EFFECT OF EUROPEAN AND SOUTHWESTERN CORN BORERS ON TRANSLOCATION OF PHOTOSYNTHETIC PRODUCTS, WATER USE AND YIELD IN *Zea mays* L.

by

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TABLE OF CONTENTS

LIST OF TABLES

LITERATURE REVIEW

Introduction

Corn producers in southern Kansas have to deal with a pest problem that few other major corn producing areas face. Both the European corn borer (*Ostrinia nubilalis* Hubner) (ECB) and the southwestern corn borer (*Diatraea grandiosella* Dyar) (SWCB) are found in this part of Kansas at economically important levels.

Many research hours have been devoted to breeding corn varieties that are resistant to borer infestation, but there seems to have been little work undertaken at this time to quantify how the borer actually reduces yields. Both species cause yield losses due to lodging, but even in hand harvested plots losses of 9% can be expected in corn infested at anthesis by SWCB (Scott and Davis, 1974) and 12% reduction by ECB infestations on susceptible hybrids (Scott et al., 1967).

In Kansas both borers are bivoltine (produce two generations of larvae per growing season). The first generation larvae are seldom of economic importance here. The second generation of larvae generally hatch near the time of anthesis. Since this time is so critical to grain fill and yield, the losses may be due to the disruption of water and/or assimilate transportation and/or photosynthetic activity which would adversely affect the source/sink relationship.

These relations become more complex when one tries to consider the effect of not just one borer species, but two. Since the tunnelling characteristics of the two species are different, there is the possibility of an interaction if both are present in one plant.

The complexity of these interactions lend themselves to the use of computers and computer modeling. One model that deals with corn growth and development is the CORNF model which was developed by Stapper and Arkin (1980). If the relationship between the borers and yield can be determined, it would be a great addition to the model and would make further work with the model reliable under more conditions.

The CORNF Model

Stapper and Arkin (1980) developed CORNF:A Dynamic Growth and Development Model for Maize (Zea mays L.). This model is made up of several subroutines dealing with accumulation of growing degree days, emergence, leaf emergence, daily leaf area index and senescence, morphological development stages, daily potential evaporation, actual evaporation, daily dry matter production and grain set and filling. Data relating to the effect of European and southwestern corn borers would be a useful addition to this model, especially for areas that have the complication of having combined infestations. The subroutines-STAGE, PHOTO, and EAR would be areas where data relating to damage by ECB and SWCB would be of the most interest.

The subroutine STAGE deals with the development of a corn plant. Here Stapper and Arkin rely very heavily on "How a corn plant develops" (Ritchie and Hanway, 1982). The timing of developmental stages can be altered by adverse conditions. The moisture content of grain is decreased by ECB infestation (Scott et al., 1967). If development is affected, these plants may have matured earlier than the uninfested controls. Information on corn borer infestation would then help this CORNF subroutine more accuratly predict premature black layer formation (Stapper and Arkin, 1980).

The subroutine PHOTO estimates dry matter accumulation and would benefit from any information acquired concerning alterations in photosynthesis due to borer infestations.

The subroutine EAR determines the number of kernels per plant and partitioning and translocation of dry matter to the kernels. If corn borer stress causes reduced kernel number or if there was a relation between timing of corn borer stress and kernel number this information could be utilized in this subroutine. If corn borer infestation caused differential partioning (into the stalk rather than the ear) this information would be useful. Many studies have shown that corn plants have the ability to remobilize stored dry matter (Kiessebach, 1948; Hume and Campbell, 1972; McPherson and Boyer, 1977; Westgate and Boyer, 1985). If borers affect the ability to remobilize stored dry matter or if borers increase respiration using a portion of the dry matter that would otherwise have been remobilized, that additional information could by utilized in this subroutine to improve the accuracy of the model for estimating yield when corn borers are present.

Southwestern Corn Borer

The southwestern corn borer is a fairly recent immigrant to Kansas. In 1931 the first infestations were reported in Morton and Stevens counties (Wilbur et al., 1950). The drought of the 1930's seemed to have checked the spread of the borer, but by 1941, borer damage was detected in 28 counties. Although Henderson et al. (1966) showed SWCB throughout the state, only the southern half is affected economically (Knutson, 1975). The northern border of the SWCB's range is determined by the severity of the winters. Sandy soils which are put into corn seem to have the heaviest infestations and are most subject to intensive infestation by first generation borers, indicating that southwesterns are better able to overwinter in such soils (Knutson, 1975).

Second generation borers will tunnel in the stalk very severely. Tunnels of 20-30 cm are not unusual. The tunnelling is generally found below the ear zone although there may be tunnelling into the shank as well. As many as 11 holes may be found in a single node, but since cannibalism is not unusual, there is seldom more than one overwintering pupae found in a plant (Wilbur et al., 1950).

The most extensive damage is done by the borer in preparation for overwintering. A hibernation chamber will be reamed out usually in the base of the stalk. Only a thin shell of rind may be left at this point on the stalk making it more prone to lodging.

Williams et al. (1983) found that a linear decline in yield accompanied an increase in numbers of SWCB eggs per plant. With each addition of 5 eggs the yield was reduced by 2.25 quintal/ha. Scott and Davis (1974) reported a yield loss of 9% with a second generation infestation of SWCB, which they attributed to a reduction in kernel number per plant rather than kernel weight or ear number.

