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Diapause in the Boll Weevil, *Anthonomus grandis* Boheman, As Related to Fruiting Activity in the Cotton Plant

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ABSTRACT

Studies in Arkansas show that boll weevil diapause is related to changes in fruiting activity of the cotton plant. Generally, when larval development took place while fruiting levels were increasing or being held at a high level, diapause in resulting adults was low (0-20%). Diapause was approximately 20-50% when larval development coincided with decreasing fruiting levels, and was 50-100% as true cut-out approached. Regrowth cotton generally lowered diapause incidence and as fruiting levels decreased, diapause increased. Therefore, the boll weevil not only responds to short photoperiods that are characteristic during the fall in the temperate zone, but also may respond throughout the season to changes in fruiting activity of the cotton plant.

INTRODUCTION

Diapause, as defined by Hanson (1962), is a period of suspended growth and development and reduced metabolism in the life cycle of many insects in which the organism is more resistant to unfavorable environmental conditions than during other periods. A more concise definition states that diapause is a state of arrested growth and development that is not reversed upon any amelioration of the environment (Simmonds, 1948). The latter definition separates diapause from cold or heat stupor or aestivation.

Hibernation in the adult boll weevil was recognized as a means of overwintering as early as 1903 (Sanderson, 1907). However, diapause as a physiologic phenomenon was not defined until 1959 (Brazzel and Newsom, 1959). Diapause was characterized in this insect by a cessation of gametogenesis and atrophy of gonads, increase in fat content, decrease in water content, and decrease in respiratory rate. Since 1959, the term diapause has been used extensively in boll weevil studies.

Earle and Newsom (1964) found that diapause in the boll weevil could be induced by 11-hr photoperiods and suppressed by 13-hr photoperiods. The immature stages were sensitive to photoperiod but the adults were not. The response to photoperiod was modified by temperature and food.

Lloyd et al. (1967) listed five environmental stimuli that are conducive to diapause in the boll weevil: (1) exposure of the larval and pupal stages to an 11-hr photoperiod, (2) exposure of adults to night temperature of 10 C, (3) adult diet of bolls, (4) limitation of the quantity of squares fed to adults, and (5) larval diet of bolls.

In previous years, boll weevil diapause initiation has been considered to occur primarily in the fall. However, recent field studies have shown that diapause initiation is not restricted to the fall, and that a midseason incidence of diapause consistently occurs. Brazzel and Newsom (1959) found diapausing boll weevils in ground trash each month of the year except June and July. They detected diapause in field individuals as early as 30 July and movement to winter quarters was observed to begin as early as 16 August during 1957. Brazzel and Hightower (1960) observed increased reproductive activity in boll weevils on September regrowth cotton and Beckham (1962) reported that the time of entry into diapause was related to maturity of the cotton plant. Findings similar to these have been reported by Lloyd et al. (1964), Mitchell and Mistric (1965), and Walker and Bottrell (1970).

The foregoing findings, in addition to reports on other insects regarding the influence of plant growth substances on insect growth and development (Carlisle et al., 1965; Nation and Robinson, 1966) and the influence of host plant maturity on diapause initiation (Gambaro, 1954; Geyspitz, 1953), led to the following studies in Arkansas on the effect of plant growth substances on boll weevil diapause.

Kimbrough (1970) found that incidence of diapause in the boll weevil could be increased or decreased when certain plant growth substances were incorporated into the artificial diet. Kinetin and ortho-chlorophenoxyacetic acid supplied in this manner reduced diapause incidence. Kimbrough also found that the adult weevil does not have to feed as an adult prior to attaining diapause. Continuing this work, Otwell (1970) also observed that kinetin and ortho-chlorophenoxyacetic acid reduced diapause incidence. Diapause reduction, when these two compounds were used in a 2:1 combination, approached 44%. Kinetin and gibberellic acid (GA_3) in a 1:1 combination also reduced diapause incidence. In late September and early October field studies, Otwell observed that diapause initiation was earlier on Rex cotton (a determinate variety) than on DPL cotton (an indeterminate variety).

