DIMBOA Concentration in Leaf Tissue at Various Plant Growth Stages in Relation to Maize Resistance to Asian Corn Borer[1]

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Summary

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The chemical analytical values obtained for MBOA (6-methoxy-2-benzoxazolinone) were related to the labile cyclic hydroxamic acid precursors DIMBOA (2,4-dihydroxy-7-methoxy-(2H)-1,4-benzoxazin-3(4H)-one) which is formed enzymatically from its glucosides when leaf tissues are crushed or placed at high temperature. The results of chemical analysis revealed that the MBOA concentrations in leaf tissue decreased as the plants grew toward maturity, inversely the TLC plate ratings increased as the plants grew older. This showed that higher MBOA concentrations existed in the leaf tissue of earlier stage plants than in those of later ones. Leaf-feeding ratings after artificial infestation with Asian corn borer (ACB), *Ostrinia furnacalis* (Gueńee) egg masses and number of surviving borer larvae per plant increased as the plants grew older, indicating that younger plants were more resistant than older ones to corn borer feeding. Of 11 inbred lines tested JT 30-1-1-1-15-3 and CI31A had lower leaf-feeding ratings, lower number of surviving larvae per plant and higher MBOA concentrations than any other lines at various stages of plant development. This implies these 2 lines possess a remarkable degree of resistance to leaf feeding by corn borer.

The correlation coefficients of MBOA concentrations with leaf-feeding ratings at the 4th, 6th, 8th, 10th, and 12nd leaf stages are as followings: −0.85, −0.84, −0.86, −0.82, and −0.84 respectively, meanwhile the correlation coefficients of MBOA

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concentrations with number of surviving larvae at the same leaf stages, in order, are as follows: −0.88, −0.83, −0.82, −0.78 and −0.80, respectively. The negative correlations of MBOA concentrations with leaf-feeding ratings and number of surviving borer larvae per plant were highly significant. This means the higher the MBOA concentrations in leaf tissue, the lower the leaf-feeding ratings and number of surviving borer larvae per plant. The results prove that DIMBOA is an important chemical factor in maize responsible for resistance to the ACB.
Key words : Corn leaf stage, DIMBOA, Asian corn borer, Insect resistance.
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Introduction

DIMBOA (2,4-dihydroxy-7-methoxy-(2H)-1,4-benzoxazin-3(4H)-one) was first found to be associated with resistance in crop plants to insect pests when Klun et al (1967)[6] isolated it from maize seedlings and bioassayed in an artificial diet for the European corn borer (ECB), *Ostrinia nubilalis* (Hubner). They found that this compound inhibited larval development and caused 25% mortality. These results and associated experimental evidence revealed that the compound is a chemical factor in the resistance maize to lst-brood ECB. As a result, DIMBOA concentration in leaf tissue was used as one of indicators for selecting resistant inbreds of maize to leaf-feeding by the ECB[7,12,13]

The concentration of DIMBOA in a maize plant was varible within the parts where it existed. Concentrations were generally highest in the roots and then in decreasing order of concentration in the stalk, whorl and leaf[7]. Moreover, the concentrations in plant parts were different for each inbred. Biosynthesis of the benzoxazinone took place throughout the development of the plant, but the overall concentration in the whole plant decreased as the plant matured[7]. The high concentration of DIMBOA in seedling corn may explain the apparent resistance of young corn to the ECB.[5,7]

DIMBOA occurs as glucoside in intact tissue. When plant tissues are crushed, the glucoside is hydrolyzed by a plant enzyme to the aglucone, 2,4-dihydroxy-7-methoxy-(2H)-1,4-benzoxazin-3(4H)-one (DIMBOA). DIMBOA is chemically labile and slowly decomposes to 6-methoxy-2-benzoxazolinone (MBOA), which is chemically stable[7] (Fig. 1). Thus, DIMBOA concentration in plant tissue could be estmiated by analyzing for MBOA. The MBOA analytical value is interpreted as a stoichiometric measure of DIMBOA formed as the result of enzymatic cleavage of its glucoside precursor[6].