European Corn Borer

The European corn borer is a major pest in the Corn Belt. Within this area it is responsible for the loss of millions of bushels of corn each year. The life cycle of the European corn borer is similar to the southwestern in some ways. In Kansas, the species is bivoltine, and the first generation infestations seldom reach an economically important level.

The tunnelling patterns, however, are very different. Since the ECB are able to overwinter in any part of the stalk, they are not found predominantly in the base. They are more evenly distributed throughout the canopy, with the highest percentage found in the ear zone. The tunnels are usually shorter and more variable in width and length. This difference makes it possible to identify which species makes a particular tunnel with a fair amount of accuracy.

Berry and Campbell (1978) reported yield losses of 1.74 and 1.54 q/ha per cavity due to a combined first and second generation infestation on two inbred lines and their F1 progeny. They also noticed a curvilinear relationship between the number of cavities and yield, indicating a decrease in loss per cavity as the number of cavities increased. Yield losses also appear to be related to hybrid. Lynch (1980) reported that losses at pretassel and pollen shedding stages were greater for long season hybrids than mid-season hybrids.

Damage also appears to depend on timing of infestation. Lynch et al. (1980) reported yield losses and damage greatest when infested at pollen shedding. Jarvis et al. (1961) reported a 2.3% loss in early planted corn and 4.1% loss in late planted corn. This article did not report the stage of development at infestation, but this could be the difference.

Developmental Stages Of Corn

Richie and Hanway (1982) published a system for the identification of developmental stages in corn. The stages are divided into vegetative (V) and reproductive (R) periods. The six reproductive stages are:

Silking (R1) begins when the silks emerge from the husk. Two or three days are required for all silks to emerge and become pollinated. Captured pollen grains take about 24 hours to grow down the silk and pollinate the ovule. Ovules that are not pollinated will degenerate.

Blister (R2) stage begins 10 days after silking and lasts for approximately 5 days. This is a time of rapid kernel development. The kernels are about 85% water during this stage and their percent moisture will decrease during the other stages.

Milk (R3) stage is approximately 18-22 days after silking. The color of the kernel changes to yellow and the fluid to milky white. This is the time of rapid dry matter accumulation. Growth is mostly due to cell expansion. Stress at this stage can affect both kernel number and weight.

Dough (R4) stage is approximately 24-28 days after silking. The starchy solids give the kernel a doughy consistency. About half of the dry matter has been accumulated by this period.

Dent (R5) stage is approximately 35-42 days after silking. Nearly all kernels are dented at this point. Kernel number is not affected by stress at this time. Kernel weight may be affected but an extreme stress such as an early frost is required.

Physiological maturity (R6) is approximately 55-65 days after silking. Maximum dry matter accumulation is now reached. Black layer is formed but further drying is needed before harvesting.

Vascular Anatomy Of Corn

Kumazawa (1961) in his studies of the anatomy of corn plants did serial microtomes of stalks. This intensive study revealed an unusual characteristic of the vascular system. There appear to be two distinct vascular systems present. These two systems derive from the same leaf. The large leaf traces enter the stalk and cross the central portion to join other bundles in the center or opposite side of the plant. The other system comes from the same leaf but consists of the smaller traces. These vessels do not cross to the middle, but follow the outside edge. These can be seen as the circle of bundles on the periphery of the node. They are more difficult to distinguish in the internodal regions.

Source/Sink Relations Of Corn

The main sink for assimilates in corn is the grain. Alternate or transient sinks are the leaves, stem and roots. The importance of these sinks usually occur prior to grain formation or as a temporary sink during rapid accumulation of assimilates. These alternate sinks also appear to be more active when there is no grain (Campbell, 1967). When assimilate production is limited these stored assimilates are remobilized (Jurgens et al., 1978; McPherson and Boyer, 1977; Daynard et al. 1969; Campbell, 1964). Daynard et al. (1969) found a 20% decrease in stalk weight from the time of the blister stage that was contributed to the final grain weight. This flexibility makes the isolation of yield reduction factors very difficult (Tollenaar, 1977).

When grain is present, the source/sink relation can be affected by manipulations at either end. This can be accomplished by either removal of photosynthetic tissue (limiting the source) or removal of kernels (limiting the sink). Comparing different combinations of source and sink removal at different plant growth phases has provided an general picture of this relationship.

As mentioned earlier, timing is important to the amount of reduction in yield caused by any agent. Early defoliation in some hybrids will actually improve yields (Crookston and Hicks, 1978; Vasilas and Seif, 1985). Defoliation during silking and blister is more consistent in its harmful effects.

Defoliation

Defoliation can reduce final grain weight in two ways. Either the total number of kernels is reduced or weight of individual kernels is reduced. Both yield components may be affected but the timing of defoliation will determine where the loss comes from (Allison and Watson, 1966; Hanway, 1969; Tollenaar, 1977; Tollenaar and Daynard, 1978 c.; Salvador, 1984). Defoliation up to 3 weeks after silking will affect kernel number and may affect kernel weight. After this time (approximately the middle of the milk stage), a defoliation treatment will affect weight of the kernels only and kernel numbers will remain constant.

