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The Southwestern Corn Borer, *Diatraea grandiosella:* Case History of an Invading Insect

G. MICHAEL CHIPPENDALE

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*G. Michael Chippendale**

INTRODUCTION

This bulletin presents a comprehensive overview of the southwestern corn borer, *Diatraea grandiosella* Dyar, a most destructive pest of corn and sorghum in the United States. An account of the bionomics of this insect is appropriate at this time because almost 25 years have elapsed since the last detailed report appeared, and a considerable amount of information has been acquired in the interim (Davis *et al.*, 1933; Walton and Bieberdorf, 1948a, b; Wilbur *et al.*, 1950; Rolston, 1955a).

Since 1913 when the insect was first reported as having migrated into the United States from Mexico, it has caused serious crop losses across the southern corn belt from Arizona to Alabama. Its economic impact can be measured in the millions of dollars lost annually to corn and sorghum farmers. The insect infests vast acreages in the southern and central United States, and is continuing to expand its range. At present it poses the greatest threat to the southern Atlantic states. In addition, a resurgence of the corn borer could occur at any time in the southwestern and southern plains states because of the expanded corn acreage made possible by modern methods of irrigation (Morrison *et al.*, 1977).

For the last 10 years we have studied the physiology, ecology, nutrition, and feeding behavior of the southwestern corn borer in the Insect Physiology Laboratory of the University of Missouri. Highlights of our research are incorporated into this report, along with summaries of other available studies dealing with the bionomics of this insect pest, many of which are located in relatively inaccessible sources. Areas for future research will also be examined. This review, therefore, will focus on the insect's biology, ecology, physiology, and management, and includes sections on (1) characteristics of the species, (2) invasion and distribution within the United States, (3) larval growth, development, and metamorphosis, (4) physiology of the larva and adult, (5) environmental control of seasonal development and time measurement, and (6) management of populations. Of these areas, the major emphasis is placed on an examination of the facultative mature larval diapause. Diapause enables the southwestern corn borer to survive under adverse environmental conditions by synchronizing its life cycle with that of its host plants.

CHARACTERISTICS OF THE SPECIES

Life Stages

Figure 1 illustrates the 4 life stages of *D. grandiosella.* Since Davis *et al.*

*Professor of Entomology, 1-87 Agriculture Building, University of Missouri, Columbia, MO 65211.

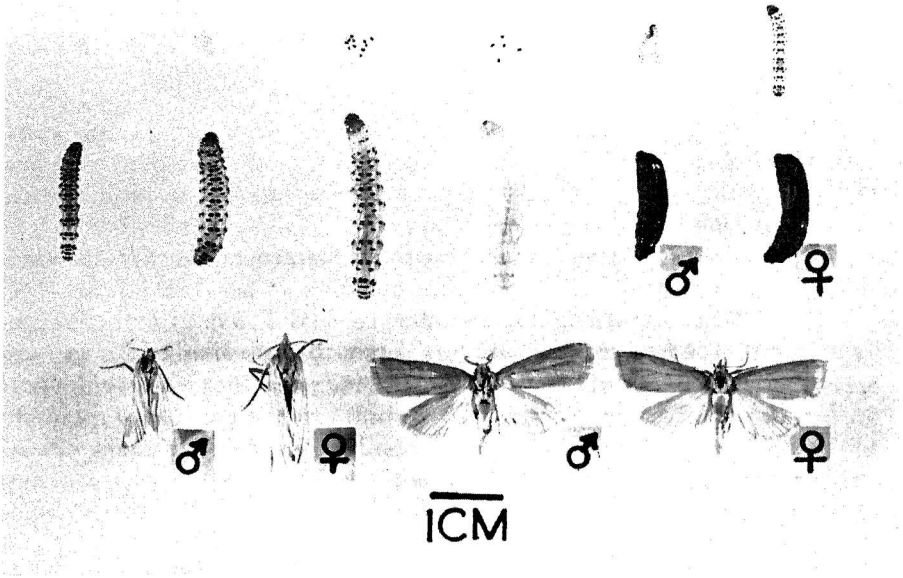

Fig. 1. Life stages of *D. grandiosella:* Top, l. to r., newly laid eggs, eggs in orange-band stage, eggs in black-head stage, 1st, 2nd, and 3rd stage larvae; Middle, 4th, 5th, 6th stage larvae, immaculate larva, male and female pupae; Bottom, male and female adults showing wings in natural position, and extended.

(1933) and Peterson (1967) have presented extensive anatomical descriptions of each stage the present account will be limited to their special characteristics.

Eggs are laid on both the upper and lower surfaces of the leaves and stalk of the host plant. Gravid females typically prefer corn plants of intermediate size as sites for oviposition. Each female lays from 100 to 400 eggs, either singly or overlapping one another in masses of several eggs. Immediately after being oviposited, each egg is flattened, elliptical, about 1 mm wide, and a uniform pale yellow. Within 36 hrs each egg develops three transverse orange bands which help to distinguish fertile eggs of *D. grandiosella* from those of several other corn feeding insects, such as the European corn borer, *Ostrinia nubilalis*. The serosa of the egg retains this orange pigment from 2 to 4 days, depending upon the temperature.

Larvae show a seasonal polymorphism. Summer-form larvae are off-white with black pinacula, whereas the winter-form larvae are uniformly light yellow due to their pigment-free pinacula (Fig. 1). After passing through at least 5 stages, summer-form (nondiapausing) larvae pupate without any prior loss of cuticular pigments. In contrast, prediapausing larvae molt from the spotted to the pigment-free "immaculate" morph (winter-form) at the onset of diapause.

Mature larvae pass through an immobile prepupal (pharate pupal) stage

which lasts about 24 hours before molting into pupae. Although larvae spin small amounts of silk, a protective cocoon is not formed around the pupa. The pupa has few characteristics to distinguish it from that of other Crambinae. It is elongate, moderately stout, lacks a cremaster and ranges from 13 to 25 mm in length. Male pupae are usually smaller than female pupae. The pupa is the earliest metamorphic stage in which sex can be determined externally. By examining the relationship between the anal and genital pores it is possible to determine sex because the genital opening of the male is located nearer to the anal opening than is that of the female (Davis *et al.*, 1933).

Davis *et al.* (1933) have provided the following general description of the adult:

> "The adult is a light straw-colored or sordid (or dull) white moth. The fore wings are slightly darker than the hind wings and their edges are nearly parallel. The hind wings are broad but lack the anal angle, thus giving them a semicircular outline. The labial palpi extend beaklike forward and downward. When at rest the wings are folded close over the body. The males are slightly smaller than the females and a very little darker in color. The antennae of the female are filiform proximad and very slightly pectinate distad and those of the male slightly pectinate. They are also a trifle shorter and thicker in the male than in the female. The tufts of hair on the top of the abdomen of the male are slightly dilated or fan shaped."

Although the dilated abdominal tufts of the male are useful for identifying the sexes, positive taxonomic identification requires a microscopic examination of the isolated male and female genitalia. Davis (1968) has described the internal anatomy of the male and female reproductive systems, including the spermatophore.

Taxonomic Position

D. grandiosella belongs to the family Pyralidae, the small snout moths, which is the third largest family in the order Lepidoptera. At least 1200 species of Pyralidae are recognized in North America alone. The borer is classed as a member of the *Chilo* group of graminaceaous stalk borers of the subfamily Crambinae. This generic group is characterized by having a closed cell in the hind wing, a sacchus and pseudo-sacchus in the male genitalia, and a free ostium pouch in the female genitalia (Bleszynski, 1969).

Dyar (1911) first described *D. grandiosella* from one female collected at Guadalajara, Mexico, and justified establishing a new species as follows:

> "A single large female differs from the series of *lineolata* in its browish color, without any yellow tint. The linings on the veins and between are very distinct; terminal dots minute black: discal dot obsolete. The front is smooth, without prominence. Hind wings soiled white."

Dyar therefore separated *D. grandiosella* from *D. lineolata,* which is a prevalent species in Central America and the Caribbean. The type specimen is now present in the U.S. National Museum. Subsequently Dyar and Heinrich (1927) provided a detailed account of the taxonomic characters of the genus *Diatraea,* including *D. grandiosella.* They pointed out that the genus is distributed throughout the world, especially in the tropics and subtropics. They stressed that taxonomic identification should be based on characters of the adult because the larvae of the various *Diatraea* species differ so little from each other, and frequently show marked seasonal polymorphism.

While undertaking an extensive taxonomic revision of the Crambinae, Box (1955) established the new genus *Zeadiatraea* in which he included *D. grandiosella.* His reclassification was based on several morphological characters, including the relative length of the juxta plate of the male genitalia. Since Bleszynski (1966) considered that these characters did not have any generic value he returned *grandiosella* to its original genus, *Diatraea.* In so doing he pointed out that the genus *Diatraea* established by Guilding in 1828 is a compact one characterized by the absence of ocelli, and often having a long uncus and gnathos in the male genitalia. Subsequently, Bleszynski (1969) provided a key to separate 7 species of *Chilo* and 21 species of *Diatraea,* including *D. grandiosella.*

Host Plant Preference

D. grandiosella is able to grow and develop successfully only on a relatively few species of wild or cultivated grasses. This restricted host range places the insect among oligophagous plant feeders which are adapted to feed on a limited variety of host plants. The grasses, the monocotyledonous family Gramineae, comprise one of the largest groups of flowering plants containing about 450 genera and 4500 species which are distributed throughout the world. They are extremely important economically because the major cereal and forage crops are found within their ranks.

Corn, *Zea mays,* serves as the primary host plant because its foliage is highly attractive for oviposition, and because corn leaf and stalk tissues permit a high growth rate of the larvae. All commercial varieties of corn appear to be equally acceptable host plants; field or dent corn, *Z. mays indentata,* sweet corn, *Z. mays saccharata,* and popcorn, *Z. mays everta,* support vigorous populations of the corn borer (Wilbur *et al.,* 1950).

In the absence of succulent corn or in situations where corn is grown close to sorghum or sugarcane, these cultivated grasses may serve as important secondary hosts. For example, larval infestations of sorghums have been found in Arizona, Arkansas, Kansas, New Mexico, Texas, and Oklahoma, and minor damage to sugarcane has been reported in Louisiana and Texas (Gifford *et al.,* 1961; Hensley *et al.,* 1963). Several varietal types of *Sorghum bicolor* support the insect:

Milo, which has relatively dry, short, slender stalks, and compact oval heads, and is grown primarily for its grain (Todd and Thomas, 1930).

Feterita, which also has relatively dry, slender stalks and few leaves, and compact oval heads, and is grown primarily for its grain (Todd and Thomas,

1930).

Kafir, which has thick succulent stalks, cylindrical heads, and is grown for both its forage and grain. Kafirita, a cross between Kafir and Feterita, is also an acceptable secondary host (Davis *et al.*, 1933).

Hegari, which also has succulent stalks, but has oval heads, matures later, and produces more suckers than Kafir. It is grown primarily as a grain sorghum (Gifford *et al.*, 1961).

Sorgo, which is characterized by sweet juicy stalks, and is grown for both forage and syrup. The sweet sorghum, "sugar drip," which is grown for forage in Oklahoma, supported larval growth and development (Gifford *et al.*, 1961).

Sudan grass, which is a grassy sorghum cultivated as a forage crop. It has smaller stems, narrower leaves, and sprouts more readily from the root than other cultivated sorghums (Rolston, 1955a).

Broom corn, which produces long brushy heads with fibrous seed branches up to 3 feet in length, and is used to manufacture broom heads (Davis *et al.*, 1933).

Besides sugarcane, *Saccharum officinarum,* the perennial grass which is cultivated widely in the tropics and subtropics, other grasses recorded as hosts include:

Teosinte, *Euchlaena mexicana.* This tall annual grass which is native to Mexico grows in large clumps and is used as a forage crop. It is closely related to maize and is an acceptable alternative host (Burkhardt and Painter, 1954).

Johnson grass, *Sorghum halepense.* This wild perennial grass has creeping rhizomes. Its usefulness as a fodder is more than counterbalanced by other characteristics which make it a noxious weed. *S. halepense* is recognized as an important secondary host (Davis *et al.*, 1933).

Pearl millet, *Pennisetum americanum.* This and other varieties of this hardy grass are grown in the tropics and subtropics as a cereal or forage crop. Although a few larvae have been shown to survive on millet under laboratory conditions, it is a minor host in the field (Rolston, 1955a).

The secondary hosts described above differ in their capacities to attract ovipositing females and to support normal larval development. They range from teosinte which virtually matches corn as a host, to millet, which at best permits a low rate of survival. While these hosts may themselves be injured, they also provide an insect reservoir for subsequent infestations of corn and protected habitats for diapausing larvae to overwinter.

Diatraea spp. Present in the United States

Four of the seven species of *Diatraea* which have been recorded in the United States are pests of cultivated grasses. Besides *D. grandiosella,* the southern cornstalk borer, *Diatraea crambidoides* (Grote), and the neotropical corn borer, *Diatraea lineolata* Walker, and the sugarcane borer, *Diatraea saccharalis* (Fabr.), are potentially or actually economically important pests of corn, sorghum, and sugarcane (Davis *et al.*, 1933; Anonymous, 1966; Bleszynski, 1969). Larvae of these closely related species can be accurately identified only through the use of

setal maps (Peterson, 1967). A brief account of their bionomics follows:

D. crambidoides is virtually indistinguishable from *D. grandiosella.* The southern cornstalk borer is found in the United States as well as in Central and South America. Within the United States largest populations are found in the southeast from Maryland to Florida though its range is reported to extend westward to Kansas and possibly Oklahoma. The life history follows a similar pattern to that of *D. grandiosella:* mature larvae of the diapause generation transform from a spotted to a pigment-free immaculate morph and overwinter in the stalk crown of the host plant. However, unlike prediapausing larvae of *D. grandiosella,* those of *D. crambidoides* do not girdle their host plant in preparation for diapause. While corn is the primary host, the larvae also feed on sugarcane, sorghum, Johnson grass, guinea corn, and gama grass. Although the larvae severely damage corn by feeding on the leaves, meristematic tissue, and stalks, but not on the ears, they are not as troublesome over their entire range of distribution as are larvae of *D. grandiosella.*

D. lineolata is a pest of corn throughout Central America and in some of the Caribbean Islands (Kevan, 1944). Although the neotropical corn borer has been reported to infest corn in south Texas in 1964, there is some doubt about whether its range includes the United States because of the close relationship between *D. lineolata* and *D. grandiosella* (Anonymous, 1966; Bleszynski, 1969). In Central America larvae become dormant and immaculate during the dry season, remain in the stalks, and pupate during the rainy season. However, unlike larvae of *D. grandiosella,* prediapausing larvae neither girdle the plant nor excavate a cell exclusively in the root crown. Corn is its principal host though Guatemala grass and teosinte are satisfactory alternative hosts. The larvae damage corn by feeding on the leaves, meristematic tissue, stalks, and ears.