Because the incidence of diapause at midseason relates directly to the reproductive potential of boll weevil populations, the ability to control, alter, or even predict the seasonal incidence of diapause would prove valuable in managing boll weevil populations. Therefore, work was begun in 1971 to evaluate the influence of host plant condition on boll weevil diapause. This paper summarizes recent work.

MATERIALS AND METHODS

Diapause incidence was compared on indeterminate and determinate lines of cotton during September and October of 1971. Mated female weevils were caged over squares and bolls of two determinate lines of cotton (Stripper 31 and Yugo 11) and an indeterminate (DPL) cotton and allowed to oviposit. Squares and bolls with ovipositional punctures were tagged, allowed to remain on the plant until abcission, then held in the laboratory until adult emergence. Adults were maintained at 25 C and a 12-hr photoperiod and fed the larval food source. Weevils were dissected for diapause determination at the end of 14 days. In male weevils criteria for diapause were the atrophy

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of the gonads and the absence of sperm packets; in the female, the criterion was atrophied ovaries with no indication of oogenesis.

Samples of squares and bolls were collected from Rex and DPL varieties in different stages of maturity. They were freeze-dried and incorporated into a modified Vandersant's diet (Vanderzant et al., 1959) at the rate of 30 g freeze-dried sample per 1000 ml diet. Diapause response was measured in weevils reared on these test diets to detect possible alterations in diapause tendencies as a result of maturity differences. Weevils were reared as immatures and held as adults at 21 C with 10.5, 11.5, 12.5, and 13.5-hr photoperiods. Adults were fed the same diets as larvae and were dissected after 21 days.

Twelve cotton entries, selected to give varying fruiting patterns and degrees of earliness, were planted near Newport, Arkansas, in 1972. Squares infested by field populations of weevils were collected from these cottons on 27 July and 7 September. A 16 August collection was obtained by artificially implanting weevil eggs in squares. The infested forms were collected after abcission and held in an open-air insectary. Adult weevils were then fed on squares from the respective cotton entries for 21 days prior to dissection.

A second objective during 1972 was to evaluate diapause response to controlled flower bud density in both determinate and indeterminate varieties of cotton. Fruiting levels of 75,000 squares per acre were maintained in one indeterminate cotton (DPL) and three determinate cottons (IX5-56, Yugo 11, and Arkugo 1). The normal fruiting level in each entry was used as control. Infested squares were collected from each of the plots and treated in the same manner as those discussed heretofore.

RESULTS

Results show that maturity of the host is reflected in incidence of boll weevil diapause (Table I). Average diapause in squares and bolls in an actively growing DPL variety was 26.7% compared to 36.1% for Stripper 31 and 45.5% for Yugo 11. The latter two were in more advanced stages of maturity. A chi-square test with diapause incidence on the DPL cotton as the expected value showed highly significant differences ($P < 0.005$) in diapause incidence between DPL cotton and the two determinate lines.

Results of laboratory tests to bioassay weevil diapause response to diet-incorporated plant part samples collected from Rex cotton in advanced maturity and an actively fruiting DPL cotton are shown in Table II. Findings in this series of tests substantiate the field observations that host plant maturity has considerable influence on the initiation of diapause in the boll weevil. For example, cut-out stage Rex bolls effected 55% diapause in contrast to 24% in peak-fruiting DPL bolls when tests were conducted under a 12.5-hr photoperiod. With the exception of tests with Rex bolls and DPL bolls at 11.5-hr, results were similar at the other three photoperiods. Mean percent diapause at all four photoperiods shows that Rex bolls effected 56% diapause, whereas DPL bolls effected 45%. More weevils (55%) diapaused from Rex cut-out stage squares than from vegetative stage DPL bollş (45%). Larval and/or adult diets have been thought to be conducive to diapause. The DPL incorporated diets, however, did not reduce diapause in comparison to diapause incidence in the standard diet controls.