There are three developmental phases during grain-filling (Tollenaar, 1977). The first is the lag period which starts at silk emergence and lasts 15 to 18 days. Following this is the period of linear grain dry matter accumulation, during which time more than 90% of the dry matter of the grain is accumulated. Finally there is the period in which the rate of dry weight accumulation of the grain declines and then terminates in black layer formation. Lag phase is the time of kernel abortion (Tollenaar and Daynard, 1978 b.).

Kernel Removal

Sink limitation appears to be the major problem in the midwestern corn production regions. Whether this is due to varietal or climatic reasons has not been clarified (Salvador, 1984). Jones and Simmons (1983) removed the tip kernels to increase assimilate supply per kernel, but found no difference in final kernel weights. Removal of basal kernels did not appear to affect kernel weight of the remaining kernels, but, if done early, then fewer kernels were aborted (Tollenaar and Daynard, 1978a.). Salvador (1984) also found this to be true, but concluded that the kernels saved at the tip did not develop enough to compensate for the loss of the basal kernels.

Photosynthesis and Assimilate Accumulation

If ears are removed making a plant barren, the alternate sinks (leaves, roots and stem) will store more assimilate than plants with actively growing ears (Kiesselbach, 1948; Hume and Campbell, 1972). Kiesselbach also noted that the stover yield of the plant was 59% higher but total dry matter was 27% lower, for barren plants than those with grain, highlighting the sink limiting situation. Greenhouse plants grown in pots showed no substitution of roots for ears. The roots of plants with ears removed showed only a 7% increase in dry weight over normal plants.

Kiesselbach (1948) came to the following conclusions:

> Carbon accumulation is influenced inversely by the concentration of water-soluble photosynthates within the vegetative parts of the plant, which in turn is modified by the degree of translocation to the grain. Gene-controlled enzyme relationships within the developing grain which lead to more complete translocation either indirectly accelerate photosynthesis within the leaves or lower the losses by respiration and thereby increase the yield of total dry matter as well as of grain. On the other hand, less efficient translocation, whether due to a different enzyme complex or to failure of grain development, results in a higher concentration of water-soluble carbohydrates within the vegetative organs, and thereby reduces the capacity for carbon accumulation and crop yield.

Neales and Incoll (1968) conducted a review of the literature and found mention of many possible mechanisms for the reduction of photosynthesis by the accumulation of assimilates. At the time of this review a negative correlation between photosynthetic rate and assimilate levels in the leaf had been adequately shown, but no biochemical mechanism had been provided.

The distribution and type of stored assimilate appear to be important factors in the negative correlation. Fairey and Daynard

(1978) found soluble carbohydrates in the stalk accumulated during early stages of kernel growth and then declined toward maturity. The major carbohydrate was sugar with only 2% as starch. They cite a report by Nishikawa and Kudo (1973) who found that 11-17% starch in the dry matter of stalk during grain fill when plant populations were high enough to produce barrenness. Allison and Weinmann (1970) found that when they removed ears after flowering, the upper leaves reached 27% starch. Premature senescence was exhibited by these leaves.

Water Stress and Assimilate Accumulation

Denmead and Shaw (1960) showed that the magnitude of yield differences due to stress depended on the growth stage at which the stress occurred. Yield losses due to moisture stress prior to silking and after silking were 25% and 21%, respectively, but 50% if stress occurred at silking and pollen shed.

Claassen and Shaw (1970b.) found significant reductions in kernel numbers if water stress occurred prior to or during silking and pollination. Kernel weights were reduced if the stress occurred during or after silking.

McPherson and Boyer (1977) found that although apparent photosynthesis was halted during periods of low leaf water potentials, translocation continued and previously accumulated photosynthate was used for grain fill. They concluded that, as long as the size of the grain sink had not been adversely affected by moisture stress, the total photosynthetic accumulation during the growing season controlled yield during stress.

Claassen and Shaw (1970a.) noted 15 to 17% reductions in total vegetative dry matter if plants were stressed by withholding water three weeks prior to silking. If water was withheld during silking there was a significant increase in dry matter of the stalk compared to the controls and all other treatments.

Westgate and Boyer (1985) concluded that a carbohydrate reserve was essential to grain production. When low leaf water potential occurred during a period when the plant had low carbohydrate reserves, such as anthesis, grain development was halted, but if reserves were present or became present after the stress then the grain or barren ear would continue to grow. This explained why shading and defoliation have similar effects to low leaf water potential.

Conclusions

1. European and southwestern corn borers contribute to losses in yields in corn not only by physical factors such as lodging, but also by physiological factors.
2. What physiological factors are involved have not yet been properly established.
3. There are only two yield components to be reduced: kernel number and kernel weight.
4. Kernel number and kernel weight can be affected differentially depending upon the timing of stress.
5. An understanding of the method of yield reduction due to ECB and SWCB could be gained from the study of the yield components of infested plants.

OBJECTIVES

Objectives of field and greenhouse studies were:

1. Determine the plant processes involved in yield losses caused by the tunneling by European and southwestern corn borers.

2. Determine the additivity of the yield loss when ECB and SWCB are found in the same plant.

The plant processes observed were assimilate accumulation/transfer, CO_2 utilization (photosynthesis) and water use. This information would then be available for use in the CORNF model giving it more accuracy in regions were SWCB and/or ECB are common.