D. saccharalis is distributed from the Gulf Coast region of the United States through Central and South America to Argentina. The sugarcane borer entered the United States around 1855 and is now found in the gulf strip of the lower austral zone in Florida, Mississippi, Louisiana, and Texas. Within the United States the life history of *D. saccharalis* is similar to that of *D. grandiosella.* The insect has a facultative mature larval diapause and overwinters in sugarcane or corn stalks above ground level. Diapusing larvae may be either spotted or unpigmented, i.e., immaculate, like diapausing larvae of *D. grandiosella.* Larvae of *D. saccharalis* cause serious damage to sugarcane by feeding on the leaves and stalks. Stalk feeding is especially destructive because it causes adulteration and loss in yield of the extracted juice. Although sugarcane and corn are its principal hosts, it has been reported to feed on about 65 species of Gramineae, including aquatic grasses (Elias, 1970).

DISTRIBUTION

The southwestern corn borer is currently found in Mexico and the United States. While its distribution in Mexico remains static, it is gradually spreading in an easterly direction in the United States and is presently established in 13

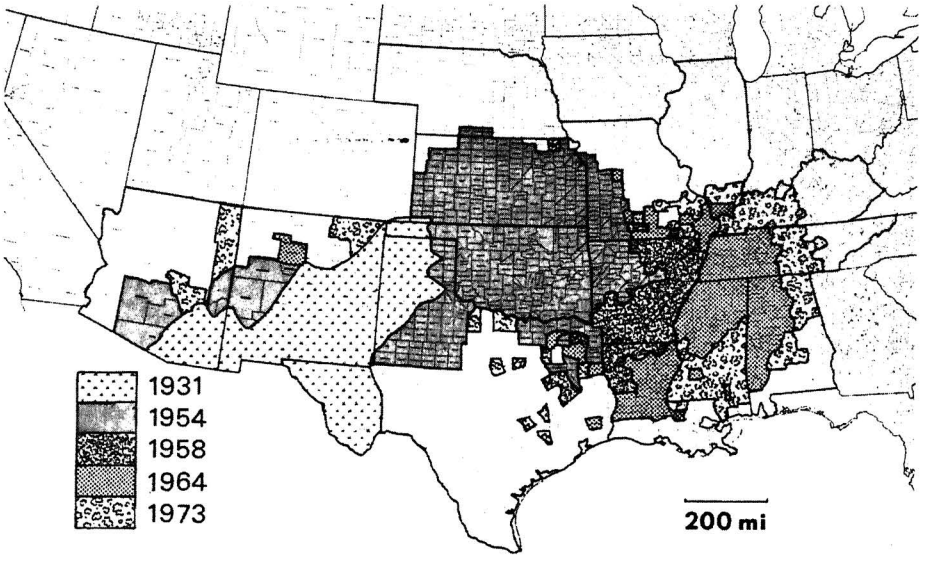

Fig. 2. Chronology of the dispersal of *D. grandiosella* across the southern corn belt of the USA. Based on information in Davis *et al.* (1933), and in the Cooperative Economic Insect Reports of the USDA.

states, ranging from Arizona to Alabama (Fig. 2).

In Mexico the insect has been reported in the south-central states of Puebla, Morelos, Guerrero, Michoacan, Colima, Jalisco, and Guanajuato, in the northwestern states of Nayarit, Sinaloa, Sonora, and Chihuahua, and in the Rio Grande Valley, Apodaca, and Rio Bravo of the northeast. *D. grandiosella,* therefore, does not appear to be present east of the northern state of Chihuahua or in the central plateau of Mexico (Elias, 1970).

The bionomics of *D. grandiosella* in Mexico have received little study because the insect causes much less damage to corn than does *D. lineolata* or *D. saccharalis.* The life history of *D. grandiosella* in Mexico is similar to that in the United States. For example, corn is planted in the northwestern state of Sonora in June or August and harvested in October or January. Mean summer temperatures are around 30°C and begin to decrease in October to give a mean low temperature of 15°C in January. Under these conditions diapausing larvae are present at harvest time. In contrast, temperatures in the subtropical state of Morelos remain relatively constant year round. With suitable irrigation, corn can be grown in the off-season, permitting the survival of a late fall-emerging brood which does not diapause (A. Ortega, personal communication).

Dispersal Across the United States

The first official records of *D. grandiosella* taken in the United States are from Lakewood and Las Palomas, New Mexico, in 1913 (Davis *et al.*, 1933). While the insect may well have entered the United States much earlier than this date, records are unavailable because the species was not named until 1911 (Dyar,

1911). A report of damage to corn at Las Cruces and Eddy, New Mexico, in July, 1891, by a borer then called *Chilo saccharalis* may in fact have been caused by *D. grandiosella* (Townsend, 1891).

Since 1913 the insect has spread in a generally eastward direction across the United States (Fig. 2). Information about the progressive colonization within the United States is presented in Henderson *et al.* (1966), Anonymous (1974), and Chippendale and Reddy (1974). From the reports of survey entomologists which are published in the Cooperative Economic Insect Reports it is possible to calculate the rate of dispersal. Fairchild *et al.* (1965) estimated an eastwardly migration of 13 miles per year from 1913 to 1931, 20 miles per year from 1932 to 1953, and 35 miles per year from 1954 to 1964. Since 1965 the migration has continued at a mean rate of about 12 miles per year. Although the species was found in southern Nebraska, northern Kansas, and central Missouri in the 1940s and 1950s, the present northern limits have receded to central Kansas and southern Missouri and Illinois, mainly because of high mortality of diapausing larvae at this latitude (38°30'N) (Tate and Bare, 1945; Wilbur *et al.*, 1950; Chippendale and Reddy, 1974). Similar temperature stresses are not encountered in a southeasterly direction, and the insect can be expected to colonize southern Atlantic states wherever suitable host plants exist.

A selection for those southwestern corn borers most resistant to freezing is undoubtedly occurring each year at the northern boundary of the species distribution. This selection may result in *D. grandiosella* gradually colonizing more northerly latitudes, although current information suggests that it has already reached the stable northern limits of its distribution in the Midwest. Field observations of diapausing populations conducted over several years in southern Missouri indicate that a high percentage of diapausing larvae die between September and May. Limited cold-hardiness, along with the depredations of predators, pathogens, and parasites, account for the attenuation of the diapausing population.

Although current evidence suggests that low winter temperatures are the principal agent regulating the northern limits of distribution, other geographic, climatic, and edaphic factors are also involved. For example, topographical barriers such as mountain ranges, forests, and deserts, where suitable host plants are absent, limit the distribution of the species. Evidence also suggests that soil type, rainfall, and snow accumulation influence overwintering survival. Mortality of diapausing larvae is higher in wet clay soils than in well-drained sandy soils in localities near the northern limits of the species distribution which are subject to similar winter temperatures (Wilbur *et al.*, 1950). This probably occurs because the wet clay soils promote the formation of ice crystals in the overwintering cells and cause inoculative freezing of diapausing larvae.

Examples of Dispersal—Kansas, Missouri, Tennessee

The distribution of the southwestern corn borer in Kansas, Missouri, and Tennessee is reviewed to illustrate multiple factors which regulate the pest's migration and distribution. Although the species was first recorded in Kansas in

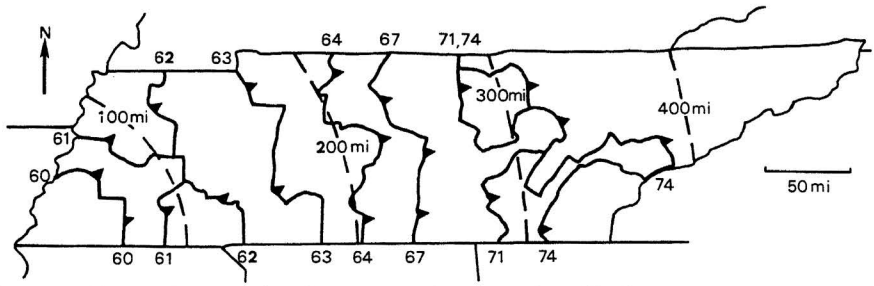

Fig. 3. Chronology of the dispersal of *D. grandiosella* from west to east across Tennessee. The dated lines indicate the successive county boundary limits of the species. Distance is indicated in 100 to 400 mile radii from the southwestern corner of state, the area of the initial infestation. Based on information in Gordon and Bruer (1975).

1931, a series of unseasonably dry years prevented any further spread until the 1940s. During that decade the species was recorded in most corn-growing counties of the state (Wilbur *et al.*, 1950). After a series of extremely cold winters in the 1950s, however, the distribution receded and the sandy land region of south-central Kansas now forms the northern limits of distribution (Knutson, 1975). Although considerable winter mortality occurs in Kansas, the highest rate of survival of diapausing larvae occurs in the south-central counties of Stafford and Reno where the well-drained sandy soils reduce mortality due to inoculative freezing (Chippendale and Reddy, 1974).

D. grandiosella was first recorded in Missouri in 1953 when infestations were found in 10 southwestern counties. Subsequently, in 1958, the insect entered the fertile cotton and corn growing Delta counties of the southeast. In the mid-1950s the borer was found in 25 western counties, but since then the overwintering populations have been restricted to about 14 southwestern and eight southeastern counties. The population decline in western Missouri can be attributed to low winter temperatures causing high larval mortality. In addition, the Ozark Mountains in south-central Missouri preclude the widespread cultivation of corn. Winter mortality tends to be higher in Missouri than in Kansas because the soils are heavier and the precipitation rate is higher (Chippendale and Reddy, 1974).

Figure 3 illustrates the time course of the migration of the insect across Tennessee. Its dispersal in this state is well documented and the mild climate does not prevent larvae from successfully overwintering in northern counties (Gordon and Bruer, 1975). The insect was first found in three counties in southwestern Tennessee in 1960 and since then has spread across West and Middle Tennessee. By 1974 southwestern corn borers had been found in 66 of the 95 counties in Tennessee. From these county records it can be estimated that between 1960 and 1964 the species dispersed eastwardly at a rate of about 38 miles per year. Between 1965 and 1974 the rate decreased to about 12 miles per year. An important reason for the lower rate of dispersal from 1965 to 1974 appears to be the limited availability of host plants on the elevated Cumberland Plateau in Middle Tennessee.

Survey data which have been gathered over the last 60 years define the rate and extent *D. grandiosella* has colonized new habitats. The many factors influencing this dispersal include availability of host plants, topographical barriers, overwintering survival, and climatic conditions, especially temperature and wind velocity. The dispersal is probably brought about solely by flight patterns of the adults. Larvae seldom leave the plant on which they hatch, and rarely feed on the ear. The inadvertent dispersal of larvae and pupae through commercial channels seems to be a highly unlikely occurrence. However, whether adult dispersal is occurring because of the presence of a true, undistracted migratory flight, or as a consequence of host-searching flights remains to be determined (Johnson, 1969).

CHARACTERISTICS OF LARVAL GROWTH AND BEHAVIOR

During the last 20 years research advances have led to the development of artificial diets for larvae of many plant-feeding insects. Since Keaster and Harrendorf (1965) demonstrated that larvae of *D. grandiosella* could be maintained on an artificial diet, specific nutritional requirements of the larvae have been determined, thereby making possible the continous mass rearing of the species (Chippendale, 1975; Davis, 1976). Improved rearing conditions have greatly facilitated research about the physiology and ecology of diapause, and the screening of resistant host genotypes.

Maintenance of a Laboratory Colony

Procedures for preparing an artificial medium (Table 1), and for handling the life stages of *D. grandiosella* have been described (Chippendale, 1975; Davis, 1976). The following methods have been used routinely in my laboratory to maintain a colony. They are satisfactory for producing a continuous supply of carefully staged insects for laboratory experiments.

Newly hatched larvae are placed on cubes of freshly-prepared artificial medium inside transparent 1 oz plastic cups. The medium is prepared in 4 liter batches and poured into four shallow stainless steel pans (21 x 31 cm). Each slab of medium is pushed through a 2.5 cm wire-mesh screen to produce small cubes. The incorporation of antimicrobial agents into the medium and strict sanitary procedures obviate a need to use sterile procedures. After the cups, each containing two or three larvae, have been sealed with laminated cardboard lids, the larvae are incubated at 30°C 16L:8D to produce a non-diapausing generation, or 23°C 12L:12D to induce the facultative mature larval diapause. Procedures for rearing large groups of larvae in single containers have not proved satisfactory, because the late instars are highly cannibalistic. Pupae are removed from the larval medium and placed on moist vermiculite in Petri dishes. Dishes containing 50 to 100 pupae are placed in a cylindrical 19 x 30 cm cage made from no. 4 hardware cloth and are held at 25°C 10L:14D. Waxed paper covers the sides and top of the cage, and eggs are deposited on these surfaces. The egg masses are collected three times a week and incubated in quart Mason jars containing moist filter paper at 25°C 10L:14D.

TABLE 1
COMPOSITION OF AN OPTIMUM ARTIFICIAL DIET FOR CULTURING LARVAE OF *D. GRANDIOSELLA*[a]

Component	Contribution to larva or medium	Specific material used	Concentration (%, wet wt.)
Nutrients			
Protein	Amino acids	Casein	4.93
Carbohydrate	Monosaccharides	Sucrose	3.25
Sterol	Cholesterol	β-Sitosterol	0.19
Polyunsaturated fatty acid	Linoleic or linolenic acid	Wheat germ oil	0.23
Salts	Inorganic anions and cations	Powdered mixture[b]	0.93
Vitamins	Vitamin B group	Aqueous mixture[b]	9.31 ml
	Choline	Choline chloride	0.10
	Vitamin C	L-ascorbic acid	0.50
Plant material	Amino acids, lipids, vitamins salts, feeding stimulants	Whole wheat germ	2.79
Water	Water	Distilled water	74.99 ml
Other additives			
Non-nutritive bulk	Texture	Cellulose powder	0.50
Gelatinizing agent	Consistency	Agar	0.25
Antimicrobial agents	Retard microbial growth	Formaldehyde, sorbic acid, methyl paraben	0.23

[a]From Chippendale (1972)
[b]For composition of mineral and vitamin mixtures see Chippendale (1975)

Nutritional Requirements

Since the adults do not feed, the larvae must consume sufficient food to meet the insect's demand for growth, metamorphosis, flight, and reproduction. Nutritional research has provided the following information about the specific dietary requirements of *D. grandiosella* (Table 1).

