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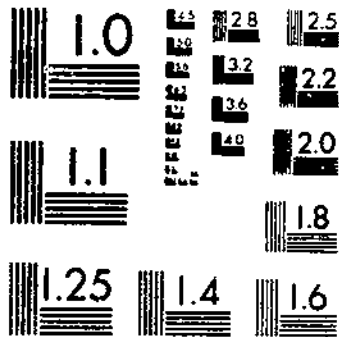
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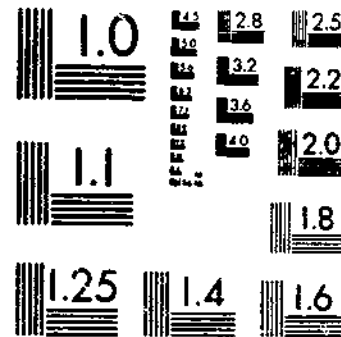
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UNITED STATES
DEPARTMENT OF AGRICULTURE
WASHINGTON, D. C.

European Corn Borer Location on the Corn Plant as Related to Insecticidal Control¹

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INTRODUCTION

The development of an effective treatment for control of the European corn borer (*Pyrausta nubilalis* (Hbn.)) is contingent upon placement of insecticides where this insect finds shelter on the corn plant. The field studies reported in this bulletin were designed to determine the sequence of biological changes that take place in the plant; what instar, when, and on what parts of the plant establishment and survival of the borer take place; and the procedures indicated by these events for the successful application of insecticides. The studies were conducted near New Haven, Conn., in commercial fields of sweet corn infested in June by first-generation corn borer larvae, and data relative to infestation are presented with special reference to plant-growth stages and varietal growth habits.

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REVIEW OF LITERATURE

The location of European corn borer larvae on infested corn plants has been described by several investigators, but the relation of growth changes in the plant to larval movement has received little attention. Vinal's (13)³ original observations included tassel infestation by first-instar larvae and their subsequent migration to the tassel stem, or peduncle. Caffrey and Wortley (5) described the feeding habits of young larvae infesting whorl leaf blades, the tassel, the stalk, and the ear. In discussing the probable causes of variations in population, Huber, Neiswander, and Salter (9, pp. 141-142) reviewed the development of plant infestation by the univoltine strain of the borer, noting the larval reactions to environmental changes and the resulting migrations. From data recorded at weekly intervals, Huber et al. drew the following general conclusion:

It is obvious that during the first part of the season the big majority of larvae are found behind the leaf sheath; a few weeks later the majority are found in the tassel or the crown of the plant. Upon the emergence of the tassel from the leaf roll or crown of the plant the larvae enter the stalk proper.

Schlosberg and Baker (12) reported a high degree of correlation between the larval population and the length of the period from infestation to silking. Houser and Huber (8) stated that the nutrition factor greatly influences the rate of larval establishment and survival, and they suggested that each instar may have particular food requirements.

Beard conducted a series of biological experiments that closely parallel the studies reported here. In his initial experiments (2), dealing with survival of first-generation larvae on the Connecticut Agricultural Experiment Station Farm at Mount Carmel, most of the early hatched borers infesting the plants became established in the tassel. In later studies by Beard and Turner (4) the experiments were designed to test the establishment and survival of borers of the second generation (August) by means of manual infestation of late-planted Marcross sweet corn. Dissections were made on three different dates during the periods of plant growth. From this test Beard concluded: "Because of the escape from oviposition and the inability to support the larvae, plants smaller than [those of] the late-whorl stage at the time of moth flight are not likely to be severely infested." Beard apparently referred here to the obvious conclusions to be drawn from his own experiments, which were restricted to midsummer Marcross corn subject to high temperatures and grown during the period of infestation by the second-generation corn borer. On the other hand, in reporting experiments with early planted Marcross grown during the first-generation infestation, Turner (See Beard and Turner, 4, pp. 567-591) showed the necessity of applying a spray during the late-whorl stage in a standard, four-treatment insecticide schedule. From studies of the relation of growth stages to infestation rates in Lexington and Marcross sweet corn, Beard (3) concluded that the

³ Italic numbers in parentheses refer to Literature Cited, p. 20.

lower survival in early planted Lexington could be attributed to differences in rates of growth in early green-tassel and mid-green-tassel stages, which prevailed at the time of maximum borer establishment. Beard also attributed differences in survival rates between first- and second-generation infestations to differential growth rates characteristic of stages critical to borer establishment.

METHODS OF PROCEDURE

The distribution of larvae in the shelter areas of the plant was determined by dissecting five 20-plant samples at each growth stage in each of the strains studied, including the commonly grown hybrid derivatives of Spanish Gold, Whipple's Yellow, Golden Early Market, and Golden Bantam. The location and instar of the borer were recorded, together with data on prevailing plant conditions. Observation of larval habits was confined to early and early midseason strains of corn, which are likely to be infested by the first generation of the borer. In most cases the hybrid Marcross C6.13 has been used as an example, because it is one of the most widely known of the early market types of sweet corn. This hybrid and others mentioned in this report are ably described by Enzie (6, 7).

