

**The Significance of Growth Stages of
Sweet Corn as Related to Infestation
by the European Corn Borer**

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CONTENTS

| | PAGE |
|---|------|
| INTRODUCTION | 173 |
| METHODS | 175 |
| OVIPOSITION | 176 |
| FATE OF EGGS | 181 |
| SURVIVAL OF BORERS | 183 |
| CORN BORER INJURY TO EARS | 186 |
| COMPARISONS BETWEEN INFESTATIONS ON MARCROSS AND LEXINGTON HYBRIDS .. | 191 |
| Oviposition | 191 |
| Borer Population | 192 |
| Survival of Borers | 192 |
| SUMMARY AND CONCLUSIONS | 198 |
| LITERATURE CITED | 199 |

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PREDICTION of insect damage to food or other commercial crops is more important now than ever before. Such prediction, if at all reliable, can be used to increase the efficiency and economy of insecticidal control measures and in some cases to eliminate these measures by the substitution of cultural practices. In such instances, a knowledge of the relationships between the destructive insect and its host plant is essential.

At the present time in the Corn Belt, delayed planting of resistant varieties is advised to reduce the damage caused by the European corn borer (*Pyrausta nubilalis* Hübn.). Now that the borer is present in increasing numbers throughout a larger area of the Corn Belt, and the bivoltine strain is extending its range, a knowledge of the pattern of insect attack becomes of greater value. Although the work reported here was done on sweet corn in Connecticut, it should have some application to field corn grown in the Midwest.

In New England and other northeastern states, where the bivoltine strain of corn borer is present, sweet corn is the principal crop infested by this insect. To provide a succession of harvests, corn is planted at successive dates, or several hybrids which mature at different times are planted at one time. In either case some plantings are more severely injured than others. The reasons for this lie in the facts that (1) the level of insect abundance changes throughout the season; that is, oviposition begins late in May, rises to a peak in mid-June, declines to a low in early July, rises to a second peak (second generation) in mid-August, and then declines again; (2) not all stages of the corn plant are equally susceptible to corn borer infestation since (a) the moths favor the older, taller plants for oviposition and (b) survival of borers is greater on older than on younger plants.

This means that if corn in susceptible stages of growth is present at the time of greatest oviposition, the maximum injury will result, and insecticidal control measures are necessary if the crop is to be profitable. Conversely, if corn in stages of growth which support the borer with difficulty is present at a time when oviposition is at a low level, minimum injury is to be expected and insecticidal treatment is a waste of time and material. Between these two extremes lie conditions which may or may not justify the use of insecticides, and some basis for judgment is essential if the most economical course is to be taken.

It is well established¹ that corn planted early is more susceptible to injury by the borer than is corn planted late; that taller corn is more heavily infested than shorter corn; that early maturing hybrids are more severely

¹ As reviewed by Beard (4).

injured than late-maturing hybrids. The lighter infestation in shorter corn is due chiefly to an escape from oviposition, whereas in late corn, whether by virtue of its longer developmental time or its late planting date, the lighter infestation is due not only to a lower oviposition rate, but also to the fact that establishment and survival of the borers themselves are less.

Unfortunately, the terms early and late, and tall and short, are relative and are meaningless if no standards of measurement are commonly employed. What constitutes an early planting date in one locality may be late in another, and a "tall" hybrid may be relatively short when grown under conditions peculiarly adverse to this hybrid. Moreover, the time required for a given hybrid to mature varies with the season. For example, the sweet corn hybrid Marcross may require 20 days longer to reach maturity when planted in mid-April than when planted in mid-June. For these reasons, the date of planting and the date of maturity may tell very little about the conditions favoring or limiting corn borer oviposition and survival. Silking date, too, has been a common point of orientation, but this has the disadvantage of too often indicating a stage after much oviposition has occurred.

It is far more desirable to know in what stages the plant may be when eggs are being deposited and borer establishment is taking place. The importance of this becomes apparent when it is considered that the susceptibility of corn during the few days marking the peak of the oviposition may make a large difference in the resultant infestation. It is common for 40 per cent or more of the eggs of the first generation to be deposited within only five days. Vance (12), working with the univoltine strain in the eastern North Central States, noted that in 1928 and 1938, respectively, 61.5 per cent and 60 per cent of the eggs were deposited within five days. Thus corn in stages unfavorable to the borer at such a time would escape a proportionately larger number of borers than at other times, even though the absolute number might be greater, due to the impact of an unusually heavy population.

In view of these considerations, the current study was designed to determine the complete pattern of attack by the corn borer, with emphasis upon the consideration of the development of corn in all stages. The classification of growth stages by Batchelder (2) was used throughout. This classification divides the characteristics of corn plant development into 11 descriptive categories, namely, primary whorl (P-W), early whorl (W-1), mid-whorl (W-2), late whorl (W-3), early green tassel (T-1), mid-green tassel (T-2), late-green tassel (T-3), early silk (S-1), mid-silk (S-2), late silk (S-3) and roasting ear (R-E). Although it must be kept in mind that the development of corn is a continuous process and that the end of one stage merges into the beginning of the next, the stages as defined by Batchelder are sufficiently distinct to serve as reliable points of reference. The present writer adds still another stage, the seedling (Sg), which includes all plants smaller than the primary whorl.

METHODS

During the summer of 1942, at the Mount Carmel experimental farm of this Station, 80 randomized plots in one field and 60 randomized plots in a nearby field were laid out. The soil and culture in the two fields were essentially alike. A separation of 6 feet between plots served to restrict migration of borers from one plot to another. Although an effort was made to grow 20 corn plants in each plot, in some plots one or more plants failed to develop due to poor germination or to cutworm, wireworm or mechanical injury. Beginning on April 17 and continuing until July 16, a sequence of plantings was made. At each planting, five plots were planted to Marcross and five to Lexington. Marcross was chosen because it is one of the most satisfactory early hybrids for this region, and Lexington, because it requires the same time for maturity as Marcross, but usually produces taller plants. The dates of planting were not spaced at regular intervals. Instead, when the seedlings of one planting appeared above ground, seed for the next series was planted. This resulted in a well-graded series of growth stages throughout the entire summer.

Complete records were taken of the development of all plantings by noting the dates on which each plant stage was reached by the corn in each plot.

Throughout the oviposition periods of both flights of moths, all plants were carefully examined for eggs at frequent intervals. During periods of unfavorable weather the interval was as great as one week, but it is believed that a very small proportion of eggs hatched without being counted. When possible, the corn was examined twice within the period of time required for hatching so that egg masses missed during the first examination would likely be found at the second. Each egg mass was counted with the aid of a hand lens and labelled by stapling a tag on the corn leaf adjacent to the mass. On the label were recorded the date of observation, the number of eggs and the stage of plant growth at the time of observation. Upon subsequent examination of the corn plant the fate of the egg mass was noted insofar as was possible.

On corn leaves which showed nothing more than a bare outline indicating the former presence of an egg mass, the mass was presumed to have sloughed off before hatching. Egg masses which had hatched or become parasitized were so recorded. Unfortunately, predation could not be determined with any degree of certainty. There was evidence of considerable predation by mites, thrips, coccinellid larvae and adults, lace-wing larvae and certain Hemiptera, but frequently the egg mass fed upon by these predators so closely resembled a hatched egg mass that it was impossible to distinguish between the two with accuracy. Because daily observations on all corn were not possible in view of the labor involved, the exact dates of oviposition and hatch are not known. Consequently, all references to date of infestation or stage of plant growth at the time of infestation, apply to the date or stage on which observation of the unhatched egg mass was made. Because of the effort made to examine the corn twice within the

time required for hatching of the eggs, it is probable that the date would be nearer that of oviposition than of hatching.

When corn of a given planting reached the later phases of the late silking stage, all plants were carefully dissected and all borers found were noted as to position in the ears, stalk or elsewhere in the main plant and tillers. It was desirable to dissect the corn before it reached the roasting ear stage, as there is a tendency for some borers to migrate from the ears at this latter stage.

OVIPOSITION

The data obtained on oviposition by the corn borer moth are summarized in Table 1, which indicates the average numbers of egg masses and of eggs per 10 plants, with the distribution as to generation, for each planting of Marcross and Lexington hybrids.