A dietary supplement of 3 to 5% protein is necessary to sustain optimum larval growth (Reddy and Chippendale, 1972). Protein is usually provided as pulverized whole casein which is readily hydrolyzed by digestive enzymes. Although casein provides a reasonably well balanced source of amino acids, the concentrations of tryptophan and the sulfur amino acids, cysteine and methionine, are low and this deficiency could result in poor growth. However, the wheat germ supplement, together with casein, provide larvae with adequate quantities of essential amino acids and amino nitrogen for the support of their metabolic processes. Although other purified proteins such as gluten and soybean protein have not yet been used extensively, they may serve as adequate cheap sources of amino acids.

Dietary supplements of 3 to 5% mono- or di-saccharides are necessary to promote larval growth and development (Chippendale and G.P.V. Reddy,

1974). Either glucose or sucrose (cane sugar) is an acceptable carbohydrate because both provide positive gustatory stimuli, and are readily assimilated by the larvae. A low growth rate is observed when dietary starch replaces sucrose because starch does not serve as a feeding stimulant and may be inefficiently digested.

The larvae do not reach maturity unless they receive an adequate supplement of dietary sterol. Larvae grow better on diets containing plant sterols, such as β-sitosterol and stigmasterol, than on those containing cholesterol because plant sterols also act as feeding stimulants (Chippendale and G.P.V. Reddy, 1972). Polyunsaturated fatty acids in the form of linoleate or linolenate have been found to promote larval growth and permit normal wing development. The fatty acids are present in whole wheat germ, along with α-tocopherol which serves as an antioxidant.

Although most of the dietary components contain inorganic contaminants, larval growth is accelerated by using a dietary salt mixture (0.5-1.0%). The salt mixture was developed originally for the flour beetle, *Tribolium confusum*, and *O. nubilalis*, and contains only nine components (Medici and Taylor, 1966; Beck *et al.*, 1968). The mixture apparently has a positive effect on feeding behavior and supplies the minerals needed for optimal growth. This supplement is necessary even in artificial diets containing wheat germ, which supplies many anions and cations (Reddy and Chippendale, 1972).

A satisfactory diet contains appropriate concentrations of water-soluble vitamins. Although many of these vitamins are supplied by wheat germ, an additional supplement is necessary. In practice, an aqueous mixture of the following B-group vitamins is used: calcium pantothenate, niacin, paraminobenzoic acid, riboflavin, pyridoxine, thiamine, folic acid, biotin, and cobalamine. *Myo*-inositol is routinely incorporated into this mixture although a requirement for it has not yet been demonstrated. The larvae also require choline chloride and ascorbic acid for growth and development (Reddy and Chippendale, 1972; Chippendale, 1975). Although the fat soluble vitamins A and E may be required they are not included as separate additives because carotenoids (mainly xanthophylls) and α-tocopherol are present in the dietary wheat germ oil.

Table 1 also lists non-nutritive dietary adjuvants which are necessary for the successful culturing of the larvae. Agar is used as the gelatinizing agent. The properties of the gel are governed by the concentration of agar and water as its pH. The addition of cellulose powder or ground corn cobs (Davis, 1976) gives the diet a suitable texture and consistency. To minimize microbial contamination, antimicrobial chemicals, such as formaldehyde, sorbic acid, and methyl paraben, are included at the lowest possible concentrations. High dietary concentrations of these chemicals have been shown to retard insect growth and development (Singh and House, 1970).

Larval Growth Rates

Larvae of *D. grandiosella* reared on an artificial diet have been shown to pass through five or six stages (Yin and Chippendale, 1976). In the field, where

temperature and food supply are more variable, up to eight larval instars have been observed, though most larvae pass through only six stages (Davis *et al.*, 1933; Rolston, 1955a). It is difficult to distinguish the instars solely on the basis of morphological characteristics. However, the head capsule and cervical shield change color beginning in the 4th instar. These structures are brownish-black in the 1st three instars and light tan in the subsequent instars.

A growth curve has been obtained for larvae reared under non-diapausing conditions, 30°C 16L:8D. The highest growth rate was found to occur between the eighth and 14th day when the larval weight increased from a mean of 23±2 to a maximum of 139±8 mg, representing about a six-fold increase in mean weight. A sex dimorphism was observed beginning in the 3rd instar. Males ecdysed into the 4th instar on days 7 and 8 and into the 5th instar on day 10. Most of the males pupated from the 5th instar, with 50% pupation observed at 16 days. The females ecdysed into the 4th instar on days 7 and 8 and into the 5th instar on days 10 and 11. Most of the females, however, entered a 6th instar and therefore pupated later than the males (50% pupation by day 18) (Yin and Chippendale, 1976).

Nutritional indices have also been calculated for 13-day-old non-diapausing larvae to determine the fate of consumed artificial diet (Jacob and Chippendale, 1971). During the experimental period each larva consumed 112 ± 12 mg dry weight diet, voided 62 ± 7 mg feces, and gained 11 ± 4 mg in live weight. Each larva, therefore, retained about 50 mg of the diet of which only 11 mg were used to produce tissue. These values yield the following nutritional indices: approximate digestibility, 44%; efficiency of conversion of ingested food, 10%; and efficiency of conversion of digested food, 22%. These last two indices provide an estimate of the larva's ability to convert nutrients into body tissues.

Pre-diapausing larvae reared at 23°C 12L:12D have been shown to have a much lower growth rate than that of non-diapausing larvae (Chippendale and Yin, 1976). Six larval instars were observed and larvae ecdysed into the 2nd, 3rd, 4th, 5th, and 6th instars on days 5, 10, 14, 18 to 19, and 24 to 28, respectively. A sex dimorphism was detected beginning on the 24th day. The head capsules of 6th instar females were significantly wider than those of the males. After reaching maturity, the larvae transform into the immaculate morph which has a mean head capsule width of 2.41 mm (male) and 2.55 mm (female). Since these head widths represent a ratio of only 1.03 over those of the spotted morph, a stationary ecdysis marks the transition to the immaculate morph. Fully grown spotted morphs collected from the field were found to have a mean head capsule width of 2.76 mm whereas immaculate morphs had head widths of 2.85 mm, suggesting that pre-diapausing field larvae pass through one additional instar (Chippendale and Yin, 1973).

Larval Feeding on the Corn Plant

The southwestern corn borer is a serious pest of corn because it damages the plant at all stages of its growth and development. Early instars of the first generation feed mainly on the succulent tissues within the whorl of young corn

plants which have not yet tasselled. In so doing they may destroy meristematic tissue of the terminal bud causing a loss of apical dominance and the development of lateral buds in leaf axils. A plant so attacked has a stunted and bushy appearance and is graphically described as having a dead heart. Dead heart injury is most likely to occur in late-planted corn. Plants have passed the critical period for dead heart injury if, as a result of early planting, the tassel stage is reached before early instars of the first generation are present. Early instars of the second generation feed primarily on the husks of the ears, the leaf sheaths, and the shanks, kernels and cobs. Although this external feeding causes superficial injury to the plant, it does not significantly reduce yields. Stalk feeding of the late instars of all generations causes substantial injury to the plant. If partly grown larvae enter the stalks before the internodes have fully extended, stunting of the plant may result. In more mature corn, larval tunneling may be so extensive as to retard translocation of nutrients to the ears, thereby causing a decrease in kernel size. In addition, pre-diapausing larvae may critically damage mature plants when they girdle the stalks just above ground level.

The feeding locations are governed by the behavior of the 1st instars which migrate from the egg masses to moist, succulent feeding sites on the corn plant. Young plants in the whorl stage are the most acceptable hosts. Tests have shown that 30 to 40% of 1st instars establish on whorl stage corn compared with less than 10% establishment on older dough or tassel stages (Stewart and Walton, 1964). A high mortality occurs on old corn plants because of the limited number of moist and succulent feeding sites for young larvae. Most larvae bore into the main stem of the plant during their 3rd instar, resulting in their spending three complete instars in the protected habitat of the stalk (Hensley and Arbuthnot, 1957).

Detailed accounts of leaf, whorl, ear, and stalk feeding sites have been provided (Davis *et al.*, 1933; Wilbur *et al.*, 1950; Davis *et al.*, 1972). Figure 4 illustrates the distribution of larvae during their first 20 days on corn plants at both the whorl and tassel stage of growth. On whorl stage plants newly hatched larvae migrate primarily to the leaves of the inner whorl where they feed on leaf, bud, and tassel tissue for 11 to 14 days before entering the stalk. In contrast, on tassel stage plants the ear husks provide the most important initial feeding sites. By the eleventh day larvae are also found in moderate numbers in the leaf sheaths and ear tissues, and by the twentieth day most of the larvae have penetrated into the stalk. The most common sites for larvae to penetrate into the stalk are the junctions between the leaf sheaths and stalks. Once inside the stalk the larvae excavate vertical tunnels from 3 to 12 in. in length. After completing its feeding cycle, each larva of the non-diapausing summer generations prepares an exit hole for the adult and then pupates within the previously excavated tunnel. In contrast, each fully fed larva of the diapausing generation migrates to the base of the stalk where it prepares an overwintering cell in the crown, and an exit hole for the adult. As part of this pre-diapausing behavior it may also girdle the plant a few inches above ground level.

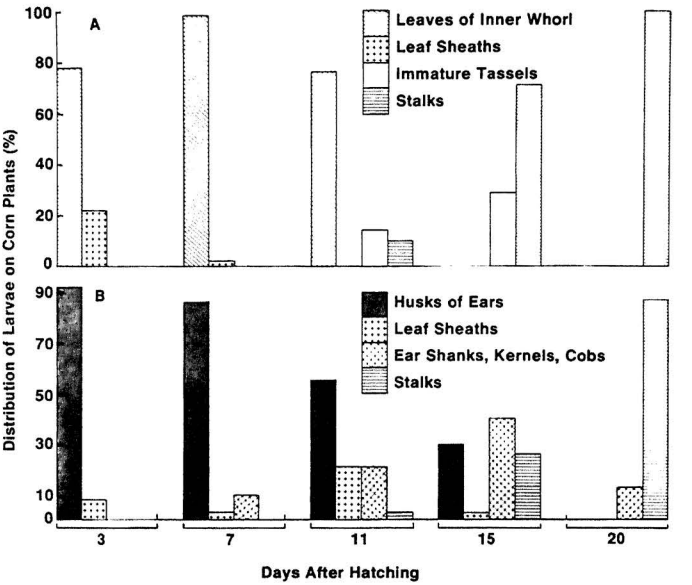

Fig. 4. Distribution of larvae of *D. grandiosella* on 30 corn plants within 3, 7, 11, 15 and 20 days of their hatching. Plants were infested in 1970 in Mississippi at the whorl (A) and tassel (B) stages of growth. Data summarized from Davis *et al.* (1972).

Larval Polymorphism

Mature larvae of *D. grandiosella* reared under diapause-inducing conditions display color polymorphism and appear, in turn, as spotted, transitional, and immaculate morphs. The spotted morph has heavily pigmented pinacula, the transitional morph lightly pigmented pinacula, and the immaculate morph has a pigment-free integument (see Fig. 1). Mature spotted larvae have been studied to determine whether they molt into immaculate morphs or whether they become immaculate as a result of fading of their cuticular pigments. The frequency with which the transitional morph appeared was also determined. The results showed that the majority of the spotted larvae molted directly in the immaculate morph. Only 7% of the larvae became transitional morphs either as a result of pigment fading or molting (Chippendale and A.S. Reddy, 1972).

Environmental influences on the transition from the spotted to the immaculate morph of *D. grandiosella* were determined (Chippendale and Reddy, 1972). The experiment was carried out by transferring 40 day old larvae from 23°C 12L:12D to 30°C 24L:OD, 30°C 12L:12D, or 30°C OL:24D. It was found that 50% of the larvae in all three 30°C regimens had ecdysed into the immaculate morph by 45 days of age as compared with 50 days of age for the 23°C control group. The transfer to a high temperature, therefore, increased the rate of ecdyses into the immaculate morph. Since similar results were obtained under all three 30°C regimens, photoperiod does not appear to have a direct influence on

the transition to the immaculate morph.

Field observations have shown that the ecdysis from the spotted to the immaculate morph occurs during September and October in southeastern Missouri. For example, counts made on October 6, 1975, showed that only 15% of the larvae were immaculate, whereas by October 27, 95% had molted into the immaculate morph. Similar observations made in 1976 showed that the 50% immaculate mark occurred about 2 weeks earlier than in 1975. Counts taken on September 10 showed that 15% of the larvae were immaculate, and by October 7, 90% of the larvae were already immaculate morphs in their overwintering cells. Observations made in November invariably show that >95% of the larvae are immaculate. The immaculate morph is, therefore, the typical diapausing stage of both laboratory and field populations.

The live weights of larvae have been measured before and after the immaculate ecdysis to determine the weight loss associated with the onset of diapause (Chippendale and A.S. Reddy, 1972). Field larvae lost 17% of their weight during the 10 days immediately preceding their immaculate ecdysis and 9% during the 10 days immediately following this ecdysis. Equivalent values for laboratory larvae were 22% and 10%, respectively. Loss of water, gut tract contents, and protein as spun silk probably account for most of the weight loss prior to the immaculate ecdysis. Since no sharp decrease in weight was detected at the time of the ecdysis, the larvae may imbibe additional water to compensate for the loss of water and exocuticle. However, larvae were partially dehydrated and had a mean water content of 65% ten days after the immaculate ecdysis. The loss of water seems to render the larvae cold-hardy and facilitates diapause development (Reddy and Chippendale, 1973).

Behavior of Pre-diapausing Larvae

Larvae display an instinctive behavioral pattern as they prepare for diapause. Pre-diapausing larvae migrate to the base of the stalk of the corn plant where they prepare an overwintering cell below ground level. In the process of preparing this cell and a plugged exit hole for the escape of the adult, the larvae may girdle the plant a few inches above ground level. Larvae of *D. grandiosella* are distinctive in the genus *Diatraea* by being the only ones which girdle the plant. Environmental stimuli including short days, low temperatures, and the state of the host plant release this behavior by acting through the larval neural and humoral systems. This behavior is typical of an instinctive trait because it is unlearned, characteristic of the species, and confers adaptive advantages. Since last instar pre-diapausing larvae, unlike non-diapausing ones, retain active corpora allata and a high juvenile hormone titer, it is possible that juvenile hormone regulates this behavioral pattern (Chippendale, 1978). The girdling behavior has been well documented and is the cause for the substantial economic losses which occur when the girdled plants lodge (Wilbur *et al.*, 1950; Rolston, 1955a). However, the girdling activity is only part of the stereotypical behavioral pattern which leads to the preparation of a secure overwintering site.