MATERIALS AND METHODS

Field Study

The field study for this experiment was conducted at the Ashland Experiment Field, Manhattan, Kansas, during the 1983 growing season to determine the effect of ECB and SWCB on assimilate transfer.

The soil is a Haynie very fine sandy loam, Mollic Udifluvent, coarse-silty, mixed, calcareous, mesic. Atrazine was applied at planting as 2.3 liters per hectare (0.48 kilograms per liter active ingredient) for weed control. The plots were irrigated weekly during July and August. The single cross hybrid, Ringaround 1502, is not known to show any resistance to European or southwestern corn borers. It is a medium season hybrid with upright leaves and medium ear height.

The experiment was a split-plot design with five replicates. Corn was planted 5 May 1983 in 76 cm rows at a population of 49400 plants per hectare. Main plots were eight rows by 15.2 meters with two border rows between main plots. Main plots were randomly designated as desiccated or nondesiccated.

Treatments were randomly assigned to rows within each main plot. Previous work (Calvin, 1985) indicated that yield reduction due to borer infestation is dependent on location in the plant. For this reason infestations were assigned to the bottom 5 or middle 5 internodes, but the top internodes were not infested. The treatments were:

LOCATION	No. ECB	No. SWCB
MIDDLE	0	2
MIDDLE	3	0
MIDDLE	3	2
MIDDLE	0	0
BASE	0	2
BASE	3	0
BASE	3	2
BASE	0	0

Ten plants per row were infested at mid-silking, during the week of 22 July. Larvae at the third instar were applied to individual plants at the indicated internodes in plastic vials with a hole in the side. The hole was surrounded with rubber foam to create a portal through which the larvae could enter the corn stalk. The plant was pricked with a nail to hasten tunneling and the vial was then rubber banded to the plant with the opening over the wound permitting the larvae to leave the vial only by tunneling into the plant at the chosen location.

The field was sprayed with BT (Bacillus thuringiensis,var. kurstaki) on 2 August for control of naturally occurring ECB. The slurry contained 12 billion International units per liter and was applied at 1.75 liters per hectare.

Two weeks after infestation, 5 August, the designated main plots were desiccated, using 3.5 liters per hectare of cacodylic acid (0.37 kilograms per liter active ingredient) and 0.39 liters per hectare of the surfactant X77. Both the BT and desiccant were applied with a hand pulled, four row, CO_2 pressurized sprayer with three hollow cone spray nozzles per row (two drop and one overhead). Weekly leaf counts (25 July; 4, 12, 19, 25, 31 August; 7 September) were kept for all nondesiccated plants from the time of infestation.

Plots were hand harvested, stalks split and tunnel lengths, widths, location and borer type were recorded for each plant. Desiccated plants were harvested first since they matured and dried down first.

Ears were weighed and shelled. Grain weights and weight per 100 seeds were recorded. Percent moisture and kernel number were calculated.

Greenhouse Study

The greenhouse study was conducted to determine the effect of ECB and SWCB on photosynthetic activity by CO_2 utilization and on water use. In a preliminary greenhouse study significant differences were found in CO_2 utilization. When calculated on a per leaf area basis, these differences disappeared. The significant difference in leaf area by treatment in the preliminary study led to further analysis in the greenhouse and field studies of leaf areas and leaf counts.

Funk's G4438 hybrid was planted day of the year 55 (24 February) 1984 in 11 liter containers using a 5:2:1 (by volume) mixture of sterile soil, peat moss and vermiculite. Overhead lighting was used to extend the day length to 16 hours.

The plants had longer internodes than field grown plants, but other wise looked normal. The plants were too tall for use in the CO_2 chamber so the plants were topped after the beginning of pollen shed (day of the year 121). Pollination was incomplete so ear development was slow.

Leaf area was measured day of the year 120. Small plants and large plants were divided as replications to remove as much variation due to leaf area as possible. Plants were then randomly designated one of the following treatments:

BORER TYPE	NUMBER	POSITION
SWCB	1	BASE
ECB	2	BASE
ECB	2	MIDDLE
ECB	4	BOTH
CONTROL	0	NONE

Plants were infested with the designated treatments day of the year

122. The applications were checked the following day and replacements were applied if the original borer did not tunnel.

These plants were then assigned to one of ten groups which would be harvested periodically throughout the experiment. Each harvest date had two replicates of five treatments for a total of 100 plants. As each group was harvested the plants were subdivided into lower stalk (first five nodes above ground level), middle stalk (next five nodes, including the ear), lower 5 leaves, middle 5 leaves, ears and roots. The stalks were split and tunnel length and volume were recorded. Roots were washed out of the soil. All plant parts were dried at 52^{o}C and weights recorded.

Water use was determined by weighing the plants twice a day between waterings from the time of infestation until harvest. The between watering period varied with the water needs of the plants, but generally plants were weighed morning and afernoon Monday through Friday then watered Friday after the final weighing of the day. No attempt was made to water to a constant weight.