NOMENCLATURE AND DEFINITIONS

In order to correlate the occurrence of larvae and the prevalence of shelter areas with definite stages of corn-plant development, it was necessary to devise a nomenclature of the growth stages of the plant. Some progress had been made in this direction by Batchelder, Turner, and Questel (1), for convenience in describing corn plants during experiments with insecticides in 1935-36. The classification of growth stages was first worked out for hybrids derived from Golden Early Market, was developed further with Golden Cross Bantam, and was later extended to various strains of sweet and field corn. Further designation of growth periods within the subdivisions is considered feasible for special purposes, but in most corn borer investigations the general classification has been found adequate in describing the stages of plant growth during which the larvae generally establish themselves and develop.

The characters found most useful in distinguishing the growth stages of the corn plant with reference to corn borer infestation are itemized in tables 1 and 2. Nine of the stages are illustrated in figures 1-3.

The terms used for convenience in designating these stages are as follows: Prewhorl, early whorl, midwhorl, late-whorl, early green-tassel, mid-green-tassel, late-green-tassel, early silk, mid-silk, late-silk, prime-milk or roasting-ear, and mature. To this list Beard (see Beard and Turner, 4) added a seedling stage, characterized by the presence of a single primary leaf blade.

TABLE 1.—Characteristics of the whorl and green-tassel growth stages of the corn plant (based on examination of 100 plants)

Growth stage	Primary leaf blades ¹	Leaf blades visible ²	Rolled leaf blades composing whorl ³	Tassel appearance	Ear shoots	Anthers	Length of husk laminae
		<i>Number</i>	<i>Number</i>		<i>Number</i>	<i>Number</i>	<i>Inches</i>
Prewhorl.....	Turgid and functional.....	1-5	2-3				
Early whorl.....	do.....	6-7	3				
Midwhorl.....	Some shriveling and tip burn.....	8-9	4-5				
Late-whorl.....	Extensive browning, or lost.....	² 10-15	5-6	Shows below edge of whorl cup.....	0-2		
Early green-tassel.....		10	2-4	Tip shows above edge of whorl cup.	2-4	0	0-5
Mid-green-tassel.....		10-11	3	Clump of adhering branches.....	2-4	0	1-8
Late-green-tassel ⁴		11-15	0-1	Branches unfurled away from stem.	3-5	⁵ 0	⁶ 2-12

¹ The first two, or primary, leaf blades are usually lost or buried prior to the mid-green-tassel stage.

² Does not include the 2 primary leaf blades. Many strains of field corn show 13 or more leaf blades during the late-whorl stage.

³ Includes all leaf blades that are rolled at least at the base and do not show a distinct line of juncture between the blade and leaf sheath.

⁴ The peduncle appears during the late-green-tassel stage, when a small part of it is visible between the topmost leaf blade and the lowermost tassel branch in some varieties.

⁵ A few.

⁶ Prominent on 2 shoots.

TABLE 2.—*Characteristics of the silk, roasting-ear, and mature growth stages of the corn plant (based on examination of 100 plants)*

Growth stage	Leaf blades visible	Tassel appearance	Peduncles	Anthers and pollen	Ear shoots and ears	Silk	Husk laminae
Early silk	Number 11-15	Branches drooped	Small part shows above top-most leaf.	Anthers dehiscing.	Husk leaves showing.	Yellowish green, fresh, only a few.	Project forward from ear tip.
Midsilk	11-15	do	May show 1 inch or more.	Maximum pollen shedding.	True ears show	Colored, tips wilted, numerous.	Turned outward from ear tip.
Late-silk	11-15	Branches straight and at angle to stem.	do	Anthers usually gone.	Husk leaves tight around ears.	Dried and brown at tips only.	Folded back along-side of ear.
Roasting-ear. ¹	11-15	do	3-6 inches long	Dry	1 ear full size	Dried and brown most of length.	Do.
Mature	11-15	do	do	do	Less than 35 percent moisture in kernels.	do	Do.

¹ Sometimes called "prime-milk," or "green-produce," ear.

Conventional terminology has been sufficiently descriptive, except for items requiring definition, as follows:

1. A rolled leaf blade is one that is spirally wound or rolled, at least at its base, and does not show a distinct line of juncture with its leaf sheath, the line of juncture being hidden by leaf blades originating at points lower on the stalk.

2. An unrolled leaf blade is one that, through expanding growth, has separated itself from the whorl and shows a distinct line of juncture with its leaf sheath, indicating the location of the ligule.

3. The peduncle, or tassel stem, is the terminal part of the stalk, which supports the tassel and is visible between the topmost leaf blade and the lowermost tassel branch.