The sequence of events leading to the formation of the intact overwintering cell usually occurs as follows. Fully grown pre-diapausing larvae descend to the root zone either by crawling down the outside of the plant and reentering just above ground level or by tunneling vertically down the stalk. The larvae then hollow out the stalk crown and ascend to about 10 cm above ground level, at a point between one of the first three internodes, where they fashion a plugged exit hole for the escape of the adult. At this time they may also girdle the plant. Girdling proceeds internally until only the thin epidermis of the stalk remains intact. Stalks may be partially or completely girdled around their circumference. The larvae then seal the central tunnel with frass and silk strands and descend to the tip of the stalk crown where they remain for the winter as immaculate morphs. In late spring, in preparation for the emergence of the post-diapausing adults, the larvae clear the tunnels and exit holes of frass and other debris before returning to their overwintering cells to pupate.

Selection for the girdling trait appears to be a fairly recent occurrence and may be associated with the northward migration of the species. Although girdling activity is rare in south-central and northwestern Mexico, a higher incidence occurs in northeastern Mexico, and up to 70% of infested stalks are girdled by *D. grandiosella* populations in the United States (Wilbur *et al.*, 1950; Rolston, 1955a; Elias, 1970). Factors controlling the rate of girdling have been investigated. Zepp and Keaster (1977a, b) have evaluated plant factors which control girdling. They concluded that high light intensity, low plant density, and the prevention of ear development, which promote vigorous stalk growth, decrease the rate of girdling. In contrast, those factors which retard stalk growth, including low light intensity, high plant density, and leaf loss, increase the rate of girdling.

Southwestern corn borers overwintering in girdled corn stalks have been shown to have a survival rate of two to three times that of larvae overwintering in ungirdled stalks (Bailey, 1962). The adaptative advantage of girdling may be associated with the prevention of root lodging and the subsequent exposure of the stalk crown, or to a reduction in the incidence of stalk rot because nutrients are not translocated from the root zone in girdled plants (Zepp, 1973).

Cannibalism is a frequent occurrence among larvae of *D. grandiosella.* It increases after larvae enter the stalk and is most pronounced in larvae immediately before they enter diapause. Fully grown spotted pre-diapausing larvae have been shown to be the most cannibalistic. They attack and kill other larvae they meet as they descend to the root zone and prepare their overwintering cells. This high degree of cannibalism associated with the pre-diapause behavior also has adaptive value because it maximizes the overwintering survival rate of the species. Although corn plants can support the growth of several larvae, usually only one pre-diapausing larva survives per plant to occupy the overwintering niche in the stalk crown. Counts taken in Arizona have shown that over 90% of the infested stalks contain a single diapausing larva (Davis *et al.*, 1933).

PHYSIOLOGY OF THE LARVA AND THE ADULT

D. grandiosella has proved to be an excellent model insect for studying the physiology of larval diapause. The mature larval diapause is instituted after the immature larval instars have been exposed to inductive short day-lengths and low temperatures. Preparatory biochemical adjustments, including the accumulation of lipid reserves, and behavioral patterns, including the migration to a protected site in the stalk crown, occur in advance. Once diapause intervenes, the metabolic and respiratory rates fall dramatically as the larva is prepared to withstand exposure to winter conditions in the absence of food and water. During the last 10 years considerable progress has been made in understanding the mechanisms controlling its diapause. Of special significance is the finding that juvenile hormone (JH) regulates diapause initiation and maintenance. Evidence related to larval physiology, as well as the more limited information available about the reproductive and flight physiology of the adults, is now reviewed.

Hormonal Control of Larval Diapause

In common with other insects the growth, development, and diapause of *D. grandiosella* is hormonally controlled. Neurosecretory cells in the brain synthesize a neurohormone, ecdysiotropin, which is released from the corpora cardiaca into the hemolymph. The function of ecdysiotropin is to stimulate the prothoracic glands to release a prohormone, α-ecdysone, which is converted to the more active 20-hydroxyecdysone (β-ecdysone) elsewhere in the body. The nature of the molt induced by 20-hydroxyecdysone depends upon the titer of the circulating JH which is secreted by the corpora allata. In the presence of a high titer of JH, 20-hydroxyecdysone initiates a larval molting cycle, whereas in the presence of an extremely low titer of JH, and in its absence, 20-hydroxyecdysone initiates pupal and adult molting cycles, respectively.

Chippendale and A.S. Reddy (1972) observed that diapausing larvae underwent stationary molts from one immaculate morph to another, thereby showing that diapausing larvae have a functional JH titer and neuroendocrine system. This stationary molting activity during diapause was found to be temperature dependent. For example, 69%, 36%, and 14% underwent one, two, and three stationary ecdyses at 20°C, whereas the frequency was only 39%, 11%, and 3%, respectively, at 30°C. Although these results in part reflect the different durations of diapause at the two temperatures they also indicate that a predetermined number of stationary ecdyses does not occur during diapause (Chippendale and Yin, 1976). While the stationary ecdyses may offer some adaptive advantages in adjusting the surface area-volume relationships of diapausing larvae, natural selection presumably favors those larvae which do not expend reserves in this manner. If the JH titer regulates the occurrence of stationary ecdyses, exposure to high temperatures may accelerate JH turnover and thereby limit the buildup of a sufficiently high titer to permit a larval ecdysis.

Yin and Chippendale (1973, 1979) experimented with the neuroendocrine system of *D. grandiosella*. A head ligature caused newly diapaused larvae to pupate

early, thereby indicating that some factor in the head sustains diapause. This interpretation was supported when an injection of 20-hydroxyecdysone into the thoraco-abdomen of diapausing larvae which had previously received a head ligature also caused them to pupate early. An ecdysone deficiency as a cause for diapause was ruled out because early diapausing larvae injected with 20-hydroxy-ecdysone underwent stationary larval ecdyses. The corpora allata in the head were identified as the diapause factor. Last instar non-diapausing larvae treated with a topical application of a JH mimic entered a diapause-like state and periodic topical JH mimic applications to diapausing larvae sustained diapause. These findings were interpretated as supporting a JH regulation theory of larval diapause (Chippendale and Yin, 1973; Chippendale, 1977). They have been supplemented with additional studies into the ultrastructure of the larval corpora allata of *D. grandiosella* (Yin and Chippendale, in manuscript). Pre-, early, and mid-diapausing larvae retain actively secreting corpora allata characterized by having extensive smooth endoplasmic reticulum, and numerous mitochondria and Golgi bodies.

To further examine JH involvement Yin and Chippendale (1976, 1979) used the *Galleria* wax test to estimate JH titers present in the hemolymph of non-diapausing, pre-diapausing, and diapausing larvae. The hemolymph of 5th instar non-diapausing larvae was found to contain a maximum JH titer of about 3000 *Galleria* Units (GU)/ml, whereas the titer in the 6th instar drops to 140 GU/ml within 6 hours of the ecdysis and continues to remain low. The corpora allata in last stage non-diapausing larvae therefore remain inactive. The JH titer in the hemolymph of 5th instar pre-diapausing larvae is similar to that of equivalent non-diapausing larvae. However, pre-diapausing larvae, in contrast to non-diapausing ones, retain a high JH titer in their hemolymph during the 6th and final instar. The highest mean titer of about 4300 GU/ml was found in 33-day-old larvae. These larvae had spent 5 days in the final instar and were nearing the end of their feeding period. Additional measurements taken from hemolymph of 35 to 41-day-old larvae showed mean JH titers ranging from about 1,230 to 2,610 GU/ml. These findings indicate that larvae retain a high JH titer prior to and immediately after the onset of diapause.

Subsequent JH bioassays were carried out on immaculate diapausing larvae between 48 and 190 days of age. During the early and mid phase of diapause the JH titer was found to remain between 700 and 1500 GU/ml and did not decline until the larvae were about 110 days old. At 130 days the mean titer was about 200 GU/ml and declined further to about 70 GU/ml by 190 days. These results, therefore, demonstrate that early and mid diapausing larvae are also characterized by the presence of a substantial JH titer in their hemolymph.

These results have been interpreted as follows. As with other insects, a high titer of JH is required at the critical period in the molting cycle to maintain the larval form while a low JH titer results in pupal differentiation. Diapause is instituted when the JH titer of last stage larvae does not decline to the low threshold required for pupal differentiation. The JH titer of immaculate diapausing larvae is slightly lower than the maximum JH titer found in the

hemolymph of non-diapausing 5th instars. This finding was confirmed by demonstrating that JH mimic treatments caused immaculate morphs to ecdyse into spotted ones which reverted to immaculate morphs if the treatment was discontinued. This relatively high JH titer is maintained throughout the refractory phase of diapause. If the JH titer in diapausing larvae remains sufficiently high to prevent differentiation and to periodically activate the ecdysiotropin-producing system, stationary ecdyses occur during diapause. This function of JH was clearly demonstrated when periodic JH mimic treatments were found to greatly increase the number of stationary ecdyses which occur in diapausing larvae. A decrease in JH titer marks the onset of the activated phase, and finally, the low JH titer present during the termination phase permits pupal differentiation (Yin and Chippendale, 1973, 1979).

Comparison of Non-diapausing, Diapausing, and JH Mimic Treated Larvae

The finding that about 60% of non-diapausing larvae treated early in their final instar with a JH mimic (alkyl-3,7, 11-trimethyl-2, 4-dodecadienoates, i.e., ZR-512, -515 or -1662) ecdysed into dormant, immaculate morphs, provided key evidence to implicate JH in the control of diapause (Yin and Chippendale, 1974, 1976). It proved necessary, however, to determine the exact physiological state of these JH mimic treated larvae. For this reason the biochemical characteristics of non-diapausing, diapausing, and JH mimic treated larvae were compared. Information was obtained about pupation and respiratory rates, metabolic reserves, and spermatogenesis. The results indicated that JH mimic treated larvae were in a state of 'diapause' solely because their JH titer had been elevated.

The rate of pupation of JH mimic treated and diapausing larvae was observed beginning at 40 days. Larvae treated with ZR-512 or ZR-1662 pupated at a high rate, but a higher incidence of larval mortality occurred in those treated with ZR-512. A low rate of pupation was observed in larvae treated with ZR-515 and about 70% larval mortality had occurred by 135 days. The normal diapausing larvae reached 50% pupation in 121 days and completed the process in 145 days. These results suggest that the JH mimics had different intrinsic hormal activities.

The oxygen consumption of mature non-diapausing and diapausing larvae (40 and 110 days of age), and JH mimic treated larvae (35 and 105 days of age) was also compared (Yin and Chippendale, 1974). The results showed that the oxygen uptake of non-diapausing larvae was about 2.6 times that of newly diapaused larvae (40-day-old) or 35-day-old JH mimic treated larvae, and about four to five times that of late diapausing larvae (110-day-old) or 105-day-old JH mimic treated larvae. The rate of oxygen consumption of all the diapausing and JH mimic treated larvae tested was significantly lower than that of the non-diapausing larvae. No significant differences were found between the rate of oxygen consumption of 40-day-old diapausing and 35-day-old JH mimic treated larvae. The respiratory rate of JH mimic treated larvae, therefore, is suppressed to the same extent as that of diapausing larvae.

Insects that enter a facultative last stage larval or pupal diapause accumulate substantial nutrient reserves during the larval stage. Numerous studies have shown that pre-diapausing insects accumulate various titers of lipids, carbohydrates (glycogen, trehalose), proteins, and amino acids. These reserves accumulate mainly in the fat body and hemolymph and are used at a low rate to sustain diapause. Sufficient reserves accumulate to provide substrates for post-diapause differentiation that takes place before feeding resumes. Pre-diapausing southwestern corn borers selectively accumulate lipids, mainly as triglycerides that make up about 90% of the neutral lipids of the fat body, and proteins. Analyses of nutrient reserves showed that the application of JH mimic to non-diapausing larvae caused them to accumulate substantial amounts of lipids and proteins between 14 and 35 days of age. The following specific observations were made (Yin and Chippendale, 1974). Non-diapausing larvae (14 days of age) had live weight of 182 mg/larva compared with 264 mg/larva for newly diapaused larvae (40 days of age) and 526 mg/larva for JH mimic treated larvae (35 days of age). Whole body analyses showed that both pre-diapausing and JH mimic treated larvae accumulated substantially more lipids and proteins than did non-diapausing larvae. Lipids comprised 40.3%, proteins 23.3%, and glycogen 1.9% of the dry weight of non-diapausing larvae. Lipids comprised 52.1%, proteins 24.0%, and glycogen 4.8% of the dry weight of newly diapaused larvae. Lipids comprised 58.5%, proteins 14.7%, and glycogen 6.7% of the dry weight of JH mimic treated larvae. When calculated per larva, newly diapaused larvae contained 2.2 times and JH mimic treated larvae contained 4.8 times the amount of lipid found in non-diapausing larvae. Similarly, newly diapaused larvae contained 1.75 times and JH mimic treated larvae contained 2.0 times the amount of protein found in non-diapausing larvae. JH mimic treated larvae appeared to be prepared for a prolonged dormancy because they accumulated significantly larger amounts of lipids and proteins than did even normal pre-diapausing larvae.

Spermatogenesis has also been examined in diapausing and JH mimic treated larvae (Chippendale and Alexander, 1973; Yin and Chippendale, 1974). Testicular volumes were measured, and the state of the germ cells was determined in larvae subjected to regimes which permitted different rates of diapause development. The principal results showed that during the first phase of diapause, germ cells which had differentiated beyond the primary spermatocyte stage degenerated, and the spermatogenesis resumed before the larvae entered the postdiapause pupal molting cycle.

Testes of diapausing larvae held at 30°C 12L:12D contained secondary spermatocytes throughout the first phase of diapause development, whereas those of larvae held at 23°C 12L:12D for the same period contained shrunken follicles which lacked secondary spermatocytes. The secondary spermatocytes eventually degenerated in the 30°C larvae so that at about 80 days the testes in both groups were made up of shrunken follicles containing only spermatogonia and primary spermatocytes. The rate of degeneration of the secondary spermatocytes is therefore temperature dependent. During the last phase of diapause develop-

ment, renewed spermatogenesis occurred in larvae held at both 23°C and 30°C 12L:12D. Resumption of spermatogenesis occurred later at 23°C, because larvae held in this regime had a lower rate of diapause development. Testicular swelling and the renewed presence of secondary spermatocytes marked the resumption of spermatogenesis. Germ cells in all stages of differentiation were eventually found before the larvae entered the postdiapause pupal molting cycle.