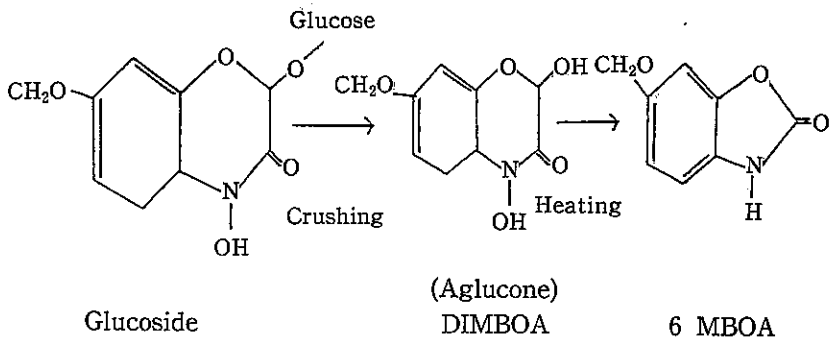


Fig. 1. Formation of DIMBOA (Aglucone) and MBOA from a glucoside occurring in maize tissue

Klun et al (1970)[9] used a diallel set of 11 inbreds of maize (55 single cross hybrids) to study the concentration of DIMBOA in whorl leaf tissue and the resistance to leaf feeding by first-generation ECB. The correlation between concentration of DIMBOA in plant tissue and level of rsistance was highly significant for the inbreds ($r = -0.89$) and the single crosses ($r = -0.74$). Genetic effects due to general and specific combining ability were highly significant for both traits, but general combining ability accounted for 84% of the variation in the resistance ratings and for 91% of the variation in the concentration of DIMBOA. These results provide further evidence that DIMBOA is a chemical factor in the resistance of maize to the ECB. Neverthless, most chemicals have their specific properties in host plant resistance (HPR) to insects[1,5]. Whether the maize inbreds with high DIMBOA concentration would exhibit similar levels of resistance to the ACB *Ostrinia furnacalis* (Gueńee) needed further study. This study was done to determine the changes of DIMBOA concentration in all stages of plant development whole life and evaluate its relation with the resistance in maize to leaf-feeding by ACB.

MATERIALS and METHODS

The 11 dent corn inbreds chosen in this study and their origins were listed in Table 1. The experiments were conducted at Potzu Branch Station, Tainan DAIS Potzu, Chiayi in four replications with a split-plot design [Main plots : inbreds; subplots: plant growth stages; sub-subplots: infesting artificial ACB egg masses[15] inside the whorl leaves and cutting the whorl leaves for chemical analysis of DIMBOA concentration (Fig.2)] The plant growth stages consisted of

4^{th}, 6^{th}, 8^{th}, 10^{th}, and 12^{nd} leaf stages. Each leaf stage is defined according to the uppermost leaf whose leaf collar is visible[10].

Table 1. Eleven dent corn inbreds used in the study and their origins

Inbred	Derivation	Origin
1. JT 30-1-1-1-15-3	JWL. 305 x Tainan DMR # 2	CIMMYT
2. YT 148-2-1-1-2-1	Yellow hard endosperm x Tainan DMR # 2	CIMMYT
3. ST 153-1-3-2-2-1	South African Yellow x Tainan DMR # 2	CIMMYT
4. CT 139-5-1-1-1-1	Cogollero x Tainan DMR # 2	CIMMYT
5. ANMT 55-1-3-2-2-1	(Amber x (B 57 x B 37) x Akbar) x Tainan DMR # 2	CIMMYT
6. PT 169-1-1-4-1-1	Pendu x Tainan DMR # 2	CIMMYT
7. ANT 176-1-3-5-13-3	Antigua Gr. x Tainan DMR # 2	CIMMYT
8. B 49	Iowa 2 ear syn.	Iowa State
9. CI31A	Midland "A" O. P.	USDA
10. B 52	Midland	Iowa State
11. WF 9	Wilson Farm Reid	Indiana State