TABLE 1. CORN BORER OVIPOSITION ON 14 PLANTINGS OF MARCROSS AND LEXINGTON HYBRIDS¹

| Planting number | Date of planting | Average number of egg masses per 10 plants | Average number of eggs per 10 plants | Per cent of eggs in: | |
|------------------|------------------|--|--------------------------------------|----------------------|-------------------|
| | | | | First generation | Second generation |
| Marcross | | | | | |
| 1 | April 17 | 82 | 1,421 | 100.0 | |
| 2 | 29 | 39 | 689 | 100.0 | |
| 3 | May 11 | 32 | 473 | 97.0 | 3.0 |
| 4 | 19 | 12 | 207 | 75.0 | 25.0 |
| 5 | 26 | 11 | 215 | 27.8 | 72.2 |
| 6 | June 1 | 27 | 632 | 1.4 | 98.6 |
| 7 | 8 | 32 | 728 | | 100.0 |
| 8 | 13 | 46 | 1,089 | | 100.0 |
| 9 | 18 | 56 | 1,235 | | 100.0 |
| 10 | 23 | 68 | 1,385 | | 100.0 |
| 11 | 29 | 52 | 1,087 | | 100.0 |
| 12 | July 6 | 41 | 858 | | 100.0 |
| 13 | 11 | 26 | 518 | | 100.0 |
| 14 | 16 | 17 | 347 | | 100.0 |
| Lexington | | | | | |
| 1 | April 17 | 76 | 1,362 | 100.0 | |
| 2 | 29 | 31 | 532 | 100.0 | |
| 3 | May 11 | 30 | 491 | 96.5 | 3.5 |
| 4 | 19 | 17 | 282 | 73.8 | 26.2 |
| 5 | 26 | 15 | 297 | 24.5 | 75.5 |
| 6 | June 1 | 26 | 582 | 2.6 | 97.4 |
| 7 | 8 | 35 | 786 | | 100.0 |
| 8 | 13 | 46 | 1,096 | | 100.0 |
| 9 | 18 | 63 | 1,338 | | 100.0 |
| 10 | 23 | 60 | 1,271 | | 100.0 |
| 11 | 29 | 56 | 1,165 | | 100.0 |
| 12 | July 6 | 44 | 909 | | 100.0 |
| 13 | 11 | 33 | 683 | | 100.0 |
| 14 | 16 | 16 | 327 | | 100.0 |

¹Total number of eggs deposited on 1,363 plants of Marcross (all plantings) was 104,762. Total number of eggs deposited on 1,335 plants of Lexington (all plantings) was 104,973.

Considering the first generation alone, the first planting received the heaviest number of eggs, not only because it was available to attack for a greater length of time, but because at the onset of oviposition it was in a stage more favorable for oviposition. There is a tendency for oviposition to be delayed on later plantings until the corn reaches more favorable growth stages. Offsetting this tendency to some extent is the fact that under the impact of an increasing oviposition rate, more of the smaller corn is attacked (see Table 3). Even so, the oviposition trend varies in time somewhat with each planting, as can be seen in Table 2, which indicates the dates on which the quartiles of the total oviposition of each planting were completed. The stage of growth reached by 50 per cent or more of the plants in a given series is indicated for each date. Only the oviposition of the first-generation moths on Marcross corn is considered.

TABLE 2. OVIPOSITION TREND OF FIRST-GENERATION CORN BORER ON MARCROSS CORN

| Date of planting | Total eggs deposited (100 plants each planting) | Oviposition first observed | Per cent of total oviposition | | | |
|------------------|---|----------------------------|-------------------------------|------------|------------|------------|
| | | | 25 | 50 | 75 | 100 |
| Apr. 17 | 14,208 | May 25 P-W | Jn. 7 W-2 | Jn. 10 W-3 | Jn. 14 T-1 | Jn. 30 S-2 |
| Apr. 29 | 6,894 | May 27 Sg | Jn. 10 W-1 | Jn. 13 W-2 | Jn. 17 W-3 | Jn. 30 S-1 |
| May 11 | 4,591 | Jn. 1 Sg | Jn. 10 W-1 | Jn. 13 W-1 | Jn. 17 W-2 | Jn. 30 T-2 |
| May 19 | 1,513 | Jn. 1 Sg | Jn. 12 P-W | Jn. 16 W-1 | Jn. 19 W-2 | Jn. 30 T-1 |
| May 26 | 599 | Jn. 6 Sg | Jn. 14 Sg | Jn. 20 W-1 | Jn. 24 W-2 | Jn. 30 W-3 |

Although the trend differences in dates between any two successive plantings may not be especially significant, the fact that differences do exist indicates the advisability of giving information relative to the stage of growth of the observed corn when comparisons of oviposition in one year or in one field are made with that in other years or in other fields.

It is usually thought that the first generation serves to build up the corn borer population so that the infestation of the second generation may exceed by two or three times that of the first. In the current study, however, no planting attacked by the second generation of borer was so heavily infested as the first planting of the season, although plantings 9 and 10 were almost as severely attacked. The infestation on planting number 1 was unusually heavy—the heaviest ever observed at the Experiment Station farm and one of the heaviest on record. If the geographic areas kept under observation are considered as a unit, regardless of the number of plants therein, a total of 53,953 eggs was deposited by moths of the first generation and a total of 155,782 eggs was deposited by moths of the second generation.

The lower infestation on a per plant basis by the second generation would seem to be an effect of dilution, although the moths of the second genera-

tion were not the offspring of the particular first-generation borers within the geographic area considered, since dissection of the corn plants was made before the borers matured. An abundance of corn of all sizes in fields within easy flight distance from the experimental plots provided an adequate population of moths for oviposition. There was no gradient of infestation across either field in any direction, and although wide variation occurred among the completely randomized plots, the infestations over the whole fields were more uniform than might have been expected.

The dilution of infestation on a per plant basis can be explained in terms of the duration of each generation, and as a direct consequence, the amount of corn available. The oviposition of the first generation rose to a pronounced peak and then declined to nothing within an interval of six weeks (see Table 7). The oviposition of the second generation, on the other hand, was distributed over a period of 11 weeks, although that of the last three weeks was negligible. Moreover, the peak of the trend was less definite than in the first generation and may be said to cover a period of four weeks during which time the number of eggs deposited exceeded 20,000 each week (on both corn hybrids).

Because of the shorter time during which the first-generation moths were in flight, only six plantings of corn (1,187 plants) were available for oviposition. For the second generation, on the other hand, 12 plantings (2,309 plants) were available. Furthermore, among the first six plantings much of the corn was too small to favor oviposition, thus the bulk of the infestation was concentrated on the first two plantings. For the most part during the second generation, corn in all growth stages was available, with the stages more favorable for egg deposition represented in all plantings subject to attack (see Table 3).

The extent to which dilution, as outlined above, affects the infestation in commercial plantings is almost impossible to determine. A uniform series of plantings with different growth stages represented in equivalent numbers is probably never attained in the usual field planting. And it has never been demonstrated whether, in the absence of corn in stages favorable for oviposition, the corn borer moths will withhold their eggs, or realize their reproductive capacities by ovipositing on very young corn or on other cultivated or weed hosts. There is little doubt, however, that in Connecticut, because so much more late than early corn is grown, the dilution factor is considerable, and frequently may mask a high total population of corn borers.

The distribution of the actual number of eggs observed relative to the growth stage of the corn is given in Table 3.