Although definition of these growth stages has been based on external structural characters predominant during plant growth, their occurrence is in general parallel with and related to characteristic periods of plant metabolism essentially as described by Kraus and Kraybill (10). The preponderance of nitrogen compounds in translocated food elements during the vegetative whorl stages, the development of a more equally balanced carbohydrate-nitrogen ratio

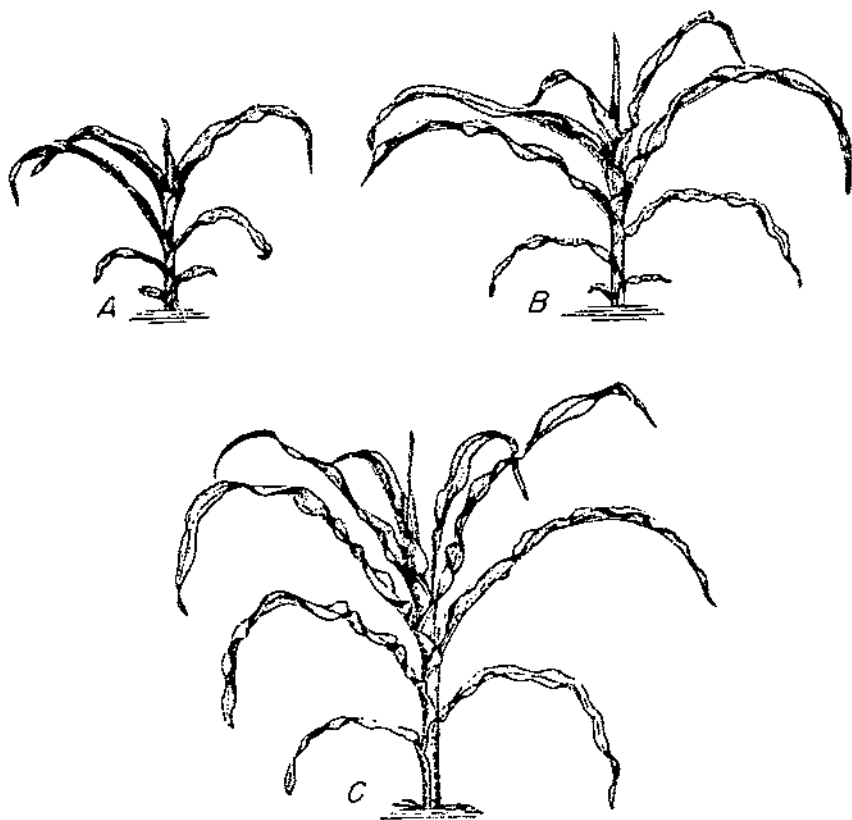


FIGURE 1.—Whorl stages of growth of the corn plant: A, Early whorl; B, mid-whorl; C, late-whorl.

during tassel growth, and the predominant carbohydrate metabolism during ear development indicate a physiological, as well as a structural, basis for this nomenclature. A growth-stage nomenclature for use in describing the corn plant at the time larvae were in its shelter areas provided a convenient standard for biological measurement. "Planting date," "plant height," "number of days from silking," and very loose terms, such as "tasseling," and "silking" were not found to be very specific or useful in comparing corn grown in different soils and during two or more seasons. These conclusions are supported by the data given in table 3 on prevailing growth stages of the same hybrid during two successive seasons.



FIGURE 2.—Tassel stages of growth of the corn plant: *A*, Early green-tassel; *B*, mid-green-tassel; *C*, late-green-tassel.



FIGURE 3.—Silk stages of growth of the corn plant: *A*, Early silk; *B*, midsilk; *C*, late-silk.

TABLE 3.—Duration and height of plant-growth stages in two similar plantings of the hybrid sweet corn *Marcross C6.13*, in 1940 and 1941 (based on examination of 100 plants)

Growth stage	Observations in 1940				Observations in 1941			
	Observation date	Period from planting date ¹	Period from prevailing growth stage to silking	Height of plants ²	Observation date	Period from planting date ³	Period from prevailing growth stage to silking	Height of plants ²
		Days	Days	Inches		Days	Days	Inches
Early whorl.....	June 12	48	27	12	June 1	47	23	10
Midwhorl.....	June 17	53	22	19	June 7	53	16	18
Late-whorl.....	June 22	58	17	22	June 10	56	13	25
Early green-tassel.....	June 27	63	12	30	June 16	62	7	35
Mid-green-tassel.....	July 2	69	7	38	June 19	65	4	41
Late-green-tassel.....	July 7							
		74	2	48	June 21	67	2	47
Early silk.....	July 9	76	0	40	June 23	69	0	51
Midsilk.....	July 12	79	3	50	June 27	73	4	56
Late-silk.....	July 24	91	15	52	July 3	79	10	58
Prime-milk, or roasting-ear.....	July 30	97	21	52	July 14	90	21	60

¹ Planted on Apr. 25, 1940.

² To tip of topmost leaf blade.

³ Planted on Apr. 15, 1941.

The prevalence of any one growth stage was found to vary with genetic strain, soil fertility, and seasonal weather. In early strains of sweet corn the plants passed from the early whorl to the late-silk stage in 30 to 45 days, depending on temperature and rainfall, in May and June. Midwhorl and late-whorl stages prevailed during 4 to 7 days, and the plant usually passed through the mid-green-tassel stage in 1 to 3 days. The same stages were greatly prolonged, however, in strains of sweet or field corn that required a longer season to reach maturity. An example of the effect of weather on the duration of growth stages is shown in table 3, in which data on two similar plantings of the hybrid *Marcross C6.13* are compared. Cool weather retarded the growth rate of the plants in 1940, but favorably high temperatures accelerated plant growth in 1941. The duration of tassel stages was 5 days longer in 1940 than in 1941, and similar differences were found in other growth stages. It is noteworthy that the development of plant-growth stages was independent of vegetative growth as expressed by height. The prevalence of growth stages in the early market hybrid *Marcross C6.13*, in a commercial field planted on April 25, 1940, is shown in table 4.