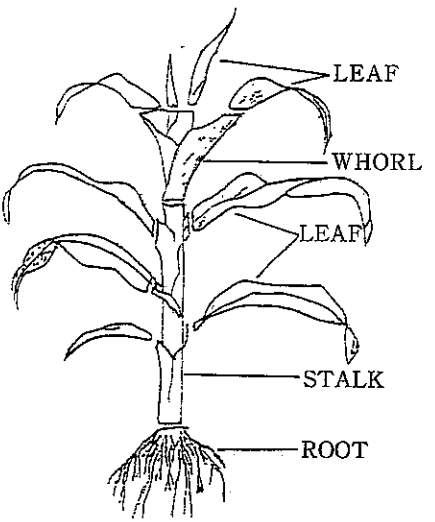


Fig. 2. Samples of plant tissues taken for chemical analysis of DIMBOA concentration (Klun & Robinson, 1969)

The 11 inbreds were each planted in 10 row-plot (twenty- four hills of two seeds/hill and thinned to one plant/hill) in 1985 and 1986. The distance between rows was 75 cm, between hills within row was 25 cm.

Five rows in each plot were infested with ACB egg masses at 4^{th}, 6^{th}, 8^{th}, 10^{th} and 12^{nd} leaf stages of plant development, respectively. Infestations were made in 3 applications of 3 egg masses (ca. 300 eggs/plant), each spaced 1 day apart. Leaf feeding damage was visually rated on a plot basis in a 9-class rating system 21 days after egg hatch[4]. After rating, 10 plants from each row were dissected to count the number of surviving borer larvae per plant.

The description for this 9-class rating system is as follows:

class 1. No visible leaf injury, or a small amount of pin or fine shot-hole type of injury on a few leaves (Fig.3).
class 2. Small amount of shot-hole type lesion on a few leaves.
class 3. Shot-hole injury common on several leaves.
class 4. Several leaves with shot-hole and elongated lesions.
class 5. Several leaves with elongated lesions.
class 6. Several leaves with elongated lesions (ca. one inch).
class 7. Long lesions common on about one-half of the leaves.
class 8. Long lesions common on about two-thirds of the leaves.
class 9. Most of the leaves with long lesions (Fig.4).

The other 5 rows in each plot were used for DIMBOA analysis. Whorl leaves from 10 plants in each row were collected at 4^{th}, 6^{th}, 8^{th}, 10^{th} and 12^{nd} leaf stages of plant development, respectively. The whorl leaves collected were placed in plastic bags and frozen at −23℃ until used. The frozen leaf tissue was thawed, dried in an oven at 45℃, and ground into a fine powder for DIMBOA analysis. The chemical determinations were actually for MBOA, expressed as mg MBOA/g of plant tissue[2,7,8,9,16]

The procedures used to obtain quantitative measurement of MBOA in leaf tissue were modified from the procedures used by Klun and Robinson (1969)[7]. For each sample, 20 ml of boiling water were added to a 70 ml jar containing 0.5 g of dried-ground leaf tissue; after shaking vigorously for 1 min., this solution was poured into a Beuchner funnel (lined with filter paper), and an aspirator vacuum filtered the filtrate into a 500 ml flask, The filtrate was poured into a 100 ml beaker and was allowed to cool (the leaf residue was discarded). Four drops of concentrated HCL were added to acidify the filtrate to pH 1. The acidified filtrate was poured into a separatory funnel 40 ml of diethyl ether were poured into the funnel. After vigorously shaking the funnel; the water and ether

Fig. 3. Resistant inbred line of dent maize rated 1 according to the visual rating system (Guthrie et al. 1960)

Fig. 4. Susceptible inbred line of dent maize rated 9 according to the visual rating system (Guthrie et al. 1960)

were allowed to separate, then each was drained into 100 ml beakers; the water was then poured back into the separatory funnel. To wash MBOA from the water layer as completely as possible, the procedure involving the separatory funnel was repeated thrice, then the water layer was discarded. Anhydrous calcium chloride was added to the ether layer to remove any water left in the ether. The ether was allowed to evaporate under a fume hood, and the ether soluble residue was dissolved in 1 ml ethyl acetate-benzene (1:1 vol/vol).