Measurements of testicular volume and rates of spermatogenesis were also obtained for JH mimic treated larvae (Yin and Chippendale, 1974). Non-diapausing larvae (13 days old) were individually treated with 3μg of a JH mimic (ZR-515) and held at 30°C 12L:12D. A significant decrease in mean testicular volume was observed from 1.0 mm^3 at 14 days to 0.17 mm^3 at 50 days. By 95 days of age, however, the testes had re-expanded to about 0.84 mm^3. Spermatogenesis was suppressed in the shrunken testes. Histological sections showed that follicles contained only spermatogonia and primary and secondary spermatocytes at 35, 50, and 65 days of age, whereas by 95 days the initiation of renewed spermatogenesis was detected. These results indicate that the JH mimic treatment caused the testes of non-diapause programmed larvae to shrink and spermatogenesis to be suppressed. The testes of JH mimic treated larvae, therefore, resembled those of a normal diapausing larvae.

Occurrence and Properties of a Diapause-Associated Protein

Recently Brown and Chippendale (1978) studied diapause-related changes in the proteins of insect fat body and uncovered a special pathway for protein metabolism in larvae of *D. grandiosella*. Electrophoretic separations showed that pre-diapausing larvae accumulate a protein fraction which accounts for a significant amount of the soluble proteins of the fat body* at the start of diapause (Fig. 5). Furthermore, the concentration of this diapause-associated protein (DAP) decreases gradually during diapause suggesting that it has a diapause-related function. Subsequently, Turunen and Chippendale (unpublished) showed that DAP is released from intact fat body of newly diapaused larvae incubated *in vitro* in macro-molecule free insect (Grace's) tissue culture medium. This study suggests that DAP may function in the hemolymph during diapause.

Since JH regulates the induction and maintenance of the larval diapause of *D. grandiosella* experiments were carried out to determine whether a relationship exists between JH and DAP. Initially such a relationship was shown when DAP was found to accumulate in the fat body of non-diapausing larvae that had been treated with a JH mimic. These larvae accumulated substantial amounts of DAP within 8 days of being treated with JH mimic. A JH involvement was further demonstrated when allatectomy retarded the accumulation of DAP in pre-diapausing larvae. This effect was partially reversed when allatectomized larvae were treated with JH mimic (Brown and Chippendale, 1978).

*In larvae of *D. grandiosella* the fat body is present as sheets of tissue which have important functions in nutrient storage and intermediary metabolism, i.e. the insect fat body is analagous to the vertebrate liver.

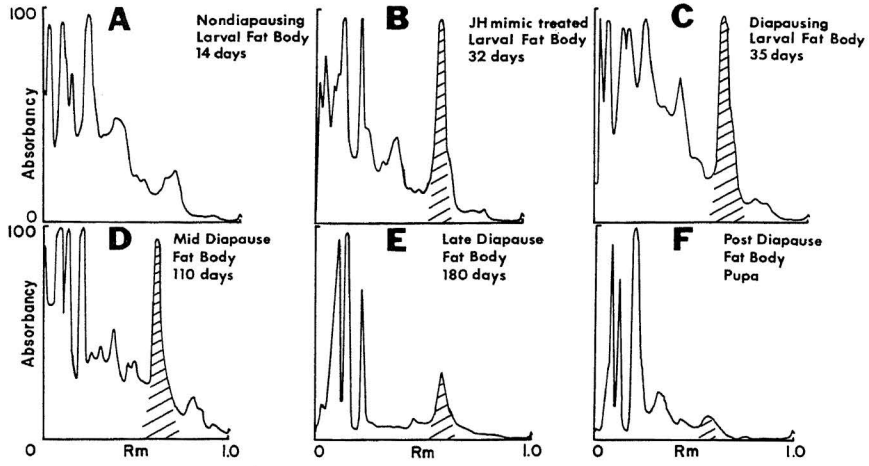

Fig. 5. Densitometric scans of disc electropherograms of fat body proteins of *D. grandiosella* illustrating the diapause-associated protein (DAP). DAP is cross-hatched; Rm = relative mobility; protein concentrations in arbitrary absorbancy units. Summarized from Brown and Chippendale (1978).

A 14 day old non-diapausing larvae showing that DAP does not accumulate in the fat body of fully grown non-diapausing larvae (0.2 fat body).

B 32 day old non-diapausing larvae which had been treated with a JH mimic at 13 days of age showing the high titer of DAP (0.15 fat body).

C 35 day old newly diapaused larvae showing the high titer of DAP (0.2 fat body).

D, E, 110 and 180 day old mid and late diapausing larvae, respectively, showing the rate of loss of DAP (0.2 fat body).

F Newly ecdysed pupa (from 214 day old post-diapausing larva) showing that only traces of DAP remain (0.2 fat body).

The synthesis of DAP in the fat body of pre-diapausing larvae of *D. grandiosella* was demonstrated using radiolabeled leucine and cycloheximide, an inhibitor of peptide bond formation. The molecular weight of DAP, isolated from the fat body of newly diapaused larvae, was estimated to be about 35,000 using sodium dodecyl sulfate electrophoresis. Analytical isoelectric focusing showed DAP to have an isoelectric point of 5.9 (Turunen and Chippendale, unpublished). Cation exchange chromatography of a hydrolyzate of DAP showed that aspartate (43), leucine (37), lysine (35), and glutamate (32 residues per molecule) predominate among the 15 to 17 constituent amino acids (Brown and Chippendale, 1978). Additional studies of the physico-chemical properties of DAP have yet to be undertaken and are needed to further characterize the protein. The finding of a specific diapause-associated protein in *D. grandiosella* has special significance because a biochemical pathway related to larval diapause has now been uncovered (Chippendale and Beck, 1967; Odesser *et al.*, 1972; LaFage *et al.*, 1974; Foster and Crowder, 1976).

The available evidence suggests that DAP has some special diapause

function, possibly related to the maintenance of the state. Brown and Chippendale (1978) offered 3 possible functions of DAP: as a latent storage form of the JH binding protein; an amino acid storage molecule; or as a proenzyme. Preliminary, and to date circumstantial, evidence suggests that DAP may function as a storage form of the JH binding protein (Turunen and Chippendale, unpublished). The available evidence focuses on the known JH involvement in diapause, the rate of change of JH titer during diapause, the physico-chemical properties of DAP, and preliminary information about the properties of the JH binding protein present in the hemolymph of diapausing larvae. Although DAP could function as an amino nitrogen reservoir for diapusing larvae, lipids serve as the primary energy source during diapause, and the fat body contains several proteins and lipo-glycoproteins of much higher molecular weight than DAP which might be preferentially mobilized to meet the small demands for amino nitrogen during diapause. In addition, a large pool of free amino acids is present in the hemolymph of diapausing larvae. Although DAP could function as a pro-enzyme which is activated during dispause, this is unlikely since it is present in rather large amounts for such a function. DAP makes up about 20% of the soluble proteins of the fat body of newly diapaused larvae, and diapause is characterized by a low metabolic rate and turnover of metabolites.

Reproductive Physiology of the Adult

Although the adults have received little study they show typical behavior and activity patterns characteristic of short-lived lepidopterans. They do not feed, and therefore depend entirely upon nutrient reserves accumulated during the larval stages to meet their energy needs for flight and reproduction. Oogenesis is completed during the pharate adult stage so that the newly emerged female is sexually competent and ready to oviposit within 24 hours of emergence.

Field observations have also shown that most adults emerge at dusk and in the early evening. After emerging, they usually crawl to the upper third of the corn plant (Rolston, 1955a; Langille and Keaster, 1973). During the day, they rest in the whorls of immature corn plants or underneath the lower leaves or brace roots of mature plants (Fairchild *et al.*, 1965). After being disturbed, they usually traverse a weaving course of 10 to 30 feet and alight on an adjacent plant. Adults become restless in the late afternoon and the daily flight begins at nightfall (Davis *et al*, 1933).

The males have a mean life span of 4.3 days, with a few individuals surviving up to 10 days (Davis *et al.*, 1933; Rolston, 1955a; Gifford *et al.*, 1961; Davis, 1965). They usually mate for the first time within 24 hours of emergence. In the absence of demonstrated feeding activity, the male's function appears to be solely related to mating. Under field conditions they have been observed to participate in weaving female-searching flights just above the tassels of corn plants between 9 and 11 p.m. Langille and Keaster (1973) caught 68 male moths in sweep nets during this period. The males usually locate females on the leaves or stalk in the upper portion of the plant and mate between 11 p.m. and 2 a.m. From current information it appears, therefore, that males have a limited flight range and are

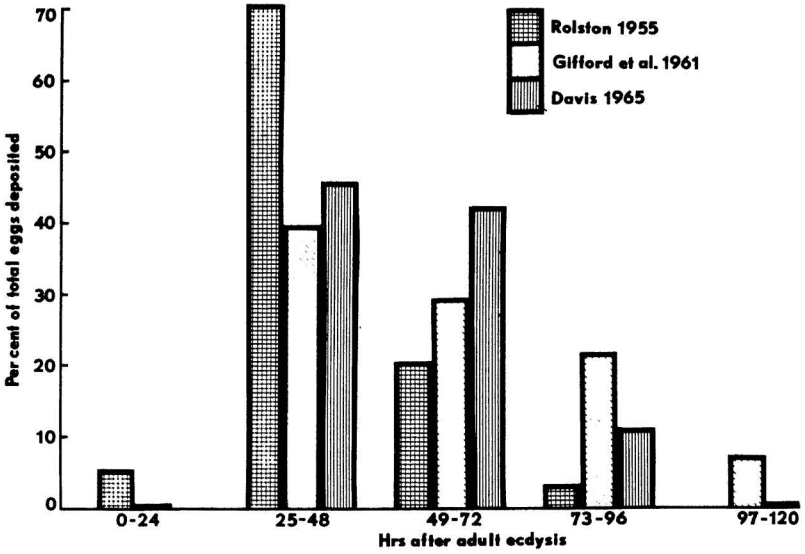

Fig. 6. The ovipositional rate of mated females of *D. grandiosella* on wax paper in small cages. Data are summarized as follows: Rolston (1955a), 15 females deposited a total of 4,698 eggs (313 eggs/female); Gifford *et al.* (1961), 22 females deposited a total of 7,535 eggs (343 eggs/female); and Davis (1965), 40 females deposited a total of 14,800 eggs (370 eggs/female).

not primarily involved in dispersal.

The females have a mean life span of 5.0 days, though exceptional individuals may survive up to 10 days. Their known activities include mating, host-searching flights, and oviposition. Rolston (1955a) and Davis and Henderson (1967) showed that about 66% of the females mated on the same night they emerged and the remainder mated on the succeeding two nights. Oviposition usually begins on the night after emergence and extends for a total of three nights. Figure 6 summarizes three studies designed to determine the ovipositional rate of caged females. Field observations also indicate a similar duration of oviposition on corn plants (Stewart and Walton, 1964). Although newly emerged females are usually quite sluggish because of their heavy egg load, they become active after they have oviposited for one or two nights (Davis *et al.*, 1933).

The females produce a sex pheromone during the first three nights after their emergence. Adler and Jacobson (1972) screened 46 short chain alcohols and acetates using isolated male antennae of *D. grandiosella*. They found that the acetates of 7-octen-1-ol, *trans*-6-dodecen-1-ol, and *cis*-8-dodecen-1-ol showed the highest sex pheromonal activity. More recently, Hedin *et al.* (1976) have isolated and tentatively identified *Z*-9-hexadecenal and *Z*-11-octadecenal as important active fractions of the sex pheromone.

Although the flight patterns involved in host searching have never been

studied, females are obviously discriminating about their choice of ovipositional sites. They prefer corn plants as an ovipositional substrate and find early whorl, dough, or tasselling stages about equally attractive for oviposition. The number of eggs deposited per plant appears to be correlated with the leaf surface available for moth contact (Stewart and Walton, 1964). In the absence of corn, females oviposit and larvae develop on sorghums, teosinte, sugar cane, broom corn, Sudan grass, and Johnson grass (Burkhardt and Painter, 1954; Rolston, 1955a; Gifford *et al.*, 1961).

Flight Physiology and Dispersal of the Adult

Although systematic studies have yet to be undertaken, the host-searching flight of mated females appears to be causing the dispersal of the species across the United States. On a local scale, Rolston (1955a) observed larval populations on corn plants in an area which required adult flights of at least 1.5 miles from known populations of *D. grandiosella*. On a regional scale, Wilbur *et al.* (1950) concluded that second generation larvae found in northern Kansas had originated from females which had dispersed 100 to 150 miles from overwintering areas in southern Kansas. In this case dispersal may have been aided by southerly winds which are common during Kansas summers (Chiang *et al.* 1965).

In common with other Lepidoptera, adults of *D. grandiosella* contain substantial lipid reserves which provide energy for flight. Adult males have a mean total lipid content of 11.3 mg, and a mean live weight of 76 mg, whereas adult females have a mean total lipid content of 18.3 mg, and a mean live weight of 117 mg (Thompson *et al.*, 1973). If the difference between the lipid content of males and females is primarily yolk lipid, then female moths contain about 11.3 mg of lipid for non-reproductive purposes.

An estimate of the flight potential of adult females can be made from a comparison of the metabolic rates of other insects which use lipid as a flight fuel. For example, the locust, *Schistocerca gregaria,* weighs about 2.5 gm and oxidizes 17 mg lipid/hr during sustained flight, whereas the aphid, *Aphis fabae,* weighs about 700 μg and oxidizes about 5 μg lipid/hr during sustained flight (Weis-Fogh, 1952; Cockbain, 1961). Therefore, females of *D. grandiosella* weighing about 117 mg probably oxidize about 800 μg lipid/hr during sustained flight. If their flight speed is similar to that of the Asiatic rice stem borer, *Chilo suppressalis,* namely 4.5 mph (Pathak, 1968), and flight continues until 75% of the available lipid is oxidized then the females of *D. grandiosella* have a maximum flight range of 48 miles over a 10-hour duration. This extensive range is made possible by the use of lipid, rather than carbohydrate, as the flight fuel.

Since the southwestern corn borer has been shown to be predominately bivoltine in Kansas (Wilbur *et al.*, 1950), Arizona (Davis *et al.*, 1933), Oklahoma (Walton and Bieberdorf, 1948a), and Arkansas (Rolston, 1955a), and trivoltine in Mississippi (David, 1965), three or four flights occur each year, depending on the geographical location. Even though a high rate of mortality occurs among diapausing larvae and low numbers of spring adults are found in most locations, the rate of dissemination of up to 35 miles/year is within the

theoretical limits of the flight capacity of the females (Fairchild *et al.*, 1965).