Table III shows the average seasonal fruiting counts of 12 cotton entries and the average diapause initiation in boll

Table I. Late Season Incidence of Diapause in Boll Weevils Reared in Bolls and Squares of an Indeterminate Cotton (DPL) and in Two Determinate Cottons (Stripper 31 and Yugo 11), Fayetteville, Arkansas, 1971

	Percent Diapause		
Entry	Squares	Bolls	$\overline{X}$*
DPL	37.2	14.3	26.7
Stripper 31	56.2	20.0	36.1
Yugo 11	50.0	42.8	45.5

*26.7 is significantly different ($P < 0.005$ from 36.1 and from 45.5.

Table II. Diapause Incidence in Boll Weevils Reared on Artificial Diet Incorporated with Lyophylized Squares and Bolls from Cut-Out Rex Cotton and an Actively Growing DPL Cotton, Fayetteville, Arkansas, 1971.

	Diapause (%) at 4 Photoperiods				
	Hours				
Sample	10.5	11.5	12.5	13.5	$\overline{X}$
Std. diet	46	48	32	32	39
Rex sq.	62	51	42	68	55
DPL sq.	48	38	32	48	42
Rex bolls	61	48	55	67	56
DPL bolls	54	51	24	54	45

Table III. Mean Fruiting Activity of 12 Cotton Entries and Mean Diapause Incidence in the Boll Weevil on These Cottons at the Dates Indicated, Newport, Arkansas, 1972.

Date	$\overline{X}$ Sq/A (1000's)	$\overline{X}$ Percent Diapause
29 June	37	
5 July	92	
12 July	137	
19 July	197	
27 July	139	21
3 August	60	
11 August	34	
16 August	41	3
23 August	59	
30 August	38	
7 September	19	87

weevils collected from the field as immatures in flared squares. A drought during June and July induced a decline in square formation after 19 July. Irrigation and rainfall in mid-August initiated a resumption of fruiting and a second fruiting peak was reached on 23 August. Weevils collected on 27 July developed from eggs deposited in squares at or subsequent to the 19 July peak fruiting. Mean diapause incidence in this collection of weevils was 21% and the incidence ranged from 5 to 40% in the 12 entries. Diapause frequencies were generally low (5-28%) on individual entries where fruiting was heavy and the plants were growing, but were higher (33-40%) in cottons that were fruiting moderately and beginning to show drought stress earlier than other entries. Diapause seemed to be influenced by drought-induced maturity of these cottons.

The 16 August group of weevils was collected 9-11 days after irrigation and rainfall. The immatures in this group of weevils were reared on plants growing and fruiting rapidly. The incidence of diapause in weevils developing on this type of plant growth ranged from 0-14% with an average of 3% on the 12 entries. These figures are based on a total of 78 weevils obtained by implanting eggs..

The 7 September group of weevils developed on cotton in advanced stages of maturity at a time when environmental stimuli were also conducive to diapause. The incidence of 87% diapause on this sample date reflects responsiveness of the weevil to these conditions.

Diapause response to adjusted versus normal fruiting level plots of determinate and indeterminate cottons is shown in Table IV. Fruiting levels were adjusted by taking weekly square counts and removing squares in excess of 75,000 squares/acre. This practice maintained plants in a more vegetative state with a high fruiting capacity. Even though excess squares were removed at weekly intervals, the adjusted fruiting level plots showed a seasonal fruiting curve similar to that of the controls. For this reason, the comparisons in Table IV are made between diapause incidence and the fruiting rate tendencies during the time of larval development on the plant. Diapause incidence was 50% on normal fruiting DPL-16 cotton with a decreasing fruiting rate compared to 44.4% on the controlled fruiting level plot with an increasing fruiting rate. Illustrations of this relationship can be seen in similar comparisons in the other cottons. The relationship of fruiting rate changes to initiation of diapause is shown in the three groups of weevils obtained from the Arkugo 1 plots. On 27 July, the normal fruiting rate was decreasing whereas the fruiting rate was heavy on the controlled plot. Diapause on the two plots was 27% and 0% respectively. On 11 August, the normal plot induced 28.6% diapause while its fruiting rate was decreasing. In contrast, the controlled plot induced 20% diapause as it was beginning regrowth after irrigation. The 16 August samples showed both plots with lower incidences of diapause as a result of their increasing fruiting rates due to regrowth. Diapause incidence was consistently higher on the normally fruited plots, with the exception of the IX6-56 samples. Conversely, the controlled fruiting level plots generally had higher fruiting rates and less diapause.