TABLE 4.—Prevalence of growth stages in the hybrid sweet corn *Marcross 06.13* at New Haven, Conn., 1940 (based on 100 plants in 4 sub-samples of 25 consecutive plants each, examined on the same day)

Growth stage	Percentage of plants in growth stage on—							
	June 12	June 17	June 22	June 27	July 2	July 7	July 12	July 24
Early whorl.....	88	7	0	0	0	0	0	0
Midwhorl.....	12	57	18	0	0	0	0	0
Late-whorl.....	0	36	52	12	0	0	0	0
Early green-tassel.....	0	0	30	72	6	0	0	0
Mid-green-tassel.....	0	0	0	16	47	17	0	0
Late-green-tassel.....	0	0	0	0	39	44	3	0
Early silk.....	0	0	0	0	8	23	31	1
Midsilk.....	0	0	0	0	0	16	58	21
Late-silk.....	0	0	0	0	0	0	8	78

SHELTER AREAS AVAILABLE FOR LARVAL ESTABLISHMENT

The locations that serve as shelter areas for European corn borer larvae in the whorl, tassel, and silk stages of the corn plant become available as the form of the plant changes through growth. In these studies some of the locations appeared to meet all the requirements of initial larval establishment, but none of them were utilized by the larvae during more than three instars. Consequently, the larvae that survived to pupate succeeded in maturing by virtue of initial establishment, escape from the hazards of migration, and fortunate reestablishment. In tables 5, 6, and 7 the distribution of larvae by instars in the various parts and growth stages of the host plant is summarized. The data in table 5 show the shift of the infesting population from one shelter area to another during successive growth stages of the plant, and the data in tables 6 and 7 give the percentages of instars found in each location and in each stage of plant growth.

WHORL STAGES

In early strains of sweet corn European corn borer larvae first enter spaces between the spirally wound leaf blades composing the whorl (table 5). There are 5 to 11 spaces in the midwhorl and late-whorl stages (fig. 1, *B* and *C*), and as the plant grows the depth of these spaces increases and the leaf blades elongate, unroll, and finally become detached from the whorl. The pressure of appressed leaf surfaces is reduced gradually and the wedge-shaped space between the leaves slowly descends toward the stalk until the outer leaf is released from the whorl. In these studies it was observed that the leaf tissues lining the unexposed parts of these spaces were relatively soft, pale green, or yellowish green, and were usually wet from plant exudates and from atmospheric moisture. The level of this film of moisture was commonly observed to rise with an increase in the rate of plant guttation, or glandular secretion of fluid materials, and it also rose with an accumu-

lation of water during rains. At other times the film receded as water was evaporated from the plant at rates in excess of the plant's capacity for replacing it.

First instars were found to feed habitually below the upper margin of the interfoliar moisture film, and they accompanied the film downward with plant growth or remained at higher levels during periods of more extensive accumulation of water and plant fluids. During periods of dry weather the larvae were observed to descend with the moisture film more deeply into the interfoliar spaces, where they became less accessible to insecticidal deposits. Some of the second instars infesting extra early and early types of corn were found to have penetrated the central shoot of the whorl, either by crawling beneath the margin of a loosely rolled leaf blade or by boring through several layers of rolled blades. Some of the larvae had reached the small, immature tassel when it consisted of white and pale-green, soft tissues, spirally wrapped in the loose but still unrolled central leaf blades of

TABLE 5.—*Distribution of European corn borer larvae in plant parts during growth stages of the hybrid Marcross C6.13, at New Haven, Conn. (based on examination of 100 plants)*

Growth stage	Percentage of larvae found in—								Number of larvae per plant	
	Interfoliar spaces	Spaces between staminate spikelets	Tassel florets	Ear shoots	Leaf sheaths	Peduncles	Ears	Stalks		Other parts ¹
Midwhorl.....	38	55	0	0	0	0	0	0	7	5.8
Late-whorl.....	12	35	47	6	0	0	0	0	0	6.3
Early green-tassel.....	12	1	58	19	4	0	0	0	6	9.5
Mid-green-tassel.....	12	0	41	33	8	5	0	0	1	12.8
Late-green-tassel.....	0	0	2	33	12	21	0	13	19	10.3
Early silk.....	0	0	2	0	11	21	40	18	8	10.4
Midsilk.....	0	0	0	0	13	16	44	21	6	5.2
Late-silk.....	0	0	0	0	7	9	51	28	6	4.4
Roasting-ear.....	0	0	0	0	5	1	55	38	5	4.0

OBSERVATIONS IN 1941										
Growth stage	Interfoliar spaces	Spaces between staminate spikelets	Tassel florets	Ear shoots	Leaf sheaths	Peduncles	Ears	Stalks	Other parts ¹	Number of larvae per plant
Midwhorl.....	88	11	0	0	0	0	0	0	2	5.6
Late-whorl.....	39	18	35	5	0	0	0	0	2	6.4
Early green-tassel.....	8	22	39	14	4	2	0	0	9	12.9
Mid-green-tassel.....	6	19	51	15	4	3	0	0	2	14.4
Late-green-tassel.....	0	24	26	16	8	12	0	5	1	14.0
Early silk.....	5	7	11	7	12	17	20	15	4	14.4
Midsilk.....	0	8	6	0	18	18	30	18	1	10.3
Late-silk.....	0	0	1	0	19	27	28	19	3	7.4
Roasting-ear.....	0	0	0	0	9	1	36	55	0	5.9