Carbon dioxide use was determined using a closed system Uris CO_2 analyzer, an Angus strip chart recorder and a plexiglass chamber 2.19 x 0.925 x 0.925m. Carbon dioxide use was measured day of the year 130, 131, 138, 141 and 144. Leaf area and light interception were recorded for each reading. Photosynthetic flux was calculated according to Jarvis and Catsky (1971).

RESULTS AND DISCUSSION

Field Study

The 1983 growing season was very hot and dry. Climatalogical data for Manhattan were incomplete for June and July, so information from Wamego which is about 16 kilometers from the Ashland experiment field was used. June had 6 days above 32°C. The average temperature was 2° higher than normal. Precipitation was 56mm above the normal of 132mm for the month. In July the average daily maximum was 35°C and there were 24 days above 32°C. There was no precipitation in the month of July which was 111mm below the average for the month. August had 31 days over 32°C with an average daily maximum of 36°C. Total precipitation for the month was 29mm which is 51mm below average. September had 12 days over 32°C. The monthly minimum was on 23 September when the temperature dropped to -1°C. The precipitation was 51mm which was 52mm below normal for the month.

YIELD

All analyses were conducted using individual plants as observations rather than on a per plot or a subplot basis since there is a great deal of variability in tunneling among borers. The splitting of individual stalks gave an estimate of the extent of this damage.

It was evident that the BT sprayings were not completely effective at controlling the natural infestation of ECB's, since tunnels were found in uninfested plants and positions on the plants. This made the source of the tunnels in the infested plants questionable and few true controls were found. Since southwestern corn borers are not a problem in northeastern Kansas and their tunnels are usually distinguishable from European corn borer tunnels an analysis was conducted to see if there was an effect due to the natural ECB infestation. Plants that were infested with SWCB's in either location on the stalk, but had no ECB's applied were analysed to see if the effect of the natural ECB tunnels was significant. The designed effects (desiccation, position, etc) were fixed variables but the natural ECB's were a continuous range with as many as six ECB's per plant. Most plants had from zero to three ECB's.

Table 1 shows that there were no effects on yield, kernel number or kernel weight due to the presence of the nontreatment ECB's. Since BT was applied during the most sensitive growth stage, it appears that the natural infestation occurred late enough that damage was minimal, but the tunnels from naturally occurring ECB could not be distinguished from treatment ECB. Therefore the designed treatments were used for further analysis.

Table 1. ANOVA for natural infestation of ECB on plants artifically infested with SWCB.

		Mean Squares		
Source	df	Yield (kg/ha)	Kernel number/ plant	Kernel weight (g/100)
Designed effects	15	30943555**	22745	255.9**
Natural ECB	1	2545512	5909	9.4
Error	240	4277487	20518	12.4
Total	256			

* significant at 5% level
** significant at 1% level

There was also a problem with the hand infested borers (Table 5). Even on the nondesiccated plants the experimental numbers were not attained. There was also a substantial decrease in the number of artificially infested borers that tunneled in plants that were desiccated. This was especially true for the SWCB's, whose numbers were very low in desiccated plants (Table 2). This is surprising since the borers had two weeks prior to desiccation in which to tunnel and greenhouse work showed the SWCB's to rapidly tunnel into the plant. The natural and artifical infestations of ECB's were also affected by desiccation. On desiccated plants the number of naturally occurring ECB per plant was reduced by not quite one with SWCB's present and on controls by about two (Table 3). On desiccated plants artifically infested with ECB the number of naturally occurring ECB per plant was reduced by about two and on controls by one (Table 4).

Table 2. Effects of desiccation and number of SWCB larvae placed on plants on mean numbers of SWCB tunnels found.

	Experimental Number SWCB	
	0	2
Nondesiccated	0.11c#	1.06a
Desiccated	- 0.02c	0.36b

#Means with the same letter are not significantly different at the 5% level using the least significant means test.

Table 3. Effect of desiccation and number of SWCB larvae placed on plants on mean numbers of ECB tunnels found.

	Experimental Number SWCB	
	0	2
Nondesiccated	2.73a#	2.66a
Desiccated	0.77c	1.81b

#Means with the same letter are not significantly different at the 5% level using the least significant means test.

Table 4. Effect of desiccation and number of ECB larvae placed on plants on mean numbers of ECB tunnels found.

	Number ECB	
	0	3
Nondesiccated	1.95b#	3.44a
Desiccated	0.79c	1.79b

#Means with the same letter are not significantly different at the 5% level using the least significant means test.

The purpose of desiccation was to determine if the disruption of the translocation of stored assimilates by tunneling was responsible for the yield losses due to infestations of ECB and/or SWCB. The desiccant was applied two weeks after silking when kernel number was stable, but kernel weight was still sensitive to stress. Desiccated plants would be dependent on their ability to remobilize stored reserves. By one week after spraying, 75% of the green leaf tissue was killed. By two weeks after application of the desiccant, 100% of the leaf tissue was dead.

Yield and kernel weight reductions due to desiccation were significant at the 5% level (Table 5). Kernel number was significant at 10% (Tables 5 and 6). The desiccation * treatment interaction was significant for yield and kernel weight but not kernel number (Table 5).

Table 5. ANOVA for yield, kernel number, kernel weight, number of SWCB tunnels and number of ECB tunnels.