A 100 μ l aliquot of this solution was then spotted on a 20 x 20 cm glass plate covered with a thin layer of silica gel (GF 254 Brinkmann Instrument^{R}, Westbury, NY). Six samples and commercial MBOA (as a reference) from Calbiochem-Behring Corp., P. O. Box 12087, San Diego, California, were spotted on an individual plate. Each sample of the 4 replications was repeated twice. The 7 spots were placed along one edge of the plate.

After spotting, the chromatogram from leaf tissue was developed with chloroform : ethyl-acetate : cyclohexane (in the ratio 4:4:2 vol/vol). After development, the plates were removed from the solution, dried, and then redeveloped in the same direction with cyclohexane : isobutanol (in the ratio 85 : 15 vol/vol). Once the chromatogram was air-dried, two observers visually rated, under short wave UV light (254 nm), the intensity of each MBOA spot from the extracts in classes of 1 to 5 (1= highest intensity, 5= lowest intensity) as described by Robinson et al. (1982)[11].

When the intensity ratings were completed, the area of the silica gel corresponding to the reference MBOA spot was scraped from the chromatogram and was transferred to a disposable pasteur pipette plugged with glass wool. MBOA was then eluted from the silica gel with 6 ml of 95% ethanol; the UV absorbance of this solution was then measured at 231 nm with a Beckman Model DB Spectrophotometer. The UV spectrophotometric percent transmission (T %) was read twice for each sample. The MBOA concentration (mg MBOA/g dried leaf tissue) was calculated from a MBOA standard curve.

Thus, we used 2 methods for measuring DIMBOA concentrations in maize leaf tissue : (1) Chemical analysis for mg MBOA/g of maize leaf tissue and (2) thin layer chromatography to rate differences visually in the concentration of MBOA (TLC plate rating).

Data on leaf-feeding ratings, number of surviving larvae per plant, mg MBOA/g dried leaf tissue and TLC plate ratings collected from above experiments were statistically analyzed to elucidate significant differences among all experimental results (Steel and Torrie. 1960)[14].

Results

MBOA Leaf Tissue Content and TLC Readings— — The results of chemical analysis for MBOA concentration and TLC plate rating for MBOA spot intensity (Table. 2) revealed that the highest MBOA concentrations were at the 4th leaf stage and the lowest were at the 12nd stage for all inbreds. Among all inbreds tested JT 30-1-1-1-15-3 and CI31A had the highest and WF 9 had the lowest MBOA concentration in all plant growth stages. The former possessed about 3 times more MBOA than the latter. The TLC plate ratings showed just the inverse, the highest ratings were at the 12nd leaf stage and the lowest were at the 4th leaf stage. JT 30-1-1-1-15-3 and CI31A had the lowest rating through all growth stages among all inbreds.

Table 2. Mean concentrations of MBOA in leaf tissue and TLC plate ratings at various leaf stages.

Inbred	Leaf stage									
	4	6	8	10	12	4	6	8	10	12
	mg MBOA/g dry weight					TLC plate ratings				
JT 30-1-1-1-15-3	3.60	3.25	2.85	2.50	2.15	1.7	1.8	2.2	3.0	3.5
YT 148-2-1-1-2-1	2.70	2.15	1.80	1.40	1.20	2.5	2.8	3.0	3.5	4.0
ST 153-1-3-2-2-1	2.51	1.81	1.65	1.10	0.85	3.5	4.0	4.5	4.5	4.5
CT 139-5-1-1-1-1	1.52	1.21	1.10	0.95	0.66	4.5	4.5	4.5	4.7	5.0
ANMT 55-1-3-2-2-1	2.01	1.80	1.41	1.20	0.95	4.0	4.5	4.5	4.8	5.0
PT 169-1-1-4-1-1	1.81	1.23	0.90	0.80	0.70	4.5	4.5	4.5	4.7	5.0
ANT 176-1-3-5-13-3	1.68	1.70	1.15	0.96	0.80	4.5	4.5	4.5	4.6	5.0
B 49	2.90	2.20	1.75	1.40	1.40	2.0	2.5	3.0	3.5	4.0
CI31A	3.56	2.90	2.60	2.45	2.10	1.7	2.0	2.5	3.0	3.5
B 52	2.31	1.80	1.45	1.30	1.25	3.5	3.5	4.0	4.5	4.5
WF 9	1.28	0.92	0.75	0.66	0.48	4.5	4.6	5.0	5.0	5.0

