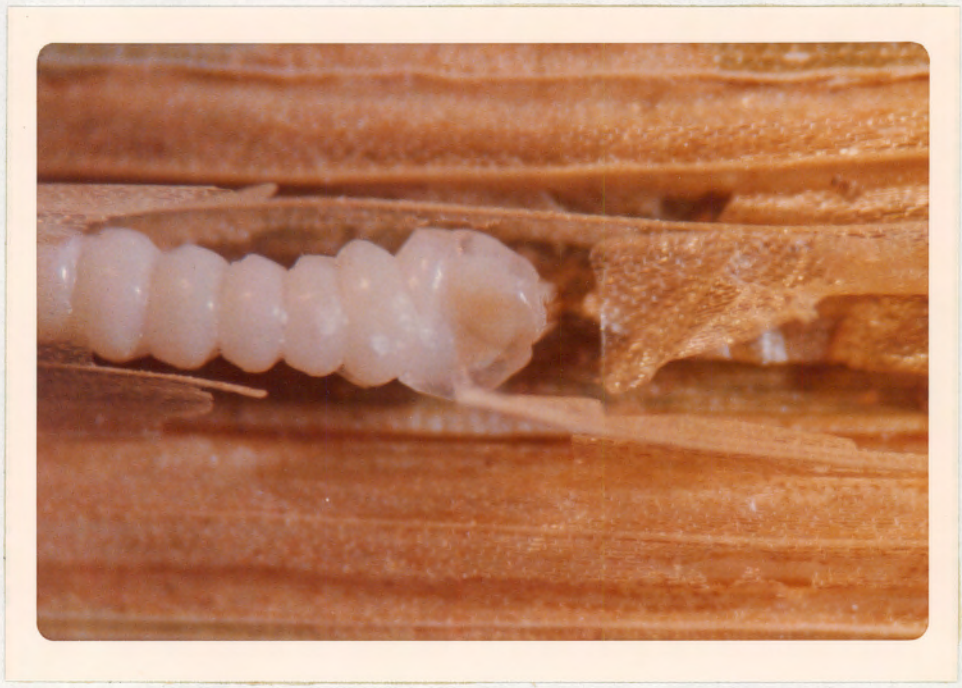

Fig. 24. Third instar larva in leaf mine.

Fig. 25. Pupa in leaf mine.

Fig. 26. Adult feeding on yellow nutsedge.

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BIOLOGY AND BIOCONTROL POTENTIAL OF *TAPHROCERUS SCHAEFFERI* NICOLAY AND WEISS (COLEOPTERA, BUPRESTIDAE), A LEAF MINER ATTACKING YELLOW NUTSEDGE (*CYPERUS ESCULENTUS* L.)

by

Richard Nathaniel Story

(ABSTRACT)

Taphrocerus schaefferi is a leaf miner of yellow nutsedge, a serious weed of many agronomic and horticultural crops. Beetles begin egg-laying in early June; the eggs have an incubation period of 16 days. There are three larval instars, the first two of which consume only the chlorenchyma and upper epidermal cells of the infested leaf. The third instar is responsible for most of the tissue destruction. Approximately one half of the vascular bundles are destroyed. Larvae are cannibalistic and only one larva per leaf can develop. The larval and pupal stadia are 20 and 11 days, respectively. Adults emerge in late July and August. The immature stages are described and illustrated.

The life cycle of *T. schaefferi* is well synchronized with that of its host. The primary mortality factor of the immature stages is two larval and pupal chalcid parasites which account for 74% of the total larval mortality. The total dry weight of plants without leaf miners is significantly greater at the $P < 0.05$ level than those plants with 5-8 leaf miners present. However,

the development of T. schaefferi causes only minimal damage to the host. Mining occurs only in mature leaves, the first and second instar mine is superficial, and the third instar mine occurs near the onset of leaf senescence. As a consequence, the biocontrol potential of T. schaefferi is limited.

A survey to detect the presence of Elliponeura debilis Loew (Diptera), a seed feeding chloropid, and Glyphipteryx impigritella Clemens (Lepidoptera, Glyphipterygidae), a leaf miner, was conducted.