Source	df	Yield (kg/ha)	Kernel number/ plant	Kernel weight (g/100)	Number SWCB tunnels	Number ECB tunnels
		Mean squares				
Block	4	10526381*	26741	165**	0.9*	1.6
Desiccation	1	891062765**	59881+	7018**	15.7**	195.9**
Error (a)	4	17698498	83158	75	1.9	6.6
Treatment	7	9466342*	44989*	46**	8.8**	26.2**
SWCB	(1)	51552262**	54679	214**	52.5**	27.3**
ECB	(1)	1636395	2956	9	2.6**	182.0**
ECB*SWCB	(1)	5245798	34188	<1	2.6**	0.3
Position	(1)	171114	35589	9	0.02	0.1
SWCB*Position	(1)	15535456*	123346*	72*	0.2	2.2
ECB*Position	(1)	2450779	47755	1	0.1	11.1*
ECB*SWCB*Position	(1)	1186550	10	8	1.1+	0.0
Des*Treat	7	16806554**	20498	63**	2.1**	13.4**
Des*SWCB	(1)	59303705**	89	419**	9.7**	36.1**
Des*ECB	(1)	17199684*	45608	4	0.2	7.2+
Des*SWCB*ECB	(1)	375513	20928	6	0.1	29.9**
Des*Pos	(1)	2081426	18788	14	1.7	1.2
Des*Pos*SWCB	(1)	7143134	32294	<1	0.9	8.7*
Des*Pos*ECB	(1)	10094452	317	8	0.1	3.8
Des*Pos*SWCB*ECB	(1)	3147050	5715	2	0.6	3.9
Error (b)	497	3943879	21051	13	0.3	2.0
Total	520					
CV		25	24	16	136	69

+ significant at the 10% level
* significant at the 5% level
** significant at the 1% level

Table 6. Effect of desiccation on yield, kernel number and kernel weight.

Treatment	Yield (kg/ha)	Kernel number/ plant	Kernel weight (g/100)
Nondesiccated	9155a#	614a	26.66a
Desiccated	6302b	591a	18.66b

#Means with the same letter are not significantly different at 5% level using the least significant means test.

Kernel number, was reduced only when SWCB's were present in the middle of the plant (Table 7). Since kernel number is fixed by two to three weeks after silking, the reduction would have to be effected by the borers rapidly stressing the plants after infestation. It would then appear that when SWCB's infest the ear zone they stress the plant more quickly than ECB's. This would indicate some interaction between the size and shape of the tunnels and function of vascular bundles in that region. The double leaf trace vascular system described by Kumazawa (1961) could be helpful in explaining the distribution and remobilization of assimilates in infested plants. The method of loading and unloading of assimilate is still unclear (Gifford and Evans, 1981), but even with the cross bridging of vascular bundles described by both articles, phloem loading and unloading could be affected by borers.

When plants depended exclusively on their stored reserves (by desiccating the leaves) the only important factor for kernel weight was SWCB infestation (Table 8). The desiccated plants which had SWCB were able to compensate for low kernel number with higher kernel weight (Table 9). These plants would have, by comparison, no respiratory demands on them. Since most water is used for transpiration, if SWCB disrupts water transport then the removal of leaves would decrease the importance of SWCB infestation.

This still does not explain how yields for nondesiccated plants could be improved by the presence of ECB and yields for desiccated plants could be improved by the presence of SWCB (Tables 10 and 11). Looking at the actual number of borer tunnels adds nothing clarify this. Even though the borer number was reduced by the desiccation, there was still more tunneling in the plants with artifical infestations than there was in the control plants both for SWCB's and ECB's. To clarify this area another experiment must be done to follow the soluble carbohydrate content of the stalk during grain fill. It may be that the plant has stored more reserves in the stalk prior to the desiccation due to a smaller sink (fewer kernels) or due to some other compensation factor.

Table 7. Effect of SWCB by position on kernel number.

	Number SWCB	
	0	2
Middle	621a#	568b
Base	606a	617a

#Means with the same letter are not significantly different at the 5% level using the least significant means test.

Table 8. Effect of SWCB by desiccation on kernel weight.

	Number SWCB	
	0	2
Nondesiccated	26.93a[#]	26.39a
Desiccated	16.90c	20.13b

#Means with the same letter are not significantly different at the 5% level using the least significant means test.

Table 9. Effect of SWCB by position on kernel weight.

	Number SWCB	
	0	2
Middle	21.66c[#]	23.79a
Base	22.16bc	22.73b

#Means with the same letter are not significantly different at the 5% level using the least significant means test.

Table 10. Effect of SWCB by desiccation on yield.

	Number SWCB	
	0	2
Nondesiccated	9179a[#]	9131a
Desiccated	5550c	6921b

#Means with the same letter are not significantly different at the 5% level using the least significant means test.

Table 11. Effect of ECB by desiccation on yield.

	Number ECB	
	0	3
Nondesiccated	8906b#	9405a
Desiccated	6368c	6104c

#Means with the same letter are not significantly different at the 5% level using the least significant means test.

LEAF NUMBER

Although there were treatment differences in the ANOVA for leaf number (Table 12), there was no treatment * date interaction. The first leaf count was taken during the week of infestation, so a loss due to infestation should have caused an interaction.