¹ Leaf surface, tillers, and midribs of leaf blades.

the midwhorl stage (fig. 1, *B*). In this position the larvae excavated the tissues of the central tassel spike and the bud tissues of the staminate spikelets composing the tassel. However, in the later hybrid, Golden Cross Bantam, larvae were not found within or between the staminate spikelets while these were enclosed in the tightly wound central shoot, which is characteristic of this hybrid during its midwhorl stage. Examination of developing tassels indicated that larvae were carried upward as the tassels emerged through the bottom of the cup at the beginning of the late-whorl stage (fig. 1, *C*), and that as soon as the tassel became exposed the population was increased by newly hatched larvae.

In early strains of sweet corn, ear shoots are exposed 4 to 6 inches during the late-whorl stage. These shoots consist largely of the streamer leaves of the husk, or husk laminae, and are closely appressed forming miniature spaces similar to the interfoliar spaces of the whorl. These spaces later become continuous with spaces between the husk leaves, thus affording permanent shelter for larvae invading the ear shoots.

TABLE 6.—*Distribution of larval instars in the various growth stages of the early market hybrid Marcross CG.13, at New Haven, Conn., 1940 and 1941 (based on examination of 100 plants)*

OBSERVATIONS IN 1940

Growth stage	Percentage of larvae in instar						Number of larvae per plant
	First	Second	Third	Fourth	Fifth	Pupa	
Midwhorl.....	100	0	0	0	0	0	5.8
Late-whorl.....	21	78	1	0	0	0	6.3
Early green-tassel.....	20	58	22	0	0	0	9.5
Mid-green-tassel.....	17	41	32	10	0	0	12.8
Late-green-tassel.....	1	25	28	34	12	0	10.3
Early silk.....	0	17	40	27	16	0	10.4
Midsilk.....	0	5	22	42	31	0	5.2
Late-silk.....	0	0	7	18	66	9	4.4
Roasting-ear.....	0	0	1	15	70	14	4.0

OBSERVATIONS IN 1941

Midwhorl.....	88	12	0	0	0	0	5.6
Late-whorl.....	73	22	5	0	0	0	6.4
Early green-tassel.....	57	27	10	0	0	0	12.9
Mid-green-tassel.....	26	38	28	6	1	0	14.4
Late-green-tassel.....	13	26	41	19	2	0	14.0
Early silk.....	4	21	35	22	18	0	14.4
Midsilk.....	4	10	29	30	27	0	10.3
Late-silk.....	0	11	26	25	38	0	7.4
Roasting-ear.....	0	0	6	20	73	1	5.9

TABLE 7.—Percentage of larval instars of the European corn borer in plant parts of the various growth stages of the hybrid sweet corn Marcross C6.13, at New Haven, Conn., 1941 (based on examination of 100 plants)

Plant parts	Midwhorl stage			Late-whorl stage			Mid-green-tassel stage			
	First instar	Second instar	Third instar	First instar	Second instar	Third instar	First instar	Second instar	Third instar	Fourth instar
Interfoliar spaces	51.8	0	0	33.6	5.7	0	3.5	1.4	0.7	6.6
Spaces between staminate spikelets	25.0	12.5	0	15.6	2.5	0	3.5	6.9	3.5	5.5
Florets of exposed tassel	0	0	0	18.8	12.3	4.1	12.2	22.6	15.9	0
Ear shoots	0	0	0	4.9	0	0	6.1	4.7	3.7	0.6
Leaf sheaths	0	0	0	0	0	0	1.4	2.0	.6	0
Peduncles	0	0	0	0	0	0	0	.6	4.2	0
Other parts ¹	10.7	0	0	0	1.6	.8	.7	.7	.6	0

Plant parts	Midsilk stage					Roasting-ear stage					
	First instar	Second instar	Third instar	Fourth instar	Fifth instar	First instar	Second instar	Third instar	Fourth instar	Fifth instar	Pupa
Spaces between staminate spikelets	0	0	2.3	3.9	1.6	0	0	0	0	0	0
Florets of exposed tassel3	.6	4.9	0	0	0	0	0	0	0	0
Leaf sheaths9	3.9	5.8	5.8	.9	0	0	4.2	2.0	2.6	0
Peduncles	0	.9	3.6	7.5	6.1	0	0	.6	0	0	0
Ears	2.3	4.2	11.0	6.2	6.8	0	0	.7	13.3	22.0	0
Stalks	0	0	1.3	5.8	11.0	0	0	0	4.2	48.1	0
Other parts ¹3	.7	.3	.3	1.5	0	0	0	0	0	1.2

¹ On surface of plants and in midribs of leaf blades.

GREEN-TASSEL STAGES

Interfoliar spaces of the whorl persist more or less into the green-tassel stages (fig. 2, *A*, *B*, and *C*), depending on the growth habit of the strain of corn. When plant growth during the early green-tassel and mid-green tassel stages causes the interfoliar spaces to dry out and become obliterated many of the larvae in the first, second, and third instars ascend to the tassel. Interfoliar spaces persist between streamer leaves, or husk laminae, projecting from newly formed ear shoots, which are produced as rudimentaries as late as the milksilk stage (fig. 3, *B*) of most types of sweet corn.