TABLE 3. NUMBER OF BORER EGGS DEPOSITED ON EACH STAGE OF MARCROSS AND LEXINGTON CORN IN 14 PLANTINGS

| Planting number | Date of planting | No. of plants | Sg. | P W | W 1 | W 2 | W 3 | T 1 | T 2 | T 3 | S 1 | S 2 | S 3 | Total |
|------------------|------------------|---------------|-----------|-------|--------------|--------------|--------------------|-------|-------|-------|-------|--------------|-------|--------|
| Marcross | | | | | | | | | | | | | | |
| 1 | April 17 | 100 | | 242 | 1,536 | 3,554 | 3,491 ¹ | 3,723 | 813 | 260 | 515 | 74 | | 14,208 |
| 2 | 29 | 100 | | 925 | <u>1,696</u> | 1,720 | 952 | 1,193 | 320 | 73 | 15 | | | 6,894 |
| 3 | May 11 | 100 | | 432 | <u>1,480</u> | 2,044 | 224 | 246 | 150 | 15 | | | | 4,734 |
| 4 | 19 | 100 | 81 | 427 | <u>358</u> | 566 | 65 | 8 | 8 | | | 73 | 70 | 2,071 |
| 5 | 26 | 100 | <u>61</u> | 191 | 89 | 258 | | | | 30 | 241 | 490 | 792 | 2,152 |
| 6 | June 1 | 100 | | 43 | 42 | | | | 119 | 46 | 541 | <u>2,186</u> | 3,338 | 6,315 |
| 7 | 8 | 96 | | | | | | 44 | 479 | 487 | 2,697 | <u>1,387</u> | 1,892 | 6,986 |
| 8 | 13 | 99 | | | | | 24 | 368 | 563 | 1,513 | 4,076 | 1,967 | 2,270 | 10,781 |
| 9 | 18 | 99 | | | | 71 | 535 | 897 | 3,488 | 884 | 3,276 | 1,930 | 1,147 | 12,228 |
| 10 | 23 | 87 | | | 12 | 351 | 641 | 2,038 | 1,817 | 1,155 | 2,177 | 2,678 | 1,176 | 12,045 |
| 11 | 29 | 86 | | | 36 | 408 | 577 | 2,154 | 1,161 | 738 | 2,448 | 1,554 | 270 | 9,346 |
| 12 | July 6 | 99 | | 30 | 116 | 907 | 694 | 1,106 | 1,301 | 1,322 | 1,980 | 797 | 244 | 8,497 |
| 13 | 11 | 97 | | 67 | 100 | 451 | 710 | 840 | 1,311 | 705 | 428 | 172 | 247 | 5,031 |
| 14 | 16 | 100 | | 70 | 354 | 502 | 566 | 964 | 509 | 118 | 211 | 20 | 160 | 3,474 |
| Lexington | | | | | | | | | | | | | | |
| 1 | April 17 | 100 | | 380 | 1,446 | 5,114 | 1,779 | 3,425 | 654 | 278 | 357 | 185 | | 13,618 |
| 2 | 29 | 89 | | 748 | <u>1,036</u> | 1,603 | 498 | 479 | 360 | 13 | | | | 4,737 |
| 3 | May 11 | 100 | | 1,021 | <u>1,294</u> | 1,975 | 194 | 225 | 29 | | | 54 | 120 | 4,912 |
| 4 | 19 | 100 | 71 | 753 | <u>415</u> | 772 | 58 | 12 | | | | 86 | 653 | 2,820 |
| 5 | 26 | 100 | <u>88</u> | 227 | 156 | 258 | | | 11 | 10 | 147 | 645 | 1,431 | 2,973 |
| 6 | June 1 | 98 | 27 | 82 | 23 | 14 | | | 79 | 107 | 776 | <u>1,981</u> | 2,613 | 5,702 |
| 7 | 8 | 96 | | | | | | 102 | 605 | 268 | 2,613 | <u>1,971</u> | 1,984 | 7,543 |
| 8 | 13 | 99 | | 14 | | 58 | 24 | 533 | 900 | 913 | 4,457 | 1,288 | 2,658 | 10,845 |
| 9 | 18 | 97 | | | | 256 | 381 | 1,574 | 2,935 | 750 | 3,664 | 1,821 | 1,598 | 12,979 |
| 10 | 23 | 83 | | | 10 | 277 | 474 | 2,021 | 2,237 | 457 | 2,496 | 1,975 | 606 | 10,553 |
| 11 | 29 | 85 | | | 69 | <u>1,174</u> | 775 | 1,714 | 999 | 654 | 2,927 | 1,271 | 331 | 9,914 |
| 12 | July 6 | 96 | | | 67 | 1,701 | 394 | 1,793 | 1,077 | 1,218 | 1,753 | 438 | 281 | 8,722 |
| 13 | 11 | 95 | | | 122 | 1,453 | 690 | 936 | 1,399 | 457 | 899 | 223 | 307 | 6,486 |
| 14 | 16 | 97 | | | 216 | 1,071 | 229 | 1,190 | 238 | 74 | 58 | | 93 | 3,169 |

¹ Underlines indicate stages of plants present during maximum abundance of moths.

These patterns bring out a number of points which are important to an understanding of corn borer infestations. Marked differences appear between the oviposition of the first and second generations of moths. It is obvious that for both corn hybrids, the bulk of the first-generation eggs go on plants of the early tassel (T-1) and earlier stages, whereas the bulk of the second-generation eggs go on the early tassel (T-1) and later stages. This is largely a matter of availability of plant material at the time of moth flight, as seen in the tendency for those stages present at the time of maximum moth abundance to receive the greatest number of eggs. This tendency is modified only when the plants are young enough to be affected by the discrimination of the corn borer moth in favor of the later growth stages. Thus in plantings 4 and 5, and 12, 13 and 14, the growth stages receiving the most eggs do not strictly coincide with those present when moth abundance was greatest.

To what extent the corn borer moth discriminates in favor of the later stages, without respect to availability, may be seen in a consideration of part of the data. Among plantings numbered 4 to 11, inclusive, plants of all growth stages were present at all times from July 15 to August 4. At any given time each stage was represented by approximately the same number of plants. The eggs deposited during this time were distributed as indicated in Table 4. Comparisons of these figures are misleading in

TABLE 4. DISTRIBUTION OF CORN BORER EGGS ON CORN GROWTH STAGES WHEN ALL STAGES WERE EQUALLY AVAILABLE

| Plant stage | Marcross | Lexington | Total |
|-------------|----------|-----------|--------|
| Sg | 142 | 172 | 314 |
| P-W | 113 | 14 | 127 |
| W-1 | 164 | 268 | 432 |
| W-2 | 1,281 | 2,492 | 3,773 |
| W-3 | 1,757 | 1,569 | 3,326 |
| T-1 | 3,422 | 4,259 | 7,681 |
| T-2 | 4,886 | 4,106 | 8,992 |
| T-3 | 2,226 | 1,261 | 3,487 |
| S-1 | 7,555 | 7,257 | 14,812 |
| S-2 | 4,106 | 4,792 | 8,898 |
| S-3 | 4,715 | 4,994 | 9,709 |

view of the fact that each stage is not equivalent in time and, hence, exposure to oviposition. Thus during the period under consideration the seedling stage averaged two weeks in length, whereas other stages ranged from two to eight days. If, then, the oviposition data indicated above are divided by the average duration (in days) of each corresponding growth stage, and the resulting figures reduced to proportions by considering the oviposition on the seedling stage as unity, indices of discrimination are obtained as shown in Table 5. A very definite trend is obvious, which

confirms observations previously reported (Beard and Turner, 4) that no significant oviposition occurs on plants younger than the mid-whorl stage, at least when older stages are available.

TABLE 5. RELATIVE NUMBER OF EGGS DEPOSITED PER UNIT OF TIME ON EACH GROWTH STAGE OF CORN, WHEN ALL STAGES ARE EQUALLY AVAILABLE

| Plant stage | Marcross | Lexington |
|----------------|----------------|----------------|
| Seedling | 1 | 1 |
| P-W | 3 | .25 |
| W-1 | 4 | 6 |
| W-2 | 15 | 26 |
| W-3 | 65 | 62 |
| T-1 | 78 | 80 |
| T-2 | 110 | 82 |
| T-3 | 77 | 50 |
| S-1 | 141 | 108 |
| S-2 | 96 | 92 |
| S-3 | — ¹ | — ¹ |

¹ Could not be calculated since the duration of the stage was not known.

It may be concluded, then, that marked differences in pattern of infestation relative to growth stages of corn appear between the first and second generations of corn borer. Except for the discrimination by the corn borer moth in ovipositing upon older plants, availability at time of maximum oviposition determines which plant stages receive the most eggs. Though the smaller corn tends to escape, it too may be attacked under the impact of heavy oviposition.

FATE OF EGGS

Observations on the fate of eggs were made only to facilitate the interpretation of borer establishment and survival relative to the growth stages of corn.

Parasitism can easily be noted, and the loss of an egg mass prior to hatching can be determined with reasonable accuracy. A predatorized egg mass, on the other hand, cannot be distinguished with real assurance from one which has hatched unless the eggs are kept under much closer observation than was possible in the present experiment. By actual comparison, egg masses fed upon by coccinellid larvae and adults resembled very closely egg masses which had hatched. In some cases, when only a portion of an egg mass was devoured, or when the predator was observed in the act of feeding or when small punctures in collapsed eggs indicated hemipterous feeding, predation was obvious. For the most part, however, the ragged appearance of an egg mass could not with accuracy be attributed to the feeding of a predator to the exclusion of the chewing by the borer at the time of hatching. For these reasons, only those egg masses actually observed to be fed upon were considered predatorized. This is unfortunate, and in the data below the survival of borers (in terms of hatched

eggs) is minimized¹ on this account, for it is known that during the summer of 1942 predation on corn borer eggs (and newly hatched larvae) was heavy. As before noted, this was principally due to predatory mites, thrips, coccinellid larvae and adults, lace-wing (*Chrysopa* spp.) larvae and the Hemiptera *Nabis fesus* L. and *Orius insidiosus* Say. The latter in particular was unusually abundant, attacking both the eggs and young larvae of the borer.