LSD (0.05)
Any two means of MBOA concentrations between leaf stages for the same inbred is 0.64
Any two means of MBOA concentrations between inbreds for the same leaf stage is 0.85
Any two means of TLC plate ratings between leaf stages for the same inbred is 0.45
Any two means of TLC plate ratings between inbreds for the same leaf stage is 0.55

Leaf Feeding Ratings and Larval Survival— — The results of leaf-feeding rating after artificial infestation with ACB egg masses and the number of

surviving larvae per plant (Table. 3) both increased as the plants matured, indicating that young plants were more resistant to leaf-feeding by ACB than older ones. Among all the inbreds tested JT 30-1-1-1-15-3 and CI31A had the lowest leaf-feeding rating and number of surviving borer larvae per plant in all leaf stages. CT139-5-1-1-1-1 and WF9 had the highest leaf-feeding ratings and numbers of surviving borer larvae per plant in all growth stages of plant development.

Table 3. Mean Leaf-feeding ratings after artificial infestation with ACB egg masses and number of surviving larvae per plant at various leaf stages.

Inbred	Leaf stages									
	4	6	8	10	12	4	6	8	10	12
	Leaf-feeding ratings					No. of surviving larvae				
JT 30-1-1-1-15-3	1.5	1.5	2.0	2.5	3.0	1.2	1.6	2.4	2.8	2.5
YT 148-2-1-1-2-1	2.5	3.0	3.6	4.5	5.5	2.2	3.0	5.0	7.5	6.5
ST 153-1-3-2-2-1	3.0	3.5	5.0	6.0	6.5	2.8	3.5	6.5	7.5	8.0
CT 139-5-1-1-1-1	5.0	4.5	6.0	6.5	7.5	5.6	6.5	7.0	8.5	8.8
ANMT 55-1-3-2-2-1	3.5	4.0	5.0	6.0	6.5	4.0	4.3	5.5	6.5	7.0
PT 169-1-1-4-1-1	4.0	4.5	6.0	6.0	7.5	4.4	6.2	7.6	8.4	8.6
ANT 176-1-3-5-13-3	4.0	4.5	6.0	6.0	6.5	4.8	5.0	6.5	7.3	6.8
B 49	2.5	3.0	4.0	5.0	5.5	2.8	3.5	5.0	5.5	4.5
CI31A	1.5	2.0	2.5	2.5	3.0	1.5	1.3	2.6	3.0	2.4
B 52	3.0	3.5	4.5	5.0	5.5	3.1	3.5	5.5	4.5	5.4
WF 9	5.0	5.5	6.5	7.5	8.5	6.5	8.0	8.5	9.8	10.5

LSD (0.05)

Any two means of leaf-feeding ratings between leaf stages for the same inbred is 1.0

Any two means of leaf-feeding ratings between inbreds for the same leaf stage is 1.5

Any two means of numbers of surviving larvae per plant between leaf stages for the same inbred is 1.1

Any two means of numbers of surviving larvae per plant between inbreds for the same leaf stage is 1.9

Correlation of MBOA Leaf Tissue Content with Leaf Feeding Ratings at various Leaf Stages— — The correlation coefficients of MBOA concentrations in leaf tissue of 11 inbreds with leaf-feeding ratings at 4^{th}, 6^{th}, 8^{th}, 10^{th} and 12^{nd} leaf stages were − 0.85,− 0.84, − 0.86, − 0.82 and − 0.84, respectively (Fig.5). The correlation of MBOA concentration with leaf-feeding rating was highly significant through all growth stages of plant development.