In some varieties tassel infestation was begun during the mid-whorl stage, and thereafter larvae accumulated in the tassels from two sources: (1) Newly hatched larvae ascending to the topmost part of the plant; and (2) first and second instars which had migrated from whorl spaces when these became unsuitable to their requirements. Between the late-whorl and the mid-green-tassel stages, while the tassel was still a clump of adhering branches, first and second instars entered spaces between staminate spikelets and between the pedicels of staminate spikelets and the tassel branch to which the pedicels were attached, and began excavations leading to entry of the florets. Many of the first-instar larvae entered the tassel through the tip of the floret and fed on the lemmas and paleae before reaching the anthers. A smaller percentage of the larvae invading the tassel during the mid-whorl or late-whorl stages became established at the juncture of the central tassel spike with a branch and bored into the central spike at that point. These larvae were found to have grown to the third or fourth instar by the time the plant had reached the mid-green-tassel stage.

In some strains of corn the tassel branches adhere in a clump during 2 or more days after emergence from the whorl (fig. 2, *B*), although high winds may cause earlier separation of the branches. When the branches become separated many of the larvae are exposed and the first four instars of these spin or drop to lower parts of the plant. Migration is then rather precipitate, unlike the subsequent migration out of the tassel florets. The florets, which contain lemma and palea bracts, as well as anthers, provide a moist environment favorable to the larvae until the anthers begin to shed pollen. After pollen shedding begins, the dryness and loss of food in the plant render it undesirable. As indicated in tables 5 and 7, movement from the tassel florets began during the late-green-tassel stage, continued through the late-silk stage, and resulted in the appearance of third instars in lower shelter areas of the plant.

A part of the peduncle below the tassel branches may be visible during the late-green-tassel stage (fig. 2, *C*), but it becomes exposed largely during the silk stages. Larvae entered this part of the peduncle before it emerged from the leaf sheath of the topmost leaf blade, and they continued to make entries as the peduncle grew upward. Later, dryness apparently made the area unacceptable to wandering larvae and a considerable number migrated from the peduncle.

Spaces beneath the leaf sheaths became available to larvae during the late-green-tassel stage. Prior to this time the plants had made vigorous vegetative growth, accomplishing approximately four-fifths of their vertical growth by the time they reached that stage. Upward growth involves the movement of each leaf sheath inside the one originating immediately below it, and this process continues until part of the stalk becomes visible. As a result of pressure caused by turgidity and growth, each overlying leaf sheath adheres tightly to the one inside it until the rate of growth upward has been materially reduced. Up to the late-green-tassel stage (fig. 2, *C*) very few larvae were found to penetrate beneath the leaf sheath, and penetration was accomplished by cutting through the ligules, as has been observed and described by Huber, Neiswander, and Salter (9, p. 45).

SILK STAGES

The silk stages of growth (fig. 3, *A*, *B*, and *C*) provide shelter areas largely in the true and rudimentary ears and beneath the leaf sheaths. Newly hatched larvae, as well as second to fourth instars migrating from the tassel, find in these areas the moisture and food necessary to establishment. Larval entry into the ears, begun in the late-whorl and early green-tassel stages, did not increase until the mid-green-tassel stage, when migrants from the tassel began to appear in the ear shoots. Increases during the silk stages (table 5) included larvae in the second, third, and fourth instars which entered by way of the silk tunnel or crawled between the sheath leaf and the husk leaves.

The routes taken by larvae in reaching the stalk were similar to those described for larvae entering the peduncle. Having reached the space beneath the leaf sheath, they made excavations in its inner surface or in the rudimentary ear developing at that point (see fig. 3, *A*, *B*). In the absence of suitable rudimentary ear tissue, the third and fourth instars began boring into the stalk. While the coincidence of unfavorable shelter in the tassel for first-instar larvae and the loosening of the ligules accounted for some increase in the number of first instars in the leaf sheath spaces, a considerable proportion of the increase in population was due to migrating third and fourth instars, as shown in tables 5, 6, and 7.

Migration out of the rudimentary ears began with deterioration of the rudimentary cob and continued through the roasting-ear stage of plant growth. By this time the infesting population had become established in the ears, or in the stalk, or beneath the leaf sheaths—the last parts to furnish moisture and food in a drying plant. As the corn plant matured the borer escaped from dryness largely by pupating or, in the case of immature larvae, by migrating from the plant as one part after another became undesirable.

Broken midribs of leaves afforded temporary shelter to migrating larvae. Although such breakage occurred during all plant-growth stages, such locations were useful to larvae only during the whorl and tassel stages, when the exposed tissues were comparatively succulent. In these studies a relatively unimportant percentage of the larvae inhabited breakage points in early types of sweet corn.