In a relatively few cases desiccation, mechanical injury and infertility prevented the eggs from hatching. Also, occasionally, unhatched eggs were present at the time the plants were dissected. The proportion of eggs lost did not vary significantly among plantings, nor among different growth stages.

The per cent of total eggs parasitized² in each planting of each hybrid is given in Table 6. Although marked differences appear among plantings, definite trends are somewhat obscured. However, when the parasitism

TABLE 6. EGG PARASITISM, BY PLANTINGS

| Planting number | Date of planting | Per cent of corn borer eggs parasitized | |
|-----------------|------------------|---|-----------|
| | | Marcross | Lexington |
| 1 | April 17 | 5.4 | 4.6 |
| 2 | 29 | 4.2 | 3.2 |
| 3 | May 11 | 2.4 | 2.5 |
| 4 | 19 | 1.0 | 0.7 |
| 5 | 26 | 0.7 | 4.6 |
| 6 | June 1 | 3.3 | 7.2 |
| 7 | 8 | 12.7 | 7.8 |
| 8 | 13 | 11.3 | 13.1 |
| 9 | 18 | 6.2 | 6.4 |
| 10 | 23 | 5.7 | 5.4 |
| 11 | 29 | 8.4 | 8.2 |
| 12 | July 6 | 14.7 | 11.5 |
| 13 | 11 | 7.4 | 11.5 |
| 14 | 16 | 8.8 | 4.2 |

is considered in terms of the total eggs deposited on both hybrids by calendar dates, it becomes clear that any appreciable per cent of parasitism is found only following a build-up of a large host density and that at the time of maximum oviposition by the corn borer moth, when a high rate of parasitism would be most effective, the rate of parasitism is 10 per cent or less. It should be pointed out that the division of the data on oviposition and parasitism into weekly units is arbitrary, in view of the fact that observations on all corn were not made at definite calendar intervals. Although the numbers involved are large enough to smooth out attendant discrepancies, the emphasis should be placed on the trend, rather than absolute values for any given date.

¹ Since mortality is attributed to larval mortality, when it should be attributed to egg mortality.

² Principally, if not entirely, by *Trichogramma pretiosa* Riley.

TABLE 7. EGG PARASITISM, BY DATES

| Date | Total eggs deposited | Number parasitized | Per cent parasitized |
|---------------|----------------------|--------------------|----------------------|
| May 30 | 571 | ... | ... |
| June 6 | 7,426 | 65 | 0.87 |
| 13 | 22,700 | 313 | 1.38 |
| 20 | 17,495 | 1,406 | 8.04 |
| 27 | 4,165 | 504 | 12.10 |
| July 4 | 1,596 | 159 | 9.96 |
| 11 | ... | ... | ... |
| 18 | 1,098 | 26 | 2.37 |
| 25 | 7,881 | 476 | 6.04 |
| Aug. 1 | 41,606 | 2,388 | 5.74 |
| 8 | 36,642 | 3,213 | 8.77 |
| 15 | 28,485 | 2,451 | 8.60 |
| 22 | 29,220 | 2,935 | 10.04 |
| 29 | 8,521 | 1,486 | 17.44 |
| Sept. 5 | 1,341 | 248 | 18.49 |
| 12 | 596 | 48 | 8.05 |
| 19 | 311 | ... | ... |
| 26 | 81 | ... | ... |
| Total | 209,735 | 15,718 | 7.49 |

It is the number of hatched eggs that is important here. For purposes of comparison on survival it is more important to refer the number of borers found to the number of hatched eggs than to the total number of eggs deposited, as the condition of the corn plant has less to do with the hatching of the eggs than with the establishment and development of the larvae. Hence the eggs which were lost, parasitized or for other reasons known not to have hatched were deducted from the total number of eggs in estimating survival.

SURVIVAL OF BORERS

In this study the term survival should not be considered in the usual bionomic sense,¹ but in reference to the number of borers present at the time the corn plants were dissected. The plants were dissected when they reached a given stage of maturity, namely in the latter phases of the late silk stages. Consequently, in some plantings, such as those numbered 6, 7 and 8, most of the borers found were in the first three instars, whereas in some of the other plantings, only fourth and fifth instar larvae and pupae were found. In a strict survival sense, there is quite a difference, for the larvae are subject to various factors of mortality from the time they become established in the plant until the time of pupation. The present treatment does not take this into consideration, and hence the term survival is used advisedly. With the exception of very few cases, the borers did not have time to mature before the plants were dissected.

Pertinent data on borers present at time of plant dissection are given in Table 8. For reference, the number of eggs deposited, expressed in num-

¹ That is, the percentage of full-grown larvae resulting from a given number of hatched eggs.

ber per 10 plants, are given, as are the average number of borers found per 10 plants. Survival is here expressed as the number of borers present at time of plant dissection out of 1,000 presumably hatched eggs.

TABLE 8. OVIPOSITION, BORER POPULATION AND BORER SURVIVAL ON 14 PLANTINGS OF MARCROSS AND LEXINGTON HYBRID CORN

| Planting number | Date of planting | Marcross | | | Lexington | | |
|-----------------|------------------|--------------------|----------------------|-------------------------------|--------------------|----------------------|-------------------------------|
| | | Eggs per 10 plants | Borers per 10 plants | Borers per 1,000 hatched eggs | Eggs per 10 plants | Borers per 10 plants | Borers per 1,000 hatched eggs |
| 1 | April 17 | 1,421 | 301 | 242 | 1,362 | 229 | 191 |
| 2 | 29 | 689 | 107 | 173 | 532 | 75 | 156 |
| 3 | May 11 | 473 | 61 | 145 | 491 | 48 | 140 |
| 4 | 19 | 207 | 18 | 118 | 282 | 21 | 100 |
| 5 | 26 | 215 | 6 | 62 | 297 | 8 | 63 |
| 6 | June 1 | 632 | 41 | 159 | 582 | 44 | 162 |
| 7 | 8 | 728 | 50 | 135 | 786 | 58 | 123 |
| 8 | 13 | 1,089 | 74 | 130 | 1,096 | 64 | 111 |
| 9 | 18 | 1,235 | 187 | 200 | 1,338 | 177 | 182 |
| 10 | 23 | 1,385 | 190 | 182 | 1,271 | 169 | 167 |
| 11 | 29 | 1,087 | 106 | 118 | 1,165 | 137 | 149 |
| 12 | July 6 | 858 | 94 | 144 | 909 | 104 | 150 |
| 13 | 11 | 518 | 48 | 116 | 683 | 50 | 99 |
| 14 | 16 | 347 | 31 | 104 | 327 | 25 | 84 |

An infestation of 30 borers per plant (301 per 10 plants), as was the case in the first planting of Marcross, is unusually high. The figures given include the borers found in the tillers as well as the main stalk but, even so, the borer population was well in excess of that usually encountered. Stalk damage, though conspicuous, was not great enough to prevent proper pollination and development of the ears. The ears, however, were so severely damaged that they would have been unmarketable.

Covering the period of the first-generation borer, each successive planting of corn is less severely attacked by the borer. The smaller number of larvae is not only a direct result of diminished oviposition but, given the same number of hatched eggs in each case, the survival of the borers decreases. Such trends on natural infestations are but confirmations of information derived from studies made on artificial infestations. It has previously been reported (Beard and Turner, 4) that when known numbers of hatching eggs were placed on plants of different growth stages, a gradient of survival, increasing with older growth stages (earlier plantings), was noted, but the survival on plants younger than the late whorl stage was of little importance.

The borer populations in corn grown during the period of the second generation tend to follow the oviposition trend, but the survival rates do not vary with such regularity as in the first generation. No definite trend appears, but a more or less uniformly high level of survival is apparent. The drop in survival rate at the very end of the season can probably be attributed to the fact that this corn was very late for such hybrids as Marcross and Lexington, and conditions late in the season were abnormal for

the development of the corn and, possibly as a consequence, abnormal for the borer.

The obvious conclusion to be drawn, however, is the difference between the two generations in the matter of survival. With the first generation, a decreasing survival is noted with successive plantings, paralleling the shift in oviposition toward the younger growth stages. With the second generation, on the other hand, the lack of such a tendency can be attributed to the distribution of corn borer eggs chiefly on growth stages of the plant more favorable for the establishment and survival of the larvae. The pattern of infestation by the first generation is not repeated by the second generation insofar as the condition of the host plant is concerned.