Table IV. Comparison of Boll Weevil Diapause with Fruiting Activity in Four Cotton Entries Adjusted Weekly to Two Fruiting Levels, Normal (Level A) and 75,000 Squares Per Acre (Level B), Newport, Arkansas, 1972

Cotton Entry	Fruit Level	Date	Fruiting Rate	Percent Diapause
DPL-16	A	27 July	decreasing	50.0
DPL-16	B	27 July	increasing	44.4
IX6-56	A	27 July	heavy	0.0
IX6-56	B	27 July	increasing	12.5
Yugo 11	A	27 July	decreasing	16.6
Yugo 11	B	27 July	heavy	0.0
Arkugo 1	A	27 July	decreasing	27.3
Arkugo 1	B	27 July	heavy	0.0
Arkugo 1	A	11 August	decreasing	28.6
Arkugo 1	B	11 August	regrowth	20.0
Arkugo 1	A	16 August	regrowth	16.7
Arkugo 1	B	16 August	regrowth	14.0

DISCUSSION

Observed changes in diapause incidence seem likely to be either a direct or an indirect response to plant growth substances which bring about changes in plant growth, fruiting, and maturity. The weevil seems to respond with a low incidence of diapause when plant growth and fruiting are stimulated. Conversely, a higher incidence of diapause is associated with slowed fruiting rates, retarded growth, and/or induced maturation of the host plant. Thus weevils respond throughout the season to these changes in plant growth and fruiting.

Midseason diapause occurs as a host plant response under conditions of long photoperiods and high temperatures which normally inhibit diapause. Fruiting activity and growth of the host plant therefore should be included in those environmental stimuli conducive to diapause. Furthermore, upon detailed study of boll weevil diapause, it seems likely that the weevil would be found to possess an array of faculties to cope with less than favorable conditions, whether they be high or low temperatures, temporary shortage of food, mature cotton host, etc. Therefore, it is apparent that the term diapause is being used in its broadest sense to include the various means of the boll weevil to circumvent a wide range of unfavorable conditions.

The data presented support Sterling's (1972) observation that plant maturity may be more useful than photoperiod in attempts to predict seasonal incidence of diapause in the boll weevil. The wide range of in-season rates of weevil population increase reported in the literature (Sterling and Adkisson, 1970) possibly could be explained by better understanding of this relationship. Midsummer diapausing weevils, as well as other types of diapausing weevils, should be given detailed study.

Boll weevil diapause has been shown to be related to changes in fruiting activity of the cotton host plant, expecially during the time of larval development on the plant. Generally, when larval development took place while fruiting levels were increasing to a peak or when a peak was being maintained, diapause incidence was low (0-20%). Diapause was approximately 20-25% when larval development took place coincident with decreasing fruiting levels, and was highest (50-100%) as true cut-out approached. Diapause incidence on cotton rapidly fruiting as a result of regrowth was generally low (0-20%) and as fruiting rates decreased, diapause increased. Therefore, diapause in the boll weevil is not only a response to short photoperiods that are characteristic during the fall in the temperate zone, but it is also a season-long response to changes in fruiting activity, growth, and maturity of the cotton plant.

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