DISTRIBUTION OF LARVAE IN PARTS OF THE PLANT

Several items in table 5 are significant because they show that the distribution of larvae in the same hybrid varies with seasonal differences and corresponding differences in establishment, migration, and reestablishment. Differences in larval distribution attributable to differences in the season are illustrated by the fact that in 1940 the larvae established themselves earlier in tassel areas, and made a shorter stay in the interfoliar spaces, than in 1941. In 1940 the ear shoots became infested earlier and by larger percentages of larvae than in 1941, but fewer borers entered the tassel florets. It is also noteworthy that, accompanying an earlier migration from the tassel during the late-green-tassel stage in 1940, a larger number of the borers were lost from the plants through accidents and a smaller percentage of the migrating larvae became established in the ear shoots.

During the 1940 infestation of the late-whorl stage 82 percent of the larvae were found to have penetrated to the immature tassels, or staminate spikelets, developing within the whorls, as compared with 53 percent in 1941. A considerable percentage of these larvae were second instars—78 percent in 1940 and 22 percent in 1941 (table 6). Apparently many of them continued to grow during the late-whorl stage, as 22 and 16 percent of the larvae in the early green-tassel plants in 1940 and 1941, respectively, were third instars, and approximately one-third of them were in that instar at the time of migration from the late green tassels.

Extensive variation in the accessibility, and utilization of midwhorl and late-whorl shelter areas was found among the four hybrids compared in table 8. Differences in availability of protective areas explain differences in the infestation, as exemplified by the ear shoots. The length of the ear shoots varied with the earliness of the hybrid. Spancross, the earliest, showed green streamers, or husk laminae, 6 inches long in the late-whorl stage, as compared with 4-inch laminae in Marcross. In Golden Cross, Bantam, and Carmelcross, on the other hand, all parts of the ear shoot were concealed beneath the leaf sheath, although, exceptionally, in plants in the late-whorl stage, 1-inch and 2-inch green laminae showed above the ligule. These differences in the amount of space available in the different varieties account for the variation in percentages of larvae inhabiting late-whorl ear shoots (table 8). Explanation is not so obvious, however, in the percentages of infestation in immature tassels developing within the whorl, including the incipient buds of the florets, or in the occurrence of instars. In 1940 approximately half the larvae (55 percent) infesting midwhorl Marcross plants had penetrated to the developing tassels, as compared with only 11 percent in the 1941 planting of this hybrid. The difference is attributable to the cool, dry weather prevailing during the midwhorl and late-whorl stages in 1940, which resulted in proportionately less vegetative growth (table 2).

Larval penetration to the midwhorl tassels of Spancross and Marcross, in contrast with the absence of larvae in the tassels of Golden Cross Bantam, was not completely explained by the looser winding of whorls characteristic of the earlier varieties, because second instars were observed to tunnel through several layers of rolled leaf blades to reach the tassel areas of the earliest and second earliest varieties.

TABLE 8.—Location of first-generation European corn borer larvae in the whorl stages of hybrids of C 13 and P 39 sweet corn at New Haven, Conn.

Growth stage and shelter area	Percentage of larvae found in plant parts of—				
	Marcross C 6.13		Span- cross C 4.13	Carmel- cross C 13×P 39	Golden- cross Bantam P 39×P 51
	1940	1941	1940	1940	1940
Midwhorl stage:					
Leaf surface.....	7	2	5	7	8
Interfoliar spaces.....	38	88	86	81	92
Spaces of developing tassel within the whorl.....	55	11	9	12	0
Late-whorl stage:					
Leaf surface.....	0	3	0	0	3
Interfoliar spaces.....	12	39	16	31	90
Spaces of developing tassel within the whorl.....	35	18	42	46	1
Florets of exposed tassel.....	47	35	21	20	2
Ear shoots.....	6	5	21	2	4

Apparently other characters were responsible for the continued high proportion (90 percent) of the larvae found in interfoliar spaces of the late-whorl stage of Golden Cross Bantam. Further examination showed 40 percent of the infesting population to be first instars, although in many plants excavation of tissues had ceased after the initial effort of the larvae had been expended. Many of the feeding areas were pin-point, trial pits, rather than the larger and elongated areas of continued excavation usually observed in early market types of corn. These pin-point feeding areas resembled those described by Patch (11) in his study of the resistant hybrid R 4. In general, larval activity in Golden Cross Bantam was in marked contrast to the continued excavation, development to second instar, and penetration to tassel areas characteristic of larvae infesting Spancross and Marcross in midwhorl and late-whorl stages of plant growth. It was concluded that the larvae infesting these stages of Golden Cross Bantam did not obtain from this food sufficient energy to continue excavation at the same rate as in the earlier varieties of corn.

Differences in the distribution of larvae in plants of the four hybrids compared in table 8 suggest the same general cause; that is, variation in the ratio of carbohydrates to nitrogen, which may occur in the larval food characteristic of these hybrids in midwhorl and late-whorl stages. It will be recalled that external differences between the four hybrids were noted in the development of the ear shoots and these differences were in the order of varietal earliness. In these four hybrids length of ear shoot and earliness were associated with the length of the predominantly vegetative period of leaf blade and stalk growth during which translocated food elements are predominantly nitrog-

enous. In the earlier varieties this period was shortened and a more equal balance of the carbohydrate-nitrogen ratio was indicated by earlier development of ear and tassel organs. With an increase in the availability of carbohydrate compounds to infesting larvae, greater provision was made for active excavation and continuous instar growth in the early Spancross and Marcross than in the midseason Golden Cross Bantam. Differences in the distribution of larvae in Marcross in 1940 and 1941 were attributed to reduction in the length of the vegetative (nitrogen) cycle of plant metabolism during the cooler 1940 season, whereas in 1941 higher temperatures and increased availability of plant food extended the period of vegetative growth.