In view of the fact that four of the plantings were infested by both generations of borers, a segregation of the composite survival data should be made. This is possible because at the time of dissection those larvae in the fourth instar, fifth instar and pupal stages could be assigned to the first generation, whereas the younger larvae were certainly offspring of the second-generation moths. There was some evidence for a slight overlap between generations, but for the most part the break between the two generations was sufficiently definite to be recognizable.

TABLE 9. NUMBER OF BORERS PRESENT AT THE TIME OF PLANT DISSECTION PER 1,000 PRESUMABLY HATCHED EGGS

| Planting number | Date of planting | First generation | | Second generation | |
|-----------------|------------------|------------------|-----------|-------------------|-----------|
| | | Marcross | Lexington | Marcross | Lexington |
| 1 | April 17 | 242 | 191 | ... | ... |
| 2 | 29 | 173 | 156 | ... | ... |
| 3 | May 11 | 148 | 112 | 0 | 0 |
| 4 | 19 | 121 | 94 | 79 | 244 |
| 5 | 26 | 90 | 58 | 30 | 68 |
| 6 | June 1 | 71 | 41 | 162 | 169 |
| 7 | 8 | ... | ... | 135 | 123 |
| 8 | 13 | ... | ... | 130 | 111 |
| 9 | 18 | ... | ... | 200 | 182 |
| 10 | 23 | ... | ... | 182 | 167 |
| 11 | 29 | ... | ... | 118 | 149 |
| 12 | July 6 | ... | ... | 144 | 150 |
| 13 | 11 | ... | ... | 116 | 99 |
| 14 | 16 | ... | ... | 104 | 84 |

The survival gradient for the first generation is even more apparent here than in the composite data, although it should be pointed out that oviposition of the first generation on plantings numbered 5 and 6 and of the second generation on plantings 3, 4 and 5 numbered less than 1,000 eggs each, so the averages as given represent an extension of the data and should be interpreted accordingly. Thus for planting number 3, hatched egg masses of the second generation numbered only four on Marcross and eight on Lexington (104 and 141 eggs respectively), and it is not surprising that no larvae were recovered. On the other hand, the observance of larvae from a few newly hatched egg masses could account for the high

survival figure for the second-generation larvae on planting number 4 of Lexington. Where the oviposition was sufficiently great, however, there is no trend of second-generation borer survival that can be correlated with the stages of plant growth at time of infestation.

In view of the increased survival attending infestation of older growth stages, it is contrary to expectation that the survival in most of the second-generation period, which reflects the infestation of tassel and silking stages, is less than that in planting number 1, which was infested principally in the whorl and tassel stages. Unfortunately, it is not known that the silking stages are more favorable for establishment and survival of the borer, although they are generally assumed to be so. The work reported by Beard (4), previously mentioned, in which hatching eggs were placed on plants of different stages, did not include silking stages, and other workers have not approached the problem in this way. This reduced survival may possibly be due to a factor only indirectly associated with the growth stage of corn, and that is predation by *Orius insidiosus* Say.

It was mentioned above that predation by this hemipteran was unusually heavy during the 1942 season, but it could not be evaluated. Barber (1) reported that *O. insidiosus*, particularly in its nymphal stages, becomes most plentiful on corn possessing moist silk. This would correspond to the early and mid-silking growth stages. Since both adults and nymphs prey upon the eggs of the corn borer, as well as on the young larvae, their effect in reducing the survival could be considerable. Dr. C. H. Batchelder (personal communication) from studies on the corn ear worm, also made in New Haven County, believes that the abundance of *O. insidiosus* in 1942 could well account for a decreased survival of the corn borer, particularly in view of the succession of plantings as was made in the present study which would provide for the continuous presence of moist silk and a consequent build-up of the population of *O. insidiosus*.

These data point to the general conclusion that, whereas the borer population tends to follow the intensity of oviposition, this tendency is modified by differential survival rates which are largely governed by the stage of corn plant growth at the time of oviposition. Differences in survival rates between the two generations of the insect can thus be explained.

CORN BORER INJURY TO EARS

Turner (4) noted that with larger infestations of the corn borer, a greater proportion of the ears became infested. This tendency can be seen readily in data obtained in the current study (Table 10). The infestation of the first four plantings, can be attributed principally to borers of the first generation, and the infestation of plantings 6 to 14, inclusive, can be attributed for the most part to borers of the second generation. Because of the small numbers of borers, of both generations, the data for planting number 5 are not considered here. If each of the four sets of data (two generations in each of the two hybrids) is considered separately, a curve may be fitted

to describe the observations. When the number of borers per 10 plants is transformed to logarithms, and the per cent of ears infested is transformed

TABLE 10. PER CENT OF EARS INFESTED RELATIVE TO BORER POPULATION

| Planting number | Date of planting | Marcross | | Lexington | |
|-----------------|------------------|-----------------------------|------------------------|-----------------------------|-------------------|
| | | Number borers per 10 plants | Per cent infested ears | Number borers per 10 plants | Per cent infested |
| 1 | April 17 | 301 | 98 | 229 | 90 |
| 2 | 29 | 107 | 85 | 75 | 66 |
| 3 | May 11 | 61 | 67 | 48 | 41 |
| 4 | 19 | 18 | 23 | 21 | 28 |
| 5 | 26 | 6 | 13 | 8 | 5 |
| 6 | June 1 | 41 | 19 | 44 | 32 |
| 7 | 8 | 50 | 32 | 58 | 33 |
| 8 | 13 | 74 | 51 | 64 | 45 |
| 9 | 18 | 187 | 82 | 177 | 71 |
| 10 | 23 | 190 | 87 | 169 | 82 |
| 11 | 29 | 106 | 71 | 137 | 79 |
| 12 | July 6 | 94 | 64 | 104 | 62 |
| 13 | 11 | 48 | 42 | 50 | 37 |
| 14 | 16 | 31 | 36 | 25 | 35 |

to probability units (probits), a rectilinear relationship pertains in each case. The slopes of the respective lines as calculated are as follows:

First generation on Marcross $b = 2.29$

Second generation on Marcross $b = 2.23$

First generation on Lexington $b = 1.86$

Second generation on Lexington $b = 1.75$

The position of each line is determined by the mean probit of the per cent of ears infested and the mean logarithm of the observed population densities. If the lines depart significantly from parallelism, any differences would have to be referred to each level of infestation. On the other hand, if the data could be fitted by lines which were parallel, they would be equidistant at all levels of infestation, and the difference in borer populations required to produce the same ear infestation could be expressed as a simple ratio or on a percentage basis. The Marcross data can certainly be expressed as parallel lines, using the combined slope of both generations, which is calculated to be $b = 2.27$.

These data are illustrated in Figure 1, in which the per cent of ears infested is plotted on a probit scale, and the number of borers per 10 plants is plotted on a logarithmic scale. It is obvious that the two generations are different and that a lower borer population of the first generation than of the second generation is required to effect the same percentage of ear infestation. Since the individual regression lines are parallel well within the limits of error, it can be stated that to cause the same percentage of ear infestation, approximately 58 per cent of the number of borers in the second generation will be required by the first generation. For example, 200 borers per 10 plants of the first generation or about 345 borers of the second generation will cause 95 per cent of the ears to become infested.

Similarly, the Lexington data can be expressed as parallel lines, using the combined slope ($b=1.80$) of the data for both generations, and it may be stated that approximately 70 per cent of the number of borers in the

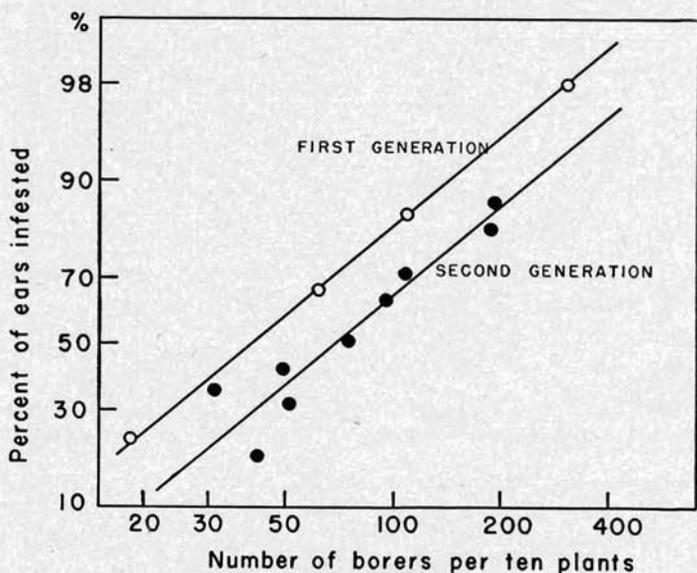


FIGURE 1. Relation of per cent of ears infested (on probit scale) to population density of borers (on logarithmic scale) on Marcross corn. Calculation of combined slope based upon probits of per cent of ears infested and logarithms of the number of borers per 10 plants.

second generation will be required by the first generation to cause the same percentage of ear infestation. In other words, there is less difference between the two generations in Lexington than in Marcross.