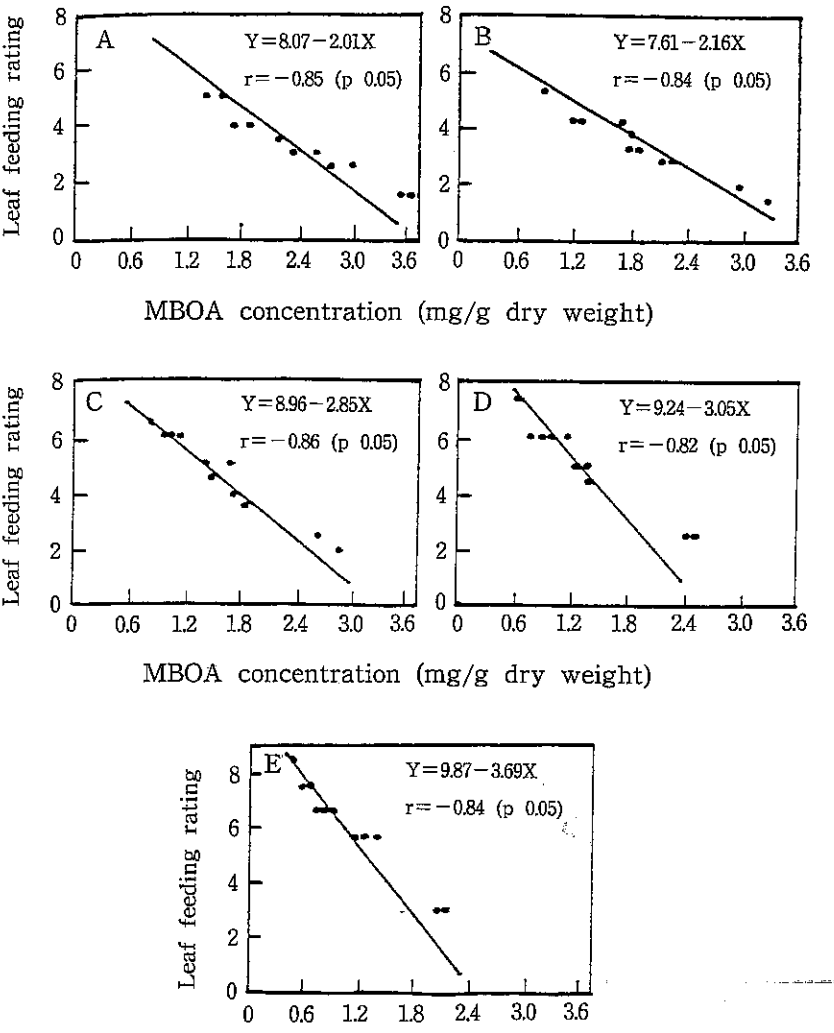
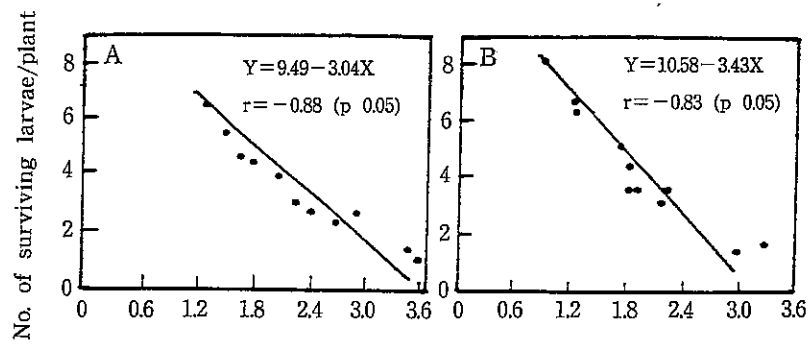
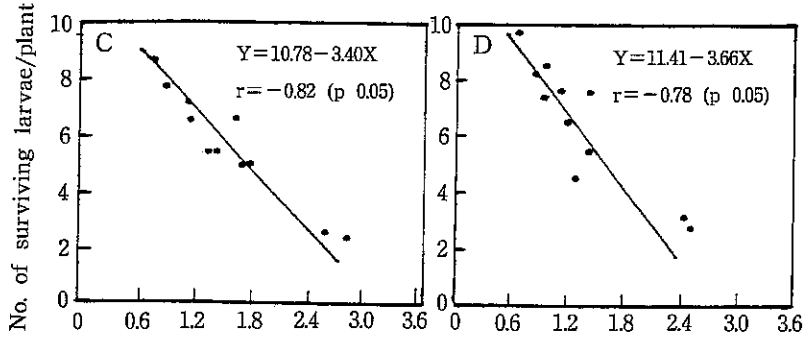