To obtain a more complete picture about the regional dispersal of populations, additional information is needed about the dispersal of females from overwintering sites to acceptable host plants, the flight of adults within and between fields of host plants, and the influence of wind, temperature, and other climatic conditions on flight activity. Field studies might profitably employ pheromone traps, dye-marked individuals (Davis, 1973), and infra-red cinematography (Lingren *et al.*, 1978).

ENVIRONMENTAL CONTROL OF SEASONAL DEVELOPMENT

The life cycle of the southwestern corn borer is tightly synchronized with that of its acceptable host plants. This synchrony is achieved by the intervention of a mature larval diapause which permits the insect to survive in a dormant state for eight months, September to May, when host plants are not available. The insect uses the environmental day length and temperature to program both the induction and termination of its diapause.

Effect of Photoperiod and Temperature on Diapause Induction

The southwestern corn borer responds to photoperiodic and temperature cues in the programming of its diapause (Chippendale and Reddy, 1973; Chippendale *et al.*, 1976; Takeda, 1978). Marked differences in the incidence of diapause were observed when larvae were reared under short day conditions (12hrL:12hrD) at constant temperatures between 20° or 30°C. A temperature response curve showed that exposure of the immature larval stages to 20° or 23°C resulted in 100% diapause whereas a 27° or 30°C exposure permitted continuous development. A partial incidence of diapause varying from about 50 to 80% occurred following exposure to 25°C. When a photoperiodic response curve was obtained at 25°C the insect was found to display a short day-long day response curve (Type III, Beck, 1968). For a southern Missouri population, the two critical photoperiods were 15hr5minL:8hr55minD (ecological threshold) and about 11hrL:13hrD (physiological threshold). Under the conditions prevailing in southern Missouri larvae are exposed to diapause-inducing conditions during August. In this month daylengths decrease from about 13.75 to 13 hours (sunrise to sunset), and temperatures range from about 32°C to 19°C.

The few available studies on the effect of thermoperiods (temperature cycles) on insect diapause have generally shown that a higher incidence of diapause occurs when the cool phase of the thermoperiod coincides with the scotophase (dark phase) than under the reversed conditions, and that in continuous darkness a thermoperiod of high amplitude substitutes for a diapause inductive photoperiod (Saunders, 1973). An examination of the effect of thermoperiods in combination with a photoperiod on diapause induction of *D. grandiosella* has corroborated these effects (Chippendale *et al.*, 1976). As already described a 12L:12D photoperiod employed with a constant temperature of 27° or 30°C suppressed the diapause response, whereas a constant 23°C caused 97% of the larvae to enter

diapause. When a 30°:23° thermoperiod was employed with 12 hour themophases all the larvae entered diapause when the low phase coincided with the scotophase, whereas only 30% entered diapause under the reversed conditions. The 12L(30°):12D(23°) regime therefore had a marked inductive effect even though its mean constant temperature (27°C) was essentially non-inductive, thereby demonstrating a thermoperiodic response.

The photoperiod-thermoperiod interaction was further explored by testing the effect of four thermoperiods combined with a 12L:12D photoperiod on the induction of diapause. The results showed that the coincidence of the high phase (30°, 32°, 34°, or 36°C) of the thermoperiod with the scotophase, suppressed the diapause response. In contrast, thermoperiods of 32°:23°C, 34°:22°C, or 36°:20°C in which the low phase coincided with the scotophase resulted in the occurrence of a high incidence of diapause. It was concluded that a thermoperiod with a 4°C amplitude (32°C:24°C) coupled with a 12L:12D photoperiod was necessary for the induction of a high incidence of diapause because a thermoperiod with a 2°C amplitude (30°C:26°C) resulted only in 18% diapause (Chippendale *et al.*, 1976).

Diapause Determination

Insects that enter a facultative diapause have been found to monitor their environment exceptionally closely and to program their life cycles by responding to seasonal cycles. Diapause is determined by the exposure of sensitive instars to critical environmental conditions that precede the unfavorable season. For example, insects entering a mature larval diapause usually have immature instars that are sensitive to short-day photoperiods and low temperatures. It is in these instars that diapause is determined.

Results obtained from diapause determination experiments are subject to strong influence from the experimental design (Beck, 1968). Insects exposed to low temperatures have lower growth rates and are exposed to more inductive cycles than are insects exposed to higher temperatures. Furthermore, the larval growth period of pre-diapausing individuals may be extended by photoperiodic stimuli alone. In the case of *D. grandiosella* pre-diapausing larvae reared at 25°C 14L:10D had a lower growth rate than did their non-diapausing counterparts reared at 25°C 16L:8D. An analysis of photoperiodic response curves at different temperatures suggested that various combinations of photoperiod and temperature influence developmental programming differently. Reciprocal exposures to 30°C 12L:12D and 23°C 12L:12D induced a higher incidence of diapause than did reciprocal exposures to 25°C 16L:8D and 25°C 14L:10D. There thus appears to be a quantitative interaction between photoperiod and temperature leading to diapause induction of *D. grandiosella* (Takeda, 1978).

The results summarized above suggest that all immature larval instars are sensitive to photoperiodic and temperature programming of diapause. A critical intermediate instar, in which the development program can be switched entirely from non-diapause to diapause or *vice-versa* by exposure to appropriate environ-

mental conditions, was not uncovered in these experiments (Chippendale and Reddy, 1973; Takeda, 1978).

In related experiments Alexander and Chippendale (1973) showed that spermatogenesis progresses at a much lower rate in pre-diapausing larvae than in non-diapausing ones. In pre-diapausing larvae they found a small increase in mean testicular volume from 0.01 to 0.11 mm^3 between the 3rd and 6th instars, whereas in non-diapausing larvae an increase of 0.01 to 1.03 mm^3 was observed between the 3rd and 5th instars. Histological data revealed that spermatogenesis progresses at a low rate in testes of pre-diapausing larvae. In the 3rd instar spermatogonia are the principal germ cells, and primary and secondary spermatocytes were not detected until larvae had entered the 4th and 5th instars. After the onset of diapause the secondary spermatocytes begin to degenerate. By contrast, the testes of 4th instar non-diapausing larvae contain secondary spermatocytes which further differentiate into spermatids and sperm bundles in the 5th instar. These observations corroborate that diapause is determined as early as the 3rd instar (see pp. 24-25).

Environmental Control of Diapause Development

Chippendale and Reddy (1973) studied the effect of five regimens on the rate of diapause development. Their results showed that diapause development occurred at a much higher rate at 30°C than at 23°C. At 23°C, diapause was sustained and 50% of the larvae did not pupate until more than 147 days had elapsed. Four regimens were tested at 30°C, and 24L:0D was found to permit the highest rate of diapause development. The data showed that 50% of the larvae had pupated around 37 days at 30°C 24L:0D, whereas those held at 16L:8D, 12L:12D, and 0L:24D required about 47, 78, and 63 days, respectively, to pupate. The results showed that the highest rates of diapause development occur under continuous illumination and long day at 30°C.

The effect of providing diapausing larvae with contact water after they have been held at 30°C 24L:0D under dry conditions for various periods has been examined (Reddy and Chippendale, 1973). Their results showed that larvae which had been held dry had a higher rate of pupation upon imbibing water than did controls which were continuously provided with water. The control larvae which received contact water from the beginning of the treatment reached 50% pupation in 48 days, whereas larvae that were provided water after 15 and 30 days attained this level in 31 and 37 days, respectively. Larvae held dry for 45 days attained 50% pupation in 49 days, just one day after the control group. Fifty percent pupation in borers held dry 60 and 75 days was delayed by 15 and 32 days, respectively, compared with the control group. This delay was approximately equal to the additional exposure to dry conditions over the 45 days dry group. However, the pupation was completed earlier than in the control in all groups which had been exposed to dry conditions except in the group held dry for 75 days. This group completed pupation 17 days after the control group because the borers were unable to enter the post-diapause pupal molting cycle until

contact water was provided.

These results show that diapause development occurs at a high rate under dry conditions and that larvae require contact water to enter the post-diapause pupal molting cycle. Diapausing larvae complete diapause development after being exposed to dry conditions for 45 days at 30°C 24L:0D. A few of the test larvae pupated before they received contact water, emphasizing that diapause development is not dependent upon the availability of water. Other findings showed a highly synchronized pupation rate when larvae imbibed water after having been maintained dry beyond the time required to complete diapause development. Those larvae that lost relatively large amounts of tissue water during early diapause completed diapause development at a higher rate than did those that retained a high water content.

Since the distribution of *D. grandiosella* is currently restricted to 14 southern and central states, diapausing larvae may be unable to withstand the cold winters in the northern states. The supercooling and freezing points of diapausing larvae have been determined to document the effect of low temperatures (Langille, 1975). Figure 7 shows that field populations of larvae exhibit moderate acclimation to low temperatures after the onset of diapause. Pre-diapausing and early diapausing larvae supercool about 7°C, whereas those in mid and late diapause supercool about 13°C. This slight increase in supercooling capacity is apprarently insufficient to protect the freezing-susceptible larvae from the more rigorous winter of the northern reaches of the Corn Belt. These results, along with other findings which revealed a high mortality rate when larvae were exposed to -4°C for up to 28 days, indicates that prolonged exposure to temperatures below about -4°C usually proves lethal (Chippendale and A.S. Reddy, 1974).

Diapausing southwestern corn borers overwinter in the stalk crown below ground level where, in southeastern Missouri, they are exposed to a low temperature between 0° and 5°C. The effect low temperature had on diapause development of field collected larvae was examined (Chippendale and Reddy, 1973). The experiment was undertaken because chilling has been found to accelerate the termination of diapause of some insects. The overall results showed that only a low rate of diapause development occurred at 5°C, and long term chilling caused some synchronization of the pupation rate. It did not appear, however, that chilling accelerated diapause development. Several specific results were obtained (Chippendale and Reddy, 1973). The experiment was carried out using larvae collected in November, 1970. These larvae had been exposed to decreasing temperatures for about two months and showed less mortality when exposed to 5°C than did larvae collected in September. After exposure for three, six, or nine weeks, a group of larvae from the 5°C OL:24D and 30°C OL:24D regimes was transferred to 30°C 16L:8D. Pupation was delayed in larvae maintained at 5°C for three to nine weeks, whereas those that were retained at 5°C remainded dormant. Pupation data showed that 50% of the larvae maintained for three weeks at 5°C pupated by 61 days, 30 days later than the 30°C control. A low rate of diapause development, however, does occur at 5°C

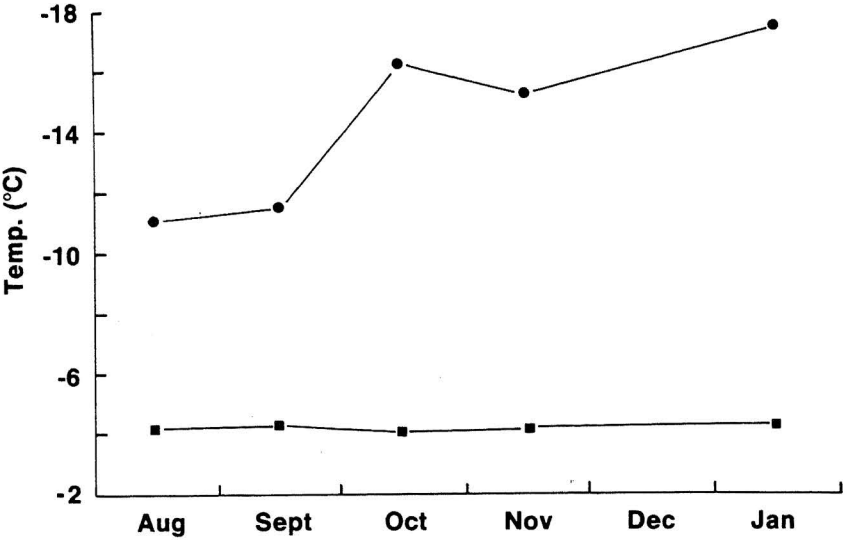

Fig. 7. Mean supercooling points (●) and nominal freezing points (■) of diapausing larvae of *D. grandiosella* collected in Aug., Sept., Oct. and Nov. 1973 and Jan. 1974 from their cells in corn plants located in southeast Missouri. Measurements were obtained from individual larvae held within balsawood blocks at -20°C using a copper-constantine thermocouple connected to a recorder. Standard deviations fell within 14% of the means. (Redrawn from Langille, 1975.)

because 50% of the larvae maintained for six and nine weeks at 5°C pupated 35 and 37 days after the respective 30°C controls.

Phenology

Since environmental factors responsible for controlling the onset of diapause differ systematically from the equator to the poles, different geographical populations of the same insect species adapt to the prevailing conditions in their locality. The local seasonal cues of photoperiod, temperature, and the availability of food, regulate the number of generations which occur each year, i.e., the voltinism of the species. Table 2 illustrates the voltinism of different geographical populations of *D. grandiosella.* Depending upon the local cues mentioned above, up to three complete generations may occur each year. Detailed information about the seasonal appearance of each generation, and factors such as soil type, exposure to sunlight, and planting date which affect the timing and duration of each generation is provided in the individual reports.

An important factor regulating the phenology of the insect is the relationship between its life stages and the availability of acceptable host corn plants (*Zea mays*) for oviposition and food. Corn plants take about 18 weeks to mature, of which nine weeks are required for both vegetative growth and grain development (Hanway, 1971). In contrast, one complete generation of the insect requires from six to eight weeks, depending upon the prevailing local conditions.

TABLE 2
VOLTINISM OF DIFFERENT GEOGRAPHIC POPULATIONS OF *D. GRANDIOSELLA*

State	Peak emergence of spring moths	Generations/ year (no.)[a]	Reference
Arizona	Mid-May	2	Davis *et al.*, 1933
New Mexico	Mid-June	1	Davis *et al.*, 1933
Texas	Early June	2 or 3	Todd & Thomas, 1930
Oklahoma	Mid-June	2	Walton & Bieberdorf, 1948a
Kansas	Late June	2	Wilbur *et al.*, 1950
Missouri	Early June	2	—
Arkansas	Early June	2	Rolston, 1955a
Mississippi	Mid-May	3	Davis, 1965

[a]Depending primarily upon temperature and the availablity of host plants a partial generation follows the last complete generation of each season. Due to the overlapping of generations the diapausing population is made up of larvae from the last complete as well as the partial generation.