Although statistical analysis demonstrates that all four individual regression lines can be expressed as parallel within the limits of error, using a combined slope of $b=2.05$, there is enough apparent difference (see Figure 2) between the Marcross data and the Lexington data to suggest that there may be a real difference between the two hybrids in the ear infestations as related to borer population, and that comparisons might better be made at each level of infestation. It seems clear, however, that in the first generation a consistently lower level of population will be required in Marcross than in Lexington to cause the same ear infestation. In the second generation, on the other hand, the differences are probably not significant, unless perhaps at the higher levels of infestation.

This discrepancy between the first and second generations can be seen in the data published by Turner (*op. cit.*).

Insofar as the data in Table 10 are applicable, corn with growth habits similar to the hybrids used here will produce more borer-free ears when

planted during the last two weeks in May and the first two weeks in June. The infested ears of plantings 6, 7 and 8 were not seriously injured since

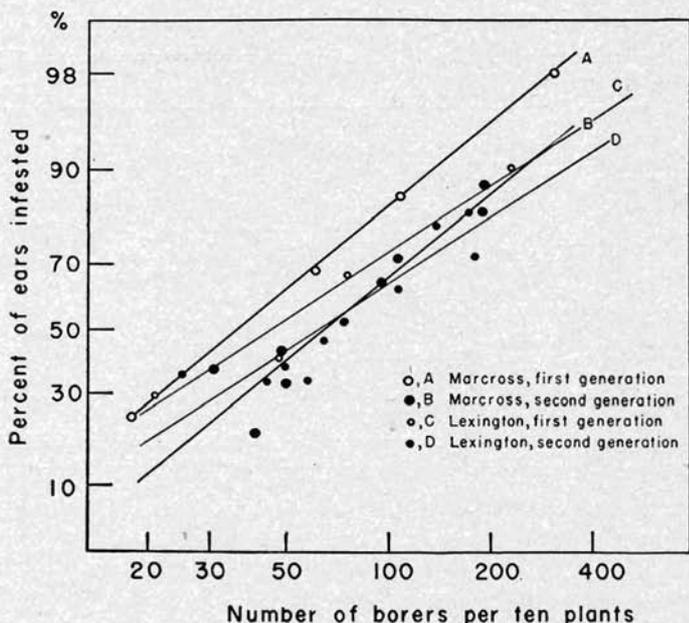


FIGURE 2. Relation of per cent of ears infested (on probit scale) to population density of borers (on logarithmic scale), on Marcross and Lexington hybrids. Calculation of combined slopes based upon probits of per cent of ears infested and logarithms of the number of borers per 10 plants.

the small larvae present were chiefly in the silk and outer husk, and would normally pass unnoticed and be removed when the ear was husked.

It was previously reported (Beard, 4) that the developing tassel is the portion of the plant most frequented by the borer until the ear shoots develop, and then the developing ears receive the larger proportion of borers. When the tassel sheds pollen and begins to dry, those borers resident there migrate to secondarily infest other parts of the plant, notably the stalk. If these conditions are applicable to field populations, those plantings infested when in growth stages showing developing ears (T-1 and subsequent stages) would show a larger proportion of the borers resident in the ears. The following table (Table 11) shows a tendency conforming to this conclusion for, although the correlation is not rigid, a decreasing percentage of borers was resident in ears of the first four plantings, and a generally higher percentage of borers was resident in ears of subsequent plantings of corn.

If the Marcross data in Table 11 (disregarding those of planting number 5) are plotted on an arithmetic grid along with the population trend

(Figure 3), it is clear that the proportion of total borers present in ears is not related to the population density, except indirectly in the first generation. Instead, the relationship is with time and, by inference, with

TABLE 11. PER CENT OF TOTAL BORERS PRESENT IN THE EARS

| Planting number | Date of planting | Marcross | Lexington |
|-----------------|------------------|----------|-----------|
| 1 | April 17 | 22.5 | 19.4 |
| 2 | 29 | 17.3 | 14.1 |
| 3 | May 11 | 11.9 | 10.6 |
| 4 | 19 | 11.2 | 12.1 |
| 5 | 26 | 47.6 | 11.8 |
| 6 | June 1 | 30.3 | 34.0 |
| 7 | 8 | 29.4 | 29.5 |
| 8 | 13 | 26.4 | 25.3 |
| 9 | 18 | 23.1 | 20.4 |
| 10 | 23 | 25.7 | 22.2 |
| 11 | 29 | 21.1 | 20.4 |
| 12 | July 6 | 20.2 | 16.0 |
| 13 | 11 | 17.4 | 15.0 |
| 14 | 16 | 19.7 | 26.9 |

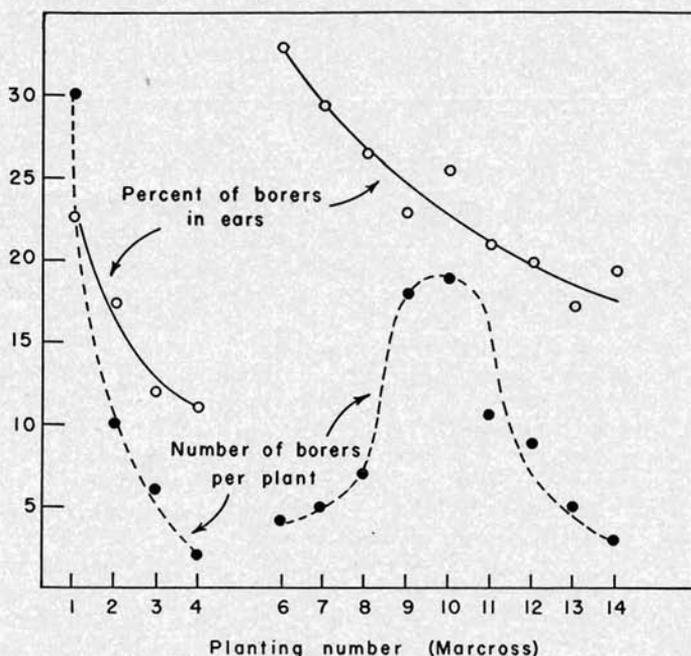


FIGURE 3. Chart showing corn borer population trend (number of borers per plant at time of dissection) and trend of the percentage of total borers resident in the ears of Marcross corn.

growth stage. When viewed in consideration of Table 3, it appears that the younger the corn at the time of oviposition, the lower is the percentage of borers resident in the ears.

The above data demonstrate that in corn attacked by the second-generation borer there are fewer ears infested, but the infested ears contain more borers than in corn attacked by the first generation. The greater number of borers present in ears seems well explained by the fact that the primary infestation is principally in the ears and ear shoots rather than in the tassel. The reason for the fewer ears becoming infested by the second generation is not apparent. It is possible that in the first generation the greater number of ears being infested is associated with the secondary infestation attending the migration of borers from the tassel in the plant stages subsequent to T-3.

Patch et al. (11) stated that the stage of plant development at the time of borer infestation is an important factor in the reduction in yield of field corn, and that plants infested early in their development suffered greater reduction due to the longer duration of borer feeding and the larger size of the borers during the period of ear production. The problem of reduced yield in field corn is somewhat different from the problem in sweet corn, where the interest is principally in the production of borer-free ears.

COMPARISONS BETWEEN INFESTATIONS ON MARCROSS AND LEXINGTON HYBRIDS

Oviposition

Because of the preference of corn borer moths to oviposit upon taller corn, as well as upon corn in older growth stages, it was hoped that a differentiation of the two conditions might be achieved by comparing oviposition on the hybrid Marcross with that on Lexington, which was expected to parallel Marcross in development, but to grow taller. The corn actually grown, however, showed no striking differences in height between the two hybrids. Time did not permit the taking of many measurements during the middle of the season, but measurements on corn in the whorl and tassel growth stages indicated no statistically significant differences between the two hybrids. Measurements taken on three plantings of corn at the time the plants were dissected (late silk-roasting ear stage) indicated a tendency for Lexington to be taller, but the difference is not great, as shown in the following table:

TABLE 12. AVERAGE HEIGHT OF CORN AT THE TIME OF DISSECTION

| Date of planting | Marcross | Lexington |
|------------------|----------|-----------|
| June 29 | 55.9 in. | 58.5 in. |
| July 6 | 57.7 | 58.4 |
| July 11 | 54.0 | 56.7 |

Likewise no marked differences in leaf area exist between the two hybrids as judged by the number of tillers produced by each. The average number of tillers produced per 10 plants of each hybrid in each of the last eight plantings is tabulated in Table 13.