Fig. 5. Correlation coefficients of MBOA concentration in leaf tissue with leaf feeding ratings at the 4^{th}(A), 6^{th}(B), 8^{th}(C), 10^{th}(D) and 12^{nd}(E) leaf stages, respectively.

Correlation of MBOA Leaf Tissue Content with Larval Survival at various Leaf Stages——The correlation coefficients of MBOA concentrations in leaf tissue of 11 inbreds with number of surviving larvae per plant at 4^{th}, 6^{th}, 8^{th}, 10^{th} and 12^{nd} leaf stages were −0.88, −0.83, −0.82, −0.78 and −0.80, respectively (Fig. 6). The correlation of MBOA concentration with number of surviving larvae per plant was also highly significant in all growth stages of plant development.





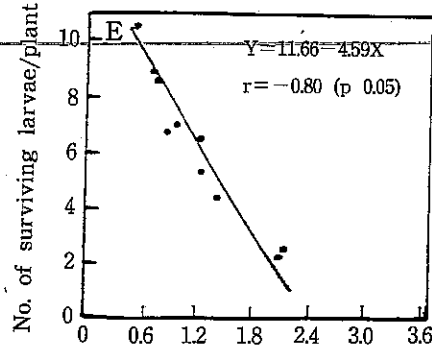


Fig. 6. Correlation coefficients of MBOA concentration in leaf tissue with number of surviving borer larvae per plant at the 4th(A), 6th(B), 8th(C), 10th(D) and 12nd(E) leaf stages, respectively.

Discussion

It is imperative to have resistant germplasm available for breeding any crop varieties with resistance to insect pests. For breeding of resistant maize cultivars to the Asian corn borer (ACB) *Ostrinia furnacalis* Gueñee. The situation is the same. The resistant maize germplasm to ACB could be obtained through:

1. Introducing or exchanging with foreign or domestic research institutes.
2. Identification from materials in stock or locally available.

However, since the resistancc mechanism in maize to ACB is unclear, it is difficult to know where to collect or how to identify the resistant germplasm[2,3]. The breeding of maize varieties resistant to ACB would be more efficient, if we knew more about their resistance mechanisms. In this study we used 11 inbreds to determine the relation of MBOA concentration in leaf tissue with resistance to ACB at various growth stages of plant development as well as to providing more information to identify resistant inbreds. The results from leaf-feeding ratings after artificial infestation with ACB egg masses at 4^{th}, 6^{th}, 8^{th}, 10^{th} and 12^{nd} leaf stages (Table. 3) indicated that the lowest leaf-feeding ratings and number of surviving borer larvae per plant were at 4^{th} leaf stages among all inbreds tested. However, leaf-feeding ratings and number of surviving larvae per plant increased as plants got matured. This indicated that the young plants were more resistant to ACB than the older ones. Therefore, if the inbreds could maintain the leaf-feeding rating and number of surviving larvae per plant in low level through all growth stages of plant development, they would possess the high resistance level to ACB. Among all inbreds tested JT30-1-1-1-15-2 and CI31A had the lowest leaf-feeding ratings and numbers of surviving larvae per plant at all leaf stages. This showed that JT30-1-1-1-15-3 and CI31A were more resistant to ACB than other inbreds.