For example, the following ranges of generation times have been estimated: 42 to 49 days in Sinaloa, Mexico (Abarca *et al.*, 1958), 40 to 50 days in Arizona (Davis *et al.*, 1933), 38 to 56 days in Oklahoma (Walton and Bieberdorf, 1948a), 45 days in Kansas (Wilbur *et al.*, 1950), and 41 days in Arkansas (Rolston, 1955a). Under field conditions, embryogenesis usually lasts five or six days while the larval growth period on corn extends from 20 to 35 days. Since corn is the most acceptable site for oviposition and for larval feeding during its first nine weeks, it is rare to find more than two complete generations per year. Three complete generations regularly occur only under mild climatic conditions, such as those found in southern Mississippi, where the generation times of the host plant and the corn borer are highly synchronized (Davis, 1965).

Chippendale *et al.* (1976) and Takeda (1978) have examined the relationship between daylength, temperature, and the number of generations of *D. grandiosella* found in Pemiscot County in southeast Missouri. At this location day lengths (sunrise to sunset) range from a shortest day of 9.6 hours to a longest day of 14.7 hours. Mean temperatures (two-week averages for 1973) ranged from a low of 2°C in January to a high of 27°C in July, whereas the deviation about the mean ranged from about 1.5°C to 6°C. Figure 8 is a photothermogram which summarizes the chronology of the natural life cycles of the southwestern corn borer in southern Missouri. The number of generations and critical photoperiod for diapause induction (about 15 hr 5 min) have been superimposed on a graph in which temperature accumulation above a 17°C base (developmental threshold is plotted against daylength, including civil twilight. About 360 degree-days above the 17°C base were estimated to be the required heat units necessary for the

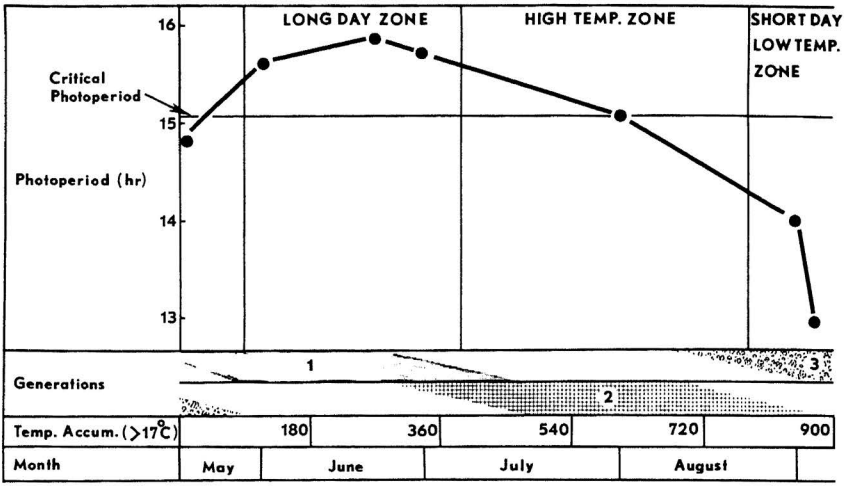

Fig. 8. Photothermogram from southern Missouri (36° 24'N) for May to August showing relationship between daylength (including civil twilight), temperature accumulation above 17°C, and the seasonal programming of the generations of *D. grandiosella*. Based on light trap records, 2 complete generations are illustrated. From laboratory experiments it has been calculated that 360 degree-days above a 17°C threshold are required for the completion of a single generation. In the high temperature zone, the mean daily temperature is above 25°C (Takeda, 1978).

insect to complete a single generation. The temperature and photoperiodic conditions present in southern Missouri permit two complete generations and a partial third generation. Larval diapause does not intervene during the first generation which is present during June and early July, because the larvae are exposed to daylengths which are longer than the critical daylength, even though the temperature at this time is still not very high (long day zone). Larvae of the second generation may or may not enter diapause, depending on the appearance of their sensitive stages relative to the critical photoperiod and prevailing temperature. Although the critical photoperiod is reached by the beginning of August, the inductive response is suppressed until mid August because the high temperatures present in early August mask the photoperiodic response (high temperature zone). Those larvae of the second and third generation which are exposed to the short days and low temperatures beginning in mid August enter diapause (short day, low temperature zone).

Geographical Races?

An important question which has not yet been investigated is whether biotypes or geographic races (ecotypes) of the insect already exist in the United States. Whenever an insect, such as *D. grandiosella,* invades new territories it is subjected to extreme selection pressures. Those individuals within the population which are better adapted to the new environmental stresses may interbreed to form populations of a new biotype or race. In such a manner, and because of the

genetic diversity within the species, several biotypes or geographical races may become identifiable over the range of distribution. A biotype may be characterized by distinctive aspects of its bionomics, behavior, physiology, or morphology.

The existence of ecological, physiological, and morphological differences among North American populations of *O. nubilalis* has been well studied. This insect has been separated into several biotypes which differ in their responses to diapause, survival, feeding habits, and even have different morphometric characteristics (Brindley *et al.*, 1975). An investigation of the incidence of diapause among larvae collected from several locations across the country and exposed to similar photoperiods and temperatures led to the conclusion that North American populations may be grouped into 3 ecotypes: a univoltine northern ecotype found in Minnesota and Quebec; a bivoltine central ecotype found in Iowa, Nebraska, Ohio, and northern Maryland; and a temperature sensitive tri- or tetravoltine southern ecotype found in Alabama, Georgia, Missouri, and southern Maryland (Showers *et al.*, 1975). The information in Table 2 indicates that a similar series of ecotypes may be identifiable for the southwestern corn borer. However, the experiments necessary to show how well each population is adapted to the local photoperiodic and temperature conditions have not yet been carried out. These experiments should include examining the diapause response of larvae from different geographical locations to common conditions of temperature, photoperiod, and food availability in the laboratory and the field.

MANAGEMENT OF POPULATIONS

Although precise information about financial losses attributable to the southwestern corn borer is not available, losses in the southwestern and southern plains states have been estimated at several million dollars annually (Morrison *et al.*, 1977). In addition, the destructiveness of the insect has caused a change in agronomic practices in portions of many states which have high populations of *D. grandiosella*. Changed agronomic practices include early planting and fall plowing, and in extreme cases a reduction in corn acreage as farmers have turned to alternative crops, usually sorghum in Kansas and Oklahoma. For example, corn acreages were reduced by as much as 50% per year when the insect migrated into and became a destructive pest in south-central Kansas in the early 1940s (Wilbur *et al.*, 1950). While it is generally considered that the insect causes less economic loss in sorghum than it does in corn, it has become a troublesome pest of sorghum in Arizona. Infested plants show retarded growth and reduced grain production, and yield losses up to 50% have been reported (Gerhardt *et al.*, 1972).

Economic losses occur in silage corn when feeding reduces plant vigor to the extent that vegetative growth is significantly retarded, and in sweet and field corn when ear production is retarded. The lodging of mature field corn due to the girdling activity of pre-diapausing larvae may cause the loss of entire plants to a mechanical harvester. Most evidence indicates that maximum losses occur in

irrigated corn which is planted and harvested late. Under these conditions plants are susceptible to dead-heart injury and to a high rate of lodging following girdling activity. Scott and Davis (1974) observed that the feeding of 1st generation larvae reduced plant height by about 16cm. They also recorded grain yield losses of up to 29% in plants infested with both 1st and 2nd generation larvae. Although these losses resulted from a reduction of the number of kernels per plant, ears harvested from girdled and lodged corn have also been shown to have a lower dry weight and higher water content than those from uninfested corn (Chada *et al.*, 1965; Daniels, 1977).

Cultural Control

Cultural methods have proven to be a practical and economical way to suppress larval populations. These methods have to be adapted to local conditions, and work best if practiced over a reasonably large area because the adults are active flyers and readily migrate from infested fields. Early planting and fall or spring plowing or discing are widely accepted agronomic practices which tend to reduce populations (Wilbur *et al.*, 1950; Rolston, 1955a).

Early planting of corn minimizes injury caused by first generation larvae to the foliage and stems of the terminal bud. For example, corn planted in April or early May in Missouri usually escapes dead-heart injury because it has passed the critical growth stage by the time large numbers of first generation larvae begin to feed. Table 3 illustrates the relationship between larval damage and the growth stage of the host plant. Corn planted on April 9 and artificially infested on May 15 suffered 36% dead-heart injury as well as disastrous yield losses. By contrast, corn planted on the same date, but artificially infested on May 26 escaped dead-heart injury and extreme grain yield losses (Arbuthnot *et al.*, 1958).

Another widely used cultural practice is to destroy the overwintering habitat of the larvae by fall or early spring plowing or by discing to bury or uproot the stubble. (Daniels and Chedester, 1975). These practices increase mortality by exposing larvae to natural hazards, and therefore decrease the number of spring moths. They could, however, be counterproductive in areas where soil erosion is a problem. The practices of no-till or minimum-till agriculture and of planting winter wheat over corn stubble tend to protect the diapausing larvae in their overwintering habitat. Under Missouri conditions spring moths emerge in May and June before winter wheat is harvested (Langille, 1975). Other sound agronomic practices include growing vigorous locally adapted hybrids in fertile soil, and harvesting the grain early to reduce yield losses due to the lodging.

Chemical Control

Foliar applications of insecticides require precise timing to be effective against the southwestern corn borer because the insect spends much of its larval life within the stalk. Early planted corn usually escapes significant damage, and while late planted corn might be heavily infested, insecticide treatments must be timed carefully to reach the larvae before they enter the stalk. Judicious early planting and harvesting of corn can, therefore, obviate a need for insecticide

TABLE 3
EFFECT OF 1ST GENERATION LARVAE OF *D. GRANDIOSELLA* OF THE GROWTH AND YIELD OF CORN[a]

Infested (date)[b]	Larvae/plant (no.)	Plants (no.)	Deadheart (%)	Dry wt/ mature plant (lbs)	Grain yield/ plant (lbs)
May 15	0	83	0	0.54	0.21
May 15	5	83	36	0.32	0.06
May 26	0	62	0	0.65	0.29
May 26	5	62	0	0.53	0.23

[a]Data summarized from Arbuthnot *et al.*, 1958
[b]Hybrid dent corn, planted April 9, 1955 on upland sandy loam in Oklahoma, was manually infested with newly hatched larvae on the designated dates.

treatments. Since most larvae enter the stalk within 12 to 14 days after hatching, insecticides must usually be applied within a week of detecting the first generation larvae. Screening tests have shown that only a few liquid or granular foliar insecticides are effective against the southwestern corn borer. For example, Rolston (1955b) found that the organophosphate, EPN, controlled larvae in early whorl stage corn plants and reduced damage caused by dead heart and stunting. Arbuthnot and Walton (1954) controlled second generation larvae in corn using EPN, or the chlorinated hydrocarbon, endrin. Larvae of the second generation are difficult to control because moths are present over long periods (early July to mid August in Missouri), and females oviposit on plants approaching physiological maturity. Granular formulations of the carbamates, carbofuran and methomyl, but not EPN, applied to whorl stage plants effectively controlled larvae in grain sorghum (Gerhardt *et al.*, 1972).

Systemic insecticides which are applied into the seed furow at the time of planting have generally proved to be more effective in controlling first generation larvae than have foliar insecticides (Whitcomb *et al.*, 1966). In fact, carbofuran applied at the time of planting and as a foliar application at the onset of pollination has been shown to control first and second generation larvae (Keaster and Fairchild, 1968). More recently, Barry and Antonio (1979) showed that a soil application of carbofuran, or the organophosphate, Nem-a-tax (diethyl-1, 3-dithietan-2-ylidenephosphoramidate), at the time of planting was effective in controlling larvae for up to 50 days.

In the 1960s two or three treatments of endrin (0.5 lb./acre) to pretasselling corn were commonly recommended for the control of second generation larvae (Fairchild *et al.*, 1965). Carbofuran is now usually recommended for systemic and foliar applications. For instance, in Missouri an application of carbofuran (1 to 3 lbs./acre) to the seed furrow followed by one or two granular applications (1 lb./acre) to the whorls or leaf sheaths, as necessary, is recommended for corn planted after April 25 in which more than 30% of the plants are infested. For corn

planted before that date insecticide treatments are not routinely advised because the losses in yield due to larval feeding do not always offset the cost of the insecticide applications (Craig *et al.*, 1978). In Kansas, the carbamate, carbaryl, is approved for use while the organophosphate, diazinon, is restricted for use against second generation larvae, and carbofuran may be used against second and third generation larvae (Gates *et al.*, 1978). Dr. Fred Poston and his colleagues at Kansas State University are currently developing a computerized phenological model to predict the seasonal program of *D. grandiosella* in south-central and southwestern Kansas (Poston *et al.*, 1978; Whitworth and Poston, 1979). When the model is perfected it should be possible to adapt it to other populations for use in scheduling insecticide applications.

Resistant Host Plants

For the past 30 years entomologists and plant geneticists have been studying the attractive possibility of reducing losses caused by the southwestern corn borer through the use of resistant strains of corn (Wilbur *et al.*, 1950). An ideal control method will result when resistant germ plasm is identified and transferred into commercial strains of corn. A few corn genotypes have already been found which differ in their resistance to feeding by both first and second generation larvae (Scott and Davis, 1974; Barry and Darrah, 1978). Plants have been rated according to their capacity to withstand leaf, sheath, and stalk feeding. To date the most resistant natural genotypes have been discovered from Central America, including Antigua, Guatemala, and Mexico. Current emphasis is being placed on breeding for resistance to leaf feeding and stalk tunnelling in artificially infested plots (Scott and Davis, 1974, 1978).

One of the earliest resistant strains was released in Arkansas in 1962 as Ark SWCB Syn. Eight inbred lines were incorporated into this synthetic strain which showed reduced stalk invasion primarily through a resistance to sheath feeding (York and Whitcomb, 1966). This resistance, however, was not confirmed when the strain was tested in southeast Missouri (M.S. Zuber and A.J. Keaster, unpubl. infor.). Since then research based at the USDA Plant Science Laboratory at Mississippi State has led to the development of mass rearing techniques to facilitate artificial infestations and the screening of corn genotypes (Davis, 1976), and to the release of some corn strains which show moderate amounts of resistance. To date, one of the most promising releases is an inbred line MP496, which shows some resistance to damage by first generation larvae because it adversely affects larval survival and growth (Davis *et al.*, 1973; Anonymous, 1975).