While keeping leaf counts I noticed some unusual abcission of green leaves, especially the ear leaf. These were otherwise healthy leaves found on plants with borer tunnels in the ear zone. This is an abnormal occurence in corn which does not abscise its leaves as do legumes. I feel this is an important observation, but it did not occur often enough to be significant in the analysis.

Table 12. ANOVA for leaf numbers.

Source	df	Number of Leaves/Plant
		Mean Squares
Replicate	4	61**
Date	6	1784**
Error (a)	24	20
Treatment	7	17**
Treatment*Date	41	3
Error (b)	2301	3
Total	2383	
cv	17	

* significant at the 5% level
** significant at the 1% level

Greenhouse

WATER USE

Treatment was significant at 5% in the ANOVA (Table 13). The means and LSD's for treatments are shown on Table 14. Water use values for all treatments were lower than the control with the SWCB treatment and the ECB in the base being significantly different from the control at the 5% level. This would indicate that transfer of water was disruted by tunneling. This was most likely due to the cutting of vascular bundles. This would indicate that water use was affected by the presence of borers.

Table 13. ANOVA for water use.

Source	df	Water use (kg)
		Mean Squares
Replication	1	0.249387**
Date	19	1.011791**
Error (a)	19	0.008656
Treatment	4	0.024972**
Treatment * date	76	0.004570
Error (b)	869	0.005143
Total	988	
cv	21.1	

* significant at the 5% level
** significant at the 1% level

Table 14. Effect of borers on water use.

Treatment	Water use (kg)
Control	0.353a#
1 SWCB (base)	0.325c
2 ECB (base)	0.333bc
2 ECB (middle)	0.345ab
4 ECB (middle and base)	0.344ab
LSD .05	0.014

#Means with the same letter are not significantly different.

LEAF AREA

Total green leaf area was measured for each plant day of the year 121 for assignment of replications. All other leaf area measurements were taken at the time of photosynthetic readings and only include the plants that were used for those readings. Thus not all dates include measurements on the same plants. Although treatments were significant at the 1% level there was no treatment by date interaction (Table 15) as would be expected if borers affected leaf area. An experiment with weekly leaf area measurements like those for the field study may have been more informative.

Table 15. ANOVA for green leaf area per plant.

Source	df	Leaf Area (cm^2/plant)
		Mean Squares
Replication	1	21710659**
Date	5	20354942**
Error (a)	5	905618
Treatment	4	6955149**
Treatment*Date	20	96228
Error (b)	174	953446
Total	209	
cv	19	

* significant at the 5% level
** significant at the 1% level

CARBON DIOXIDE FLUX

The ANOVA for CO_2 flux is found in Table 16. Only date was significantly different. There was no treatment effect or treatment*date interaction. There appeared to be no shut down of photosynthesis due to borer infestation.

Table 16. ANOVA for photosynthetic flux.

Source	df	Photosynthetic Flux mg $CO_2/(m^2$ leaf s)
		Mean Squares
Replication	1	0.050835
Date	4	0.131057**
Error (a)	4	0.035528
Treatment	4	0.048236
Treatment * Date	16	0.021445
Error (b)	75	0.032161
Total	104	
cv	24.8	

* Significant at the 5% level
** Significant at the 1% level

DRY MATTER

No significant treatment differences were found for dry weight of leaves or roots (Table 17), but stem, ear and total weights were significant at the 5% level. When single degree of freedom contrasts were there were some significant effects for roots and leaves. Plants with four ECB had higher leaf weights than plants with two borers at either location (32.78g vs 27.10g for middle leaves and 10.99g vs 9.30g for lower leaves). Roots for all infested plants were decreased from controls (44.30g vs 52.23g).

Controls had the highest means for the dry weights of lower stems, ears and total dry weight (Table 18). The controls were significantly higher than all treatments for total dry weight and were significantly higher than the four ECB (2 in the middle and 2 in the base) and the two in the base treatments for ear weight. There were no differences among the four infestation treatments in total dry weight.

The location of the borer tunnels correspond to the portion of the stalk with decreased dry weights (Table 18). The amount of stalk actually consummed by the borer is relatively small in comparison to the dry weight differences found for these locations. Decreased stalk dry weight could be related to increased respiration or decreased translocation and/or decreased photosynthetic activity for these regions.

Table 17. ANOVA for dry matter.

		Middle		Base				
Source	df	Leaf (g)	Stem (g)	Leaf (g)	Stem (g)	Ears (g)	Roots (g)	Total (g)
		Mean Squares						
Replication	1	590.1	249.7**	75.9**	154.6+	498.1+	289.4	5394.0**
Harvest date	9	52.1	275.5**	11.6	570.1**	237.0**	2622.4**	14023.5**
Treatment	4	130.8	81.6*	12.4	119.7*	400.5*	423.0	1799.1*
None vs any	(1)	1.2	18.1	2.9	297.5**	793.5*	992.0+	6671.4**
SWCB vs ECB	(1)	78.2	1.4	6.5	47.9	679.5*	138.2	7.8
#2 vs 4	(1)	429.8*	204.9*	38.2*	26.8	10.4	464.5	298.0
#Mid vs Base	(1)	15.7	103.7+	0.0	95.2	149.4	67.3	69.9
Hdate*Treat	36	49.8	45.1	9.3	55.3	63.9	306.3	910.0+
Error	49	66.2	33.0	7.2	40.4	133.0	344.1	590.1
Total	99							
cv		28.7	18.8	27.5	16.6	48.9	40.4	13.8

+ significant at the 10% level
* significant at the 5% level
** significant at the 1% level
# Only ECB treatments were used in this comparison.