DIMBOA [2,4-dihydroxy-7-methoxy-(2H)-1,4-benzoxazin-3(4H)-one] is chemically labile and slowly decomposes to 6-methoxy-2-benzoxazolinone (MBOA), which is chemically stable.[2,8] Thus, DIMBOA concentration can be determined by chemical analysis of dried plant tissue for MBOA[7,8,9]. The results of chemical analysis of MBOA concentrations and TLC plate ratings (Table. 2) revealed that MBOA concentration decreased as plants grew toward maturity. Inversely, TLC plate rating increased as plants grew older. This showed that young plants contained more MBOA concentration than that of older ones. Among 11 inbreds tested JT 30-1-1-1-15-3 and CI31A had the highest MBOA concentrations and the lowest TLC plant ratings. The correlation coefficients of MBOA concentrations with leaf-feeding ratings at 4^{th}, 6^{th}, 8^{th}, 10^{th} and 12^{nd} leaf stages were -0.85, -0.84,

−0.86, −0.82 and −0.84 respectively (Fig. 5) and the correlation coefficients of MBOA concentrations with numbers of surviving borer larvae per plant at the same leaf stages were −0.88, −0.83, −0.82, −0.78 and −0.80 respectively (Fig.6). These clearly indicated that the relation of MBOA concentration with leaf-feeding rating and number of surviving borer larvae per plant was highly significant. In other words, the higher the MBOA concentration in leaf tissue the lower were leaf-feeding rating and number of surviving larvae per plant. This means that the inbreds with greater MBOA concentration would possess a higher resistant level to ACB. The experimental data proved that DIMBOA was a significant biochemical factor in maize responsible for ACB resistance.

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不同生育期玉米葉部組織 DIMBOA 含量與其對亞洲玉米螟之抗性關係[1]

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摘 要

DIMBOA（2,4-dihydroxy-7-methoxy-(2H)-1,4-benzoxazin-3(4H)-one）是以葡萄甙（Glucoside）型態存在玉米（*Zea mays* L.）組織內。當組織受壓榨或在高溫下時，葡萄甙會漸次分解產生 DIMBOA，DIMBOA 性不穩定會再分解成 MBOA（6-methozy-2-benzoxazolinone）。MBOA 性穩定，因此 DIMBOA 在葉部組織之含量，可藉由分析定量 MBOA（mg MBOA/g dry weight）而推知。化學分析結果葉部組織 MBOA 含量及色層分析板上 MBOA 亮度級數于玉米生長過程中，前者隨葉齡增長而遞減，後者隨葉齡增長而增多，顯示幼期玉米葉部組織 MBOA 含量較老期者爲高。玉米葉部受玉米螟〔*Ostrinia furnacalis* (Guenee)〕爲害等級及幼蟲存活數／株，以人工接種螟蟲卵塊，每株接種 9 個卵塊（約 300 卵粒／株）進行測試，試驗結果兩者均隨著葉齡增長而增多，顯示幼期玉米之抗螟性較老期者爲强。供試十一玉米自交系中，以 JT 30-1-1-1-15-3 及 CI31A 二品系在生長過程中其葉部受螟蟲爲害級數及幼蟲存活數／株均較其他品系爲少，同時二品系在各葉齡期之葉部組織 MBOA 含量亦較其他品系爲高，顯示二品系具有相當程度之抗螟性。而葉部組織 MBOA 含量與葉部受螟害等級在第 4、第 6、第 8、第 10 及第 12 葉齡之相關值分別爲：－0.85、－0.84、－0.86、－0.82 及－0.84，同時葉部組織 MBOA 含量與幼蟲存活數／株在以上各葉齡下之相關值依序爲：－0.88、－0.83、－0.82、－0.78 及 －0.80，由此顯示葉部組織 MBOA 含量與葉部受螟害等級及幼蟲存活數／株之負相關極顯著，亦即玉米葉部組織 MBOA 含量越高之品系，其葉部受玉米螟爲害程度及幼蟲存活數／株越少，而其抗螟性也越强，由是可知 DIMBOA 是玉米抗亞洲玉米螟之重要化學成分而無疑。

關 鍵 詞：玉米葉齡、DIMBOA、亞洲玉米螟、抗蟲性。
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