Research and screening efforts are continuing in Mississippi, Missouri, Kansas, and Texas to select varieties which show even greater resistance to leaf and sheath feeding than does MP496. Dr. Dean Barry, a USDA entomologist who is studying host plant resistance in Missouri, has screened over 6,000 selected lines of corn for resistance to first generation larvae from 1976 to 1978. Although four lines have shown reproducible resistance to larval feeding, several years of research and development are needed to produce commercial varieties

which have substantial resistance to the southwestern corn borer (Barry and Darrah, 1978).

Biological Control

The highest rate of natural mortality occurs during the winter. Diapausing larvae are subject to many lethal agents during the eight months of their hibernation. Field observations from most states indicate that overwintering mortality usually ranges from about 50% to a high of >95%. These high mortality rates result in relatively few spring moths and first generation larvae. However, as Wilbur *et al.* (1950) have noted, a winter survival rate of 2% in heavily infested areas is adequate to restore population levels in the second generation.

Figure 9 illustrates the rate of mortality of diapausing larvae at two locations in southeast Missouri. At both locations the highest mortality rates occurred from December to mid-February when about 50% of the larvae died. By late May, less than 20% of the diapausing larvae remained alive (Langille, 1975). Many reasons exist for the high rate of winter mortality. Corn plants which are infected with stalk rot provide a less suitable host for diapausing larvae than do healthy plants. The causative agents of stalk rot penetrate into the larval cell and allow seepage of soil water into the overwintering habitat. Under these conditions the entrance of pathogens is promoted. A similar effect is achieved by termites (e.g., *Reticulitermes humilis)* which have been observed in Arizona, New Mexico, and Texas to excavate stalk crowns of corn plants during winter months (Davis *et al.*, 1933). Nutrient reserves are not usually the limiting factor in larval survival. An inadequate supply of nutrients contributes to overwintering mortality only under those conditions in which pre-diapausing larvae do not complete their normal feeding cycle on the corn plant (Chippendale, 1973).

In Missouri, the insect is at the northern limits of its distribution and the primary factors controlling populations appear to be subzero (°C) winter temperatures and bird predators. The detrimental effects of low midwinter temperatures are enhanced in wet clay soils by inoculative freezing. The higher mortality of diapausing larvae in wet clay or loam soils than in porous sandy soils is well documented (Wilbur *et al.*, 1950; Langille, 1975). The rate of survival in sandy soils is increased because of a decreased likelihood of inoculative freezing, and the presence of fewer disease pathogens than occur in wet clay soils.

The migration of the insect across the southern corn belt has been aided by the absence or low populations of natural enemies necessary to keep field populations in check. Table 4 lists four egg and two larval parasites known to attack the insect. Of these, only three species, *Trichogramma minutum, Apateles diatraeae,* and *Lixophaga diatraeae* have been studied in any detail, and quantitative information about their effects is scarce.

The hymenopteran, *T. minutum*, appears to be the most effective parasite of *D. grandiosella.* The two species have been found in association in several states. The adults of the parasite are most abundant in late summer and are therefore most effective in parasitizing eggs of the third generation, thereby decreasing the

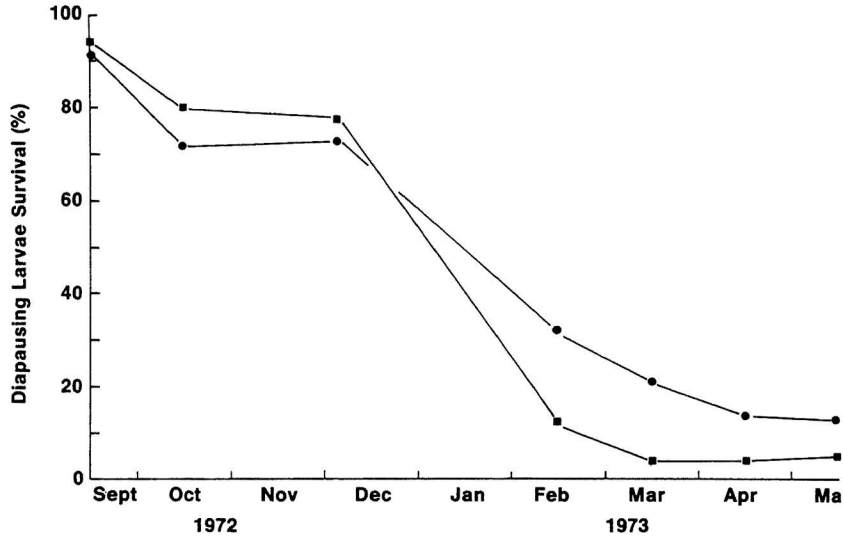

Fig. 9. Survival rates of diapausing larvae of *D. grandiosella* in Pemiscot (■) and Mississippi (●) Counties of southern Missouri, during the winter and spring of 1972 and 1973. 100 undisturbed and infested stalks were examined at each date. (Redrawn from Langille, 1975.)

TABLE 4
HYMENOPTERA AND DIPTERA KNOWN TO PARASITIZE EGGS AND LARVAE OF *D. GRANDIOSELLA*

Parasite	*Host stage attacked*	*Region*	*Reference*
Trichogramma minutum (Hymen.)	Egg	Arizona, New Mexico	Davis *et al.* (1933)
		Arkansas	Rolston (1955a)
		Missouri	Fairchild *et al.* (1965)
Prospaltella sp. (Hymen.)	Egg	Arizona	Davis *et al.* (1933)
Telenomus sp. (Hymen.)	Egg	New Mexico	Davis *et al.* (1933)
Chelonius annulipes (Hymen.)[a]	Egg	—	Hensley & Arbuthnot (1955)
Apanteles diatraeae (Hymen.)	Larva	Arizona	Davis (1944)
Lixophaga diatraeae (Dipt.)	Larva	Mississippi	Beland & King (1977)
		Louisiana	McPherson & Hensley (1978)

[a]About 280,000 progeny of a colony of the braconid hymenopteran, *C. annulipes*, imported from northern Italy were released in the United States between 1930 and 1940 as an egg parasite of the European corn borer. The parasite has not become sufficiently abundant or widely enough distributed to be a practical control agent. It parasitizes eggs of the southwestern corn borer only under laboratory conditions.

number of pre-diapausing larvae. High rates of parasitism of third generation eggs of *D. grandiosella* have been observed in Arkansas, Arizona, and Missouri. For example, egg masses on late planted corn in southeast Missouri in 1963 showed the following percent parasitism by *T. minutum:* August 29, 26%; September 4, 53%; and September 9, 96% (A.J. Keaster, unpubl. infor.).

The braconid hymenopteran, *A. diatraeae,* is a larval parasite of *D. grandiosella* and *D. saccharalis.* Females oviposit directly into the hemocoel of the larva. After feeding on the body tissues the mature larvae pupate within the corn stalk. Three or four generations are present in Arizona and the parasite overwinters as an immature larva within diapausing southwestern corn borers. *A. diatraeae* was an effective natural parasite of second and third generation larvae between 1931 and 1934 in Arizona when values of 32% and 78% parasitism, respectively, were recorded (Davis, 1944).

The tachinid fly, *L. diatraeae,* a native of the West Indies introduced into Louisiana as a parasite of *D. saccharalis,* also parasitizes *D. grandiosella.* The female flies larviposit on fresh frass of actively feeding larvae. The maggot enters the larva through an intersegmental membrane and completes its growth within the hemocoel. Fully grown maggots usually migrate from their hosts and pupariate in tunnels previously excavated by their hosts. Studies have shown that large larvae may encapsulate the invading maggot and complete their metamorphosis to produce viable eggs. *L. diatraeae* appears to have little promise for controlling field populations because the release of flies in 1974 and 1975 in Mississippi resulted in only 1% parasitism among collected larvae of *D. grandiosella* (Beland and King, 1977).

Larvae of *Chaetopsis debilis* (Diptera: Otitidae) have been observed in the overwintering chambers of *D. grandiosella* in Missouri (Langille, 1975). These maggots usually invade the partially rotted stalks in early October and remain active throughout the winter. They may feed on living or dead larvae and become attached to the larval cuticle. They undergo metamorphosis in early spring. In summer, larvae and pupae of *C. debilis* are found frequently among the frass of southwestern and European corn borers.

Pathogens have been shown to cause considerable mortality of diapausing larvae. Both fungal and bacterial pathogens have been observed to invade diapausing larvae in their overwintering cells (Davis *et al.,* 1933; Langille, 1975). A fungus of *Beauveria* sp. kills up to 6% of diapausing larvae in Missouri by entering the hemocoel of diapausing larvae in the fall. Initially, attacked larvae turn pink, and then after a few days appear white after the fungal hyphae have apread over the entire cuticle. Similarly, a bacterium of *Bacillus* sp. reduces fall populations of diapausing larvae by about 10% (Langille, 1975). Although larvae have been shown to be susceptible to *Bacillus thuringiensis* under laboratory conditions, attempts have not been made to exploit this agent in the field (Sikorowski and Davis, 1970).

Those larvae overwintering in stalks which disintegrate as a result of fungal-induced stalk rot are more likely to be invated by lethal pathogens than are

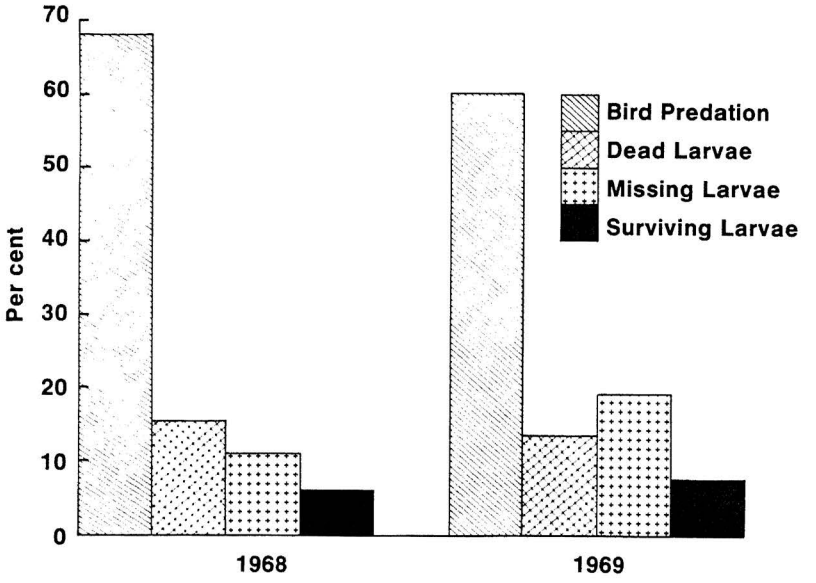

Fig. 10. Bar chart illustrating factors contributing to the mortality of diapausing larvae of *D. grandiosella* in Mississippi. Information is based on average values per acre, and on infestation rates of 50.3% and 58.7% of 11,223 and 10,406 plants/acre, respectively. (Data summarized from Black *et al.*, 1970.)

larvae in intact stalks. The decaying corn plant provides a suitable environment for the growth of microorganisms which may ultimately invade the diapausing larvae. However, any conclusions about the lethal effects of assumed pathogens must be drawn from controlled laboratory studies. Under field conditions it is difficult to exclude the possibility that the observed microorganism is saprophytic and therefore did not contribute to larval death.

While several arthropods, including ants, thrips, predaceous bugs (Hemiptera), and beetles (Coccinellidae) may feed on various life stages of *D. grandiosella* little information is available about their effect on population levels (Davis *et al.*, 1933; Fairchild *et al.*, 1965). In contrast, bird predation of diapausing larvae is well documented and accounts for more overwintering mortality than any other single factor. Bird predation has been shown to be important in supressing populations of diapausing larvae in Arkansas (Wall and Whitcomb, 1964), Louisiana (Floyd *et al.*, 1969), Mississippi (Davis *et al.*, 1973, and Missouri (Langille, 1975). The yellow-shafter flicker, *Colaptes auratus* (L.), is the most important predator. Fig. 10 illustrates the contribution of bird predation to the mortality of diapausing larvae in Mississippi. In the winters of 1968 and 1969 the flickers destroyed 68% and 60% of the diapausing larvae, respectively. The flicker seeks larvae in stalk crowns of plants which show external signs (entrance holes, girdle stalk) of their presence. The bird pecks a hole about 0.5 cm in diameter near ground level among the brace roots, and in so doing gains entrance to the overwintering cell. Most predation occurs from

December to early March. By late March the population density of *D. grandiosella* has declined and other food sources are becoming available. It is clear, therefore, that the foraging of the flicker among corn stubble is important in keeping in check populations of diapausing larvae in several states.

CONCLUDING REMARKS

The southwestern corn borer is a member of a group of lepidopterous larvae which causes severe damage to corn (Dicke, 1977). Its status as a pest of corn and sorghum remains assured until more effective means of control than are currently available are developed. The modern practices of no-tillage agriculture, which leaves undisturbed the overwintering habitat, and extensive irrigation, which increases corn acreage within the insect's range, tend to favor the buildup of populations of *D. grandiosella.*

At present, cultural methods combined with precisely timed insecticide applications offer the most practical approach to reduce populations and to limit economic losses. Early planting of corn minimizes dead-heart injury because plants reach the tassel stage of development by the time first generation larvae hatch, and fall or spring plowing or discing destroys diapausing larvae. These cultural methods represent well established techniques which will remain important in future pest management programs.

Improvements in control practices are likely to come from the development of varieties of corn which are resistant to feeding by first generation larvae. Other future control strategies may employ techniques to disrupt the genetically-controlled larval diapause. These may include the use of conditional lethal traits to desynchronize the insect's life cycle with that of its host plant (Klassen *et al.*, 1970), or the use of anti-hormones or hormone mimics to deregulate the larval diapause. Improvements in control methodology require a commitment to further studies into the population ecology, behavior, genetics, physiology, and biochemistry of the insect.

D. grandiosella is an excellent laboratory model for studies dealing with the developmental physiology of plant-feeding Lepidoptera. The larvae rank high for such studies because they: (a) are easy to rear on artificial food in highly synchronized populations, (b) enter a facultative diapause, the onset and termination of which is easily regulated by manipulating photoperiod and temperature, (c) are relatively large and do not feed during diapause, thereby enabling surgical operations to be performed on their neuroendocrine system without disturbing their normal growth processes, and (d) molt from the spotted to the immaculate morph at the onset of diapause. This transformation provides a positive identification that diapause has begun, and offers a tremendous advantage over most insects in which the diapause state has to be identified by negative criteria, i.e., the insect does not molt or metamorphose. These characteristics, together with the known involvement of juvenile hormone in the regulation of the insect's diapause, provide the basis for future research which hopefully will lead to the development of new methods for controlling *D. grandiosella* and related insects.

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