TABLE 13. AVERAGE NUMBER OF TILLERS PER 10 PLANTS

| Date of planting | Marcross | Lexington |
|------------------|----------|-----------|
| June 1 | 22 | 23 |
| 8 | 23 | 23 |
| 13 | 23 | 25 |
| 18 | 25 | 23 |
| 23 | 25 | 25 |
| 29 | 22 | 23 |
| July 6 | 19 | 20 |
| 11 | 18 | 21 |
| 16 | 10 | 13 |

Just as these differences in plant size are slight, the increased oviposition on Lexington over Marcross is very slight, and it may be concluded that either the differences are meaningless or the discrimination on the part of the moths to oviposit on taller, more leafy plants is extremely acute. Statistical analysis indicates that on only one planting, that made on May 29, was the difference in oviposition between the two hybrids great enough to exceed the 5 per cent level of significance (t-test). There is no obvious reason why this one planting should show significant differences, and this significance is minimized by the fact that fewer eggs were deposited on this planting than on any other.

Borer Population

The seasonal trends of the borer populations in the two hybrids parallel each other. In seven of the plantings the borer population is greater in Marcross than in Lexington, and in the remaining seven the reverse is true. To a large extent the differences can be attributed to the differences in numbers of eggs present, but differential survival rates also appear.

Survival of Borers

Reference to Table 9 shows that the survival of corn borers in Lexington is less than that in Marcross in every planting attacked by the first generation. The survival of second-generation borers, however, is not so sharply divided. In five of the plantings survival was greater in Lexington and in six of the plantings survival was greater in Marcross. Subjected to statistical analysis, however, the data show that only the differences between the two hybrids in planting number 1 and planting number 3 are significant, and the others are only suggestive, or non-significant statistically. The trend for the first generation seems too consistent to be due to mere coincidence.

In view of the differences in susceptibility to the borer by corn in different growth stages, an analysis of the development of the two hybrids is essential. If the silking date alone is considered, it was found that in six of the plantings, 50 per cent or more of the plants in a given planting of Lexington were in silk on the same day as a comparable number of Marcross plants. In the other eight plantings, Lexington was one day behind Mar-

cross. Considering the maturity of the two hybrids, comparisons cannot be made because, for the most part, plant dissections were made prior to the roasting ear stage. Lexington was probably from zero to four days behind Marcross, although in Figure 4, which illustrates four representative ears of each hybrid picked on the same day, no appreciable difference in maturity is evident, with the exception of the fourth ear of Lexington, which is definitely immature. As before mentioned, however, dates of silking and

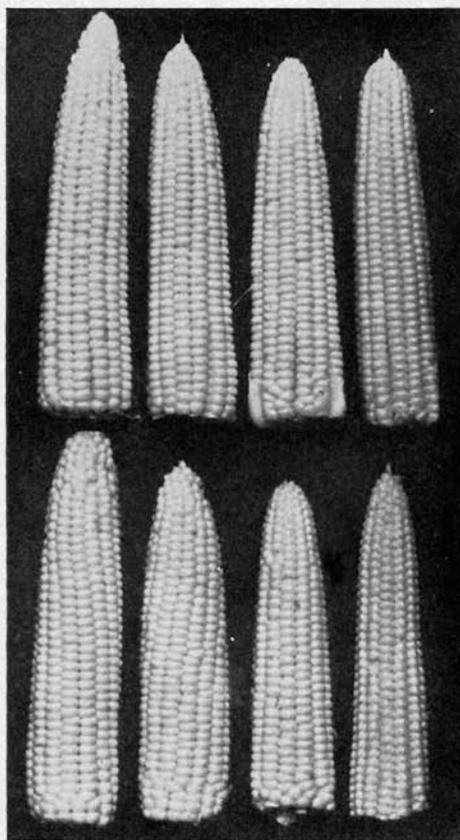


FIGURE 4. Illustration of ears of Marcross (above) and of Lexington (below) picked on August 4 from corn planted June 1.

maturity are inadequate to compare the growth of the two hybrids, and so a comparison of all growth stages yields the following table, in which are given the number of days difference between Marcross and Lexington in the reaching of each plant stage by 50 per cent or more of the plants in each planting.



FIGURE 5. A. View looking down into whorl of Lexington plant in late W-2 stage. Tassel still enclosed by rolled leaves. B. Marcross plant of same age as Lexington plant in A, but tip of tassel can be seen. W-3 stage. C. Row of Marcross corn in W-2 stage. D. Row of Marcross corn in W-3 stage.

It is apparent that no difference in growth of the two hybrids occurs through the mid-whorl stage. In reaching the last whorl stage, however, Lexington is delayed by from one to three days in every planting. In no

TABLE 14. NUMBER OF DAYS DIFFERENCE IN DEVELOPMENT BETWEEN MARCROSS AND LEXINGTON AT EACH PLANT STAGE¹ + LEXINGTON AHEAD; - LEXINGTON DELAYED

| Planting | Sg | P W | W 1 | W 2 | W 3 | T 1 | T 2 | T 3 | S 1 | S 2 | S 3 |
|----------|----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| 1 | 0 | 0 | 0 | -1 | -2 | -1 | -1 | -2 | -1 | -3 | 0 |
| 2 | 0 | -1 | -1 | 0 | -3 | -2 | -3 | -2 | -1 | -2 | -1 |
| 3 | +1 | 0 | 0 | 0 | -3 | -3 | -2 | -1 | -1 | -4 | -3 |
| 4 | 0 | 0 | +1 | +1 | -1 | -1 | 0 | -1 | 0 | -1 | -2 |
| 5 | -1 | +1 | +1 | +1 | -1 | 0 | 0 | -1 | 0 | -1 | -1 |
| 6 | 0 | 0 | 0 | +1 | -2 | -1 | 0 | -1 | -1 | -1 | -1 |
| 7 | 0 | 0 | +2 | 0 | -2 | -1 | -1 | 0 | -1 | -1 | -1 |
| 8 | 0 | 0 | +1 | 0 | -2 | -2 | -2 | -1 | -1 | 0 | -1 |
| 9 | 0 | 0 | -1 | -1 | -2 | -1 | -1 | -1 | 0 | 0 | -1 |
| 10 | 0 | 0 | -1 | 0 | -1 | -1 | -4 | -1 | -1 | -2 | -2 |
| 11 | 0 | 0 | 0 | -1 | -3 | -3 | -3 | -2 | 0 | 0 | -1 |
| 12 | 0 | 0 | 0 | 0 | -2 | -1 | 0 | -1 | 0 | -2 | 0 |
| 13 | 0 | 0 | 0 | 0 | -2 | -2 | -3 | -2 | 0 | 0 | -2 |
| 14 | +1 | 0 | -1 | 0 | -2 | -1 | -1 | -1 | -1 | -1 | 0 |

¹ Based on date each stage reached by 50 per cent or more of the plants in a given planting.

other growth stage is the delay so consistent, although Lexington is never ahead of Marcross in any subsequent stage. This delay is not maintained uniformly for, as before mentioned, the silking date may be considered to be the same or to differ by no more than one day.

Characteristic of the delay in reaching the late whorl stage by Lexington is the reluctance of the terminal leaf to unroll and expose the developing tassel (cf. A, B, Figure 5). This tendency is one of those which characterizes a resistant corn. This is particularly marked in the resistant inbred Illinois R 4, and in hybrids with R 4 as one parent. According to Patch (8), the hybrid R 4 x Hy may have its tassel enclosed by a roll of leaves for 7.6 days longer than a comparable, less resistant hybrid (A x Tr). Patch concluded, however, that this tendency was not a real delay in the corn development since the dates of pollen shedding and silking were essentially the same for the two hybrids. A delay of 7.6 days could be highly significant if the bulk of the infestation occurred at this time for, as before mentioned, 60 per cent of the oviposition may occur within five days, and it is at the late whorl stage that larval survival becomes increasingly significant.