APPLICATION OF INSECTICIDES

The sequence of biological events during growth stages of the corn plant indicated the physical properties needed in insecticide materials to combat corn borer and the procedure required in their application. The shelter areas entered by corn borer larvae are more accessible to insecticides having penetrating properties, but in the studies discussed in this publication, the larvae as they migrated from one plant part to another were all subject to the effect of deposits or barriers of insecticides at points of entry.

As many of the second and third instars had already become established in the concealed tassel, insecticides applied during the whorl stages were effective largely against first-instar invaders of interfoliar spaces. The insecticide must either be able to penetrate deeply or the insoluble deposits must be mobile. Early market types of sweet corn were found to be subject to a relatively high infestation rate, with extensive establishment and survival during midwhorl and late-whorl stages (fig. 1, *B* and *C*), which indicated the importance of insecticidal treatment during these stages.

When treatments are applied during the early green-tassel (fig. 2, *A*) or the mid-green-tassel (fig. 2, *B*) stage, more than 50 percent of the larvae on the plant occupy shelter areas in the furled tassel, where many of them are accessible to insecticide deposits. To insure maximum reduction of borers at this time the insecticide must be capable either of penetrating closely felted and waxy components of the tassel or of providing barriers that will be effective against successful migration out of the tassel by second-, third-, and fourth-instar borers.

The stalk can be protected by penetrant or barrier insecticides deposited at leaf sheath openings during late-green-tassel (fig. 2, *C*) and early silk (fig. 3, *A*) stages of plant growth.

It was evident during these studies of initial and secondary establishment that probably no single application of an insecticide will suffice to protect the ears. It was concluded that ear protection can be accomplished only by the following procedures: (1) Reduction of the total larval population, as some of the larvae from other parts of the plant are potential contributors to ear infestation; (2) use of an insecticide sufficiently effective to protect the ear from third- and fourth-instar migrants; and (3) so directing the application as to insure deposits on the developing ear shoots.

SUMMARY

The areas of the corn plant that serve as shelter for larvae of the European corn borer (*Pyrausta nubilalis* (Hbn.)) were studied to determine their relation to insecticide deposits.

Types of shelter area characteristic of each of 12 stages of plant growth were examined, and the prevalence of larvae in them was found to be affected by the growth stage and varietal growth rate of the plant and by the growing season.

Successive locations used by the larvae for entry during growth of the plant were as follows: (1) Interfoliar spaces, (2) immature tassels, (3) tassel florets, (4) ear shoots, (5) leaf sheaths, and (6) ears. The extent to which the respective locations were utilized for initial establishment varied with the maturity of the plants when the larvae were hatching. Feeding areas were either obliterated through growth or were made unsuitable for tenancy by changes resulting from plant development. Spaces inside leaf sheaths became available to the larvae during the late-green-tassel stage, when the completion of internodular growth and the loosening of the sheaths permitted the larvae to enter.

Migration of larvae from less protective to more protective areas was found to accompany the development of specific plant-growth stages. The direction and sequence of these migrations were as follows: (1) From interfoliar whorl spaces to spaces of the partially enclosed tassel; (2) from interfoliar whorl spaces to space areas of the exposed tassel; (3) from spaces between parts of the unfurling tassel to its stem, or peduncle, and to ear shoots; (4) out of the tassel florets to the leaf sheaths and the ears; and (5) from the tassel peduncle to the leaf sheaths and the ears. These migrations were proportionately more important during the late-whorl, mid-green-tassel, and mid-silk stages.

First-instar larvae were found to feed habitually below the upper margin of the interfoliar moisture film, and accompanied this film downward with plant growth or remained at higher levels when water and plant fluids were more abundant. During dry weather the larvae descended with the moisture film more deeply into the interfoliar spaces, where they became less accessible to insecticidal deposits. In the earlier hybrids, Spangcross and Marcross, second instars penetrated from the interfoliar spaces to the partially enclosed tassel during the mid-whorl and late-whorl stages.

The distribution of larvae and their development to maturity in shelter areas of plants in mid-whorl and late-whorl stages of growth varied with the earliness and seasonal growth of the hybrid sweet corn strains. Evidence suggested that the variations were due to differences in the carbohydrate-nitrogen ratio during the stages of plant growth. The earlier increase of carbohydrate constituents in the earlier hybrids, Spangcross and Marcross, resulted in earlier differentiation and development of ear shoots. In the later variety, Golden Cross Bantam, larvae failed to penetrate deeply and to feed extensively, probably because the preponderance of vegetative metabolism characteristic of the mid-whorl and late-whorl stages deprived them of sufficient carbohydrate, energy-producing nutrients to enable them to excavate the plant tissues.

The data obtained on the occurrence and utilization of shelter areas by the larvae should be useful in interpreting the performance of insecticides tested for European corn borer control. Direct application of this type of information would indicate the physical properties an insecticide must have if it is to be effective against the borer, and the degree of plant protection to be expected from treatments directed at specific shelter areas.

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