Table 18. Effect of borers on dry matter weights.

Treatment	Middle stem(g)	Base stem(g)	Ears (g)	Total (g)
Control	31.47ab#	41.69a	29.34a	192.98a
1 SWCB (base)	30.47abc	35.91b	27.13ab	171.26b
2 ECB (base)	33.24a	36.75b	22.84abc	175.63b
2 ECB (middle)	30.02abc	39.84ab	18.98c	173.01b
4 ECB (middle and base)	27.71c	36.88b	20.03bc	169.59b
LSD .05	3.65	4.04	7.32	15.43

#Means with the same letter are not significantly different.

Conclusions

From the field and greenhouse studies some general conclusions can be drawn.

1. There appear to be differences in the effect of ECB's and SWCB's. The Southwesterns appear to act more rapidly and are more likely to decrease kernel numbers if they both infest at the same time. For some reason plants infested with SWCB's were better able to call on their reserve carbohydrates or had more reserve carbohydrate.

2. Water use appears to be sensitive to borer infestation. It also appears to be location sensitive with tunneling in the ear zone decreasing water use more than tunneling in the base.

3. Neither leaf area nor photosynthetic flux was significantly affected by the presence of either species, even though there were instances of unexplained abscission of green leaves in the field.

How plants infested with SWCB's could yield more than controls (even though it was under the nonnormal conditions of desiccation) is very difficult to explain. The tunneling characteristics could possibly be a key. If damage was done early enough so that major paths to the ears were disturbed and assimilates were stored in the stalk then there could be more carbohydrate to remobilize during the later stress.

The total plant dry weight differences in the greenhouse were similar to the the grain yield losses of 9% in SWCB reported by Scott and Davis (1974) and 12% for ECB reported by Scott et al. (1967). Since the greenhouse experiment was thorough in covering the possible physiological causes for yield decreases and there were no significant differences, it would seem likely that the precision of the experiment was not high enough to identify the cause of loss. A gradual decrease in assimilate accumulation due to slightly decreased photosynthetic ability would be very hard to distinguish with the few readings that were taken (coefficent of variation 25%). A study that would look at the distribution of soluble sugars during grain fill and CO_2 utilization under high intensity lighting (so the experiment would not be weather dependent for the measurement of CO_2 uptake), would perhaps provide the needed information.

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EFFECT OF EUROPEAN AND SOUTHWESTERN CORN BORERS ON TRANSLOCATION OF PHOTOSYNTHETIC PRODUCTS, WATER USE AND YIELD IN *Zea mays* L.

by

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Farmers in south central Kansas are plagued by both the European corn borer Ostrinia nubilalis Hubner (ECB) and the southwestern corn borer Diatraea grandiosella Dyer (SWCB). Both can cause yield losses due to lodging, but both are known to cause nonmechanical losses also. Whether the presence of both species in one plant has a different affect than either alone has not been studied. The plant process or processes the borers affect (water use, assimilate transfer or photosynthesis) has not been shown nor how these processes contribute to the yield loss.

This study was conducted 1. to determine the method of nonmechanical yield losses due to infestations by ECB and SWCB and 2. to determine the losses when both are present in the same plant.

The plant processes observed were assimilate accumulation/transfer, CO_2 utilization (photosynthesis) and water use. This information would then be available for use in the CORNF model giving it more accuracy in regions with natural populations of ECB and SWCB.

A field study was conducted at the Ashland Experiment Field, Manhattan, Kansas to study the ability of corn to remobilize stored carbohydrates when infested with three European (ECB) and/or two southwestern (SWCB) corn borer larvae either in the middle or the base of the stalk.

One half of the plots were desiccated to study translocation of stored carbohydrate to the ear. Weekly leaf numbers were also kept to see if leaf number was affected by borer infestation.

The greenhouse experiment was conducted to study water use and photosynthetic activity for plants infested with 1SWCB in the base or two ECB in the base or middle or four ECB, two in the middle and two in the base. Plants were weighed twice a day between waterings to determine water use. CO_2 uptake measurements were taken and photosynthetic flux was calculated. Plants were periodically harvested and dry weights and tunneling data were recorded.

From the field experiments there appear to be differences in the effect of ECB's and SWCB's. The southwesterns appear to act more rapidly and are more likely to decrease kernel numbers when both infest at flowering. For some reason plants infested with SWCB's were better able to call on their reserve carbohydrate or had more reserve carbohydrate.

In the greenhouse a significant difference of approximately 10% was found between the total dry weight of the controls and infested plants. This was similar to the yield differences found in the literature for SWCB and ECB, but none of the plant processes tested showed significant differences to show were the loss occurred. It is doubtful that there was an plant processes missed that would have accounted for that loss. It is possible that the work done on photosynthetic flux by CO_2 utilization had too much variation to find the small changes in photosynthetic activity that would produce a loss of 10%.