It is obvious that a delay at this point would favor resistance to the corn borer, provided the delay were real, and not just apparent. What constituted a real delay in terms of corn borer survival will not be known until the fundamental factors affecting corn borer survival are understood. These would seem to include nutritional factors. Although Bottger (5, 6) has approached the problem of nutritional requirements of the corn borer, the chemical changes in the intact plant associated with plant development

are largely unknown. Aside from vegetative growth, the principal change occurring in the late whorl stage is the appearance of the tassel which has been developing within the whorl of leaves. The stage of pollen formation within the anthers should indicate whether there is any actual delay in development which is reflected by the enclosure of the tassel by leaves. Consequently, cytological examination¹ was made to determine the stages of pollen formation in plants of the late whorl stage and the beginning and latter phases of the early tassel stage. The anthers on the terminal branch of the tassel develop before those on lateral branches, so samples of both were taken from representative plants of each hybrid. The stages of pollen formation² as found are tabulated in Table 15. These observations demon-

TABLE 15. STAGES OF POLLEN FORMATION IN LATE WHORL AND EARLY TASSEL STAGES

| Plant stage | Marcross | | Lexington | |
|-------------------------------|--|--|---|------------------------|
| | Nuclear stage | Starch | Nuclear stage | Starch |
| W-3 Lateral anther | Microspore 1 nucleus | Not evident | Microsporocyte Diakinesis of meiosis | None |
| Terminal anther | Microspore 2 nuclei; shortly after division I | Not evident | Microspore 1 nucleus | Not evident |
| T-1 (Early) Lateral anther | Microspore 2 nuclei | Little, just starting to develop | Microspore 1 nucleus | Very little, if any |
| Terminal anther | Microspore 2 nuclei | Little | Microspore 1-2 nuclei | Little |
| T-1 (Late) Terminal anther | Microspore 2 nuclei | Little | Microspore 2-3 nuclei; stages of division II | Well filled |

strate that Lexington does actually lag behind Marcross in pollen formation until the early tassel stage, when it not only catches up with Marcross but may be further developed in the latter phases of this stage. To what extent pollen formation is associated with corn borer survival is not known, but it is true that in the later whorl stages and the early tassel stages the developing tassel is the plant structure most favorable to the borer, and it is at this time that the rate of larval survival is markedly increased.

A lag in development at this time would result in a lower survival of the corn borer only if the infestation occurred on the plant stages centering around the mid-whorl stage, for the delayed appearance of the tassel implies

¹ Made by Dr. Frances Clark Beard.

² In the formation of the pollen grain the microsporocyte undergoes two meiotic divisions to form four microspores, each of which undergoes division into a vegetative cell and a generative cell. The latter cell further divides into two sperm cells. A pollen grain thus contains a vegetative cell and two sperm cells. Storage of starch begins in the microspore stages.

a longer time spent in the mid-whorl stage. This condition is met with only in the early plantings attacked by the first generation of the corn borer. In fact, as mentioned above, it is only in plantings numbered 1 and 3 that the differences in survival of borers in the two hybrids are statistically significant. On theoretical grounds, planting number 2 should also show significant differences, but no explanation can be given why it does not. Because in the tassel and silking stages establishment and survival of the corn borer is at a much higher level than in the early stages of plant development, infestations on the later stages of plant growth should result in little or no differences in survival between the two hybrids. Here is found an explanation for the absence of a tendency towards lower survival in Lexington than Marcross in those plantings attacked by the second-generation corn borer.

If, then, these two hybrids were observed during the first generation alone, Lexington would be considered somewhat resistant to the borer as compared with Marcross. And, since this resistance can be correlated with some degree of assurance with the pattern of infestation relative to the growth stages of the corn, a parallel is observed between this resistance and the gradient of borer survival with later growth stages. This is emphasized when the survival rates (borers per 1,000 eggs) of the first generation are arranged in a descending numerical order,

| Planting number | Marcross | |
|--------------------|----------|-----------|
| | | Lexington |
| 1 | 242 | |
| 1 | | 191 |
| 2 | 173 | |
| 2 | | 156 |
| 3 | 148 | |
| 4 | 121 | |
| 3 | | 112 |
| 4 | | 94 |
| 5 | 90 | |
| 5 | | 58 |
| 6 | 71 | |
| 6 | | 41 |

wherein Lexington behaves, insofar as supporting the borer is concerned, as corn planted at a later date than its corresponding planting of Marcross, or as a hybrid which matures more slowly than was actually the case.

Although admittedly only two hybrids are compared, and the differences and similarities are not entirely discrete, these data suggest that the resistance of one hybrid as compared with another and the resistance of a young growth stage compared with an older growth stage are but two expressions of the same fundamental factor or factors responsible for a lower rate of borer survival. In other words, there may not be anything chemical or physical inherent in one hybrid or inbred, and not in another, which is responsible for decreased corn borer survival. Rather, due to differential growth rates during those plant stages in which the corn becomes increasingly able to support the borer and at a time when oviposition is heavy, one strain of corn is less heavily infested and is considered "resistant". Indeed, Flint et al. (7) stated that "in a strain of corn in which resistance to attack by the borer is to be developed, three protective characteristics are con-

sidered desirable: 1. Delayed emergence of the tassel. 2. Slow, early development of the plant and rapid late development 3. Relatively late maturity." The relationship between differential growth and the time of oviposition has not been sufficiently emphasized. Recently, however, Patch (10) has reported that differences in borer survival between the resistant field corn hybrid, Ill. Hy X R4, and the susceptible hybrid, Ill. A X Ind. Tr, diminished as the plants approached the pollen shedding stage at the time of the borer hatching.

If the data presented above have any general applicability, a very important implication arises. If, as appears to be the case, the resistance of hybrids and inbreds of field corn depends upon a retardation of growth during less susceptible stages of growth at a time when corn borer attack is at its peak, the resistance will not be apparent if the bulk of the infestation occurs on the older, more susceptible growth stages. Thus resistant strains of field corn, when planted relatively late in areas harboring the bivoltine strain of corn borer, may be as susceptible to borer attack as the less resistant strains, simply because the second-generation borer is well supported by susceptible growth stages of the otherwise "resistant" hybrid or inbred. This conclusion has some observational support for, although definite data were not recorded, Dr. D. F. Jones, geneticist at the Connecticut Experiment Station, noted that among field corn inbreds some of the so-called resistant strains, including the highly resistant Illinois R.4 and Iowa L 317 (Patch; 9), were fully as susceptible as other inbreds attacked by the second-generation borer in 1942. This is very significant in view of the fact that in the recent major spread of the European corn borer throughout the extensive Corn Belt the bivoltine strain of borer is involved.

SUMMARY AND CONCLUSIONS

In order to study the pattern of corn borer infestation relative to growth stages of sweet corn, 14 plantings of Marcross and Lexington hybrids were observed for borer oviposition and survival. The initial planting was most severely attacked, and successive plantings attacked by the first generation were less severely infested. Subsequent plantings became increasingly infested by the second-generation borer until the ninth planting, and thereafter the infestation declined.

Except for growth stages too small to favor oviposition, availability of growth stages at time of maximum oviposition determines which stages receive the most eggs. The tendency for oviposition to be delayed on some plantings until the plants reach a favorable size is responsible for shifts in the oviposition trend as related to time. The total number of eggs deposited by the second-generation corn borer greatly exceeded that of the first generation, although on a per plant basis, the first planting of the season received the greatest number of eggs. Because of the presence of the second-generation moths over a much longer period of time than the first generation, much more corn was available to attack by the second generation. The bulk of the first-generation eggs was deposited on corn in the early tassel stage and younger, whereas most of the second-generation eggs were deposited on corn in the early tassel and later stages. The pattern of infestation by the first-generation borer, relative to corn growth

stage, was not repeated in any planting attacked by the second-generation borer.

The fate of eggs was considered only as an aid in estimating survival. The tendency for the borer population to parallel the intensity of oviposition was modified by differential survival rates, which seem to be governed principally by the growth stage of the plant at the time of borer establishment. At the same level of borer population, corn attacked by the second generation has fewer infested ears than that attacked by the first generation, but the ears which are infested contain more borers. The percentage of infested ears is related to the total borer population, whereas the percentage of borers resident in the ears is related to the growth stage of corn at the time of infestation.

In growth habit, Lexington differs from Marcross chiefly in a tendency for increased height and a delay in reaching the late whorl stage. Oviposition on the two hybrids did not differ significantly, but survival of the first-generation borer was consistently lower in Lexington than in Marcross. Survival of the second-generation borer did not differ significantly between the hybrids. The difference between the two generations in regard to survival is explained on the basis of differential growth rates at growth stages critical to borer establishment. It is suggested that the resistance of corn at different growth stages and the resistance of one strain of corn as compared with another are but two expressions of the same fundamental phenomenon, and that a "resistant" strain may owe its resistance to a differential growth rate at a particular time relative to the pattern of infestation. If the pattern is different, the resistance may be lost.

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