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PHYSIOLOGICAL BASIS OF FALL ARMYWORM (LEPIDOPTERA: NOCTUIDAE) RESISTANCE IN SEEDLINGS OF MAIZE INBRED LINES WITH VARYING LEVELS OF SILK MAYSIN

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ABSTRACT

To assess both foliage- and ear-feeding insect resistance in the same maize inbred lines, fall armyworm, *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae) resistance at the seedling stage was examined in 6 corn inbred lines, including 4 CIMMYT maize inbred lines (CML333, CML335, CML 336, and CML338) with varying levels of silk maysin that confers corn earworm, *Helicoverpa zea* (Boddie), resistance and controls (fall armyworm-resistant Mp708 and susceptible AB24E). Fall armyworm injury rating and chlorophyll content were examined under greenhouse and field conditions. Plant height, plant stem circumference, and photosynthesis-related measurements were recorded on uninfested and infested plants only under greenhouse conditions. Injury ratings on CML333, CML336, and CML338 (with a range of low to high levels of silk maysin) were the same as for the resistant control (Mp708), and were significantly lower than for the susceptible control AB24E and CML335 (without silk maysin). Plant height, plant stem circumference, and chlorophyll content varied among the 6 inbred lines, but were not consistently correlated to resistance at the seedling stage. Photosynthetic rate was negatively affected by injury in AB24E, CML333, CML335, and CML336, but not affected in CML338 and Mp708. The reduction in photosynthetic rate of fall armyworm-susceptible AB24E, and in resistant CML333 and CML336 indicated that insect resistance in CML333 and CML336 might not be related to photosynthetic rate. At the same time, the data suggest that CML338 and Mp708 were tolerant to herbivory because no difference in either photosynthetic rate or photosynthetic capacity was detected in either inbred line between uninfested and injured corn seedlings. Further examination of photosynthetic capacity based on A/Ci and light response curves supported this resistance mechanism categorization. This experiment indicated that corn earworm-resistant corn inbred lines with varying levels of silk maysin could confer resistance to foliage-feeding fall armyworm at its seedling stage.

Key Words: CO_2 exchange rate, light response curve, A/Ci curve, host plant resistance, tolerance

RESUMEN

Para evaluar la resistencia de insectos que se alimentan del follaje y el elote en las mismas líneas endogámicas de maíz, la resistencia de la etapa de la plántula hacia el gusano cogollero, *Spodoptera frugiperda* (J. E. Smith) (Lepidóptero: Noctuidae) fue examinada en 6 líneas endogámicas de maíz, incluyendo 4 líneas endogámicas de maíz CIMMYT (CML333, CML335, CML 336 y CML338) con varios niveles de maysin en la seda que proveen resistencia y control contra el gusano del elote de maíz, *Helicoverpa zea* (Boddie), (Mp708 resistente al gusano cogollero y AB24E susceptible al gusano cogollero). La tasa del daño causado por el gusano cogollero y el contenido de clorofila fueron examinados bajo condiciones de invernadero y de campo. La altura de la planta, la circunferencia del tallo de la planta y medidas relacionadas con la fotosíntesis fueron registrados sobre plantas no infestadas y en plantas infestadas bajo condiciones en el invernadero. La tasa de daño sobre CML333, CML336 y CML338 (con bajos a altos niveles de maysin en la seda) fue igual que el control resistente (Mp708), y fue significativamente mas baja que en los controles susceptibles AB24E y CML335 (sin maysin en la seda). La altura de la planta, la circunferencia del tallo y el contenido de la clorofila varían entre las 6 líneas endogámicas, pero no fueron correlacionados consistentemente con la resistencia en la etapa de la plántula. La tasa fotosintética fue afectada negativamente por el daño en AB24E, CML333, CML335 y CML336, pero no afectada en CML338 y Mp708. La reducción en la tasa fotosintética de AB24E susceptible al gusano cogollero, y en las líneas resistentes, CML333 y CML336, indicó la posibilidad que la resistencia de los insectos en CML333 y CML336 no es relacionada con la tasa fotosintética. A la vez, los datos sugieren que CML338 y Mp708 son más tolerantes a las herbívoras por

que ninguna diferencia en la tasa fotosintética y la capacidad fotosintética fue detectada en ninguna de las dos líneas endogámicas entre las plántulas de maíz no infestadas versus en las plantas dañadas. Un examen adicional de la capacidad fotosintética basada sobre las curvas de A/Ci y la respuesta hacia la luz apoyó esta categorización del mecanismo de resistencia. Este experimento indicó que las líneas endogámicas de maíz resistentes a gusano del elote con niveles de maysin en la seda variables pueden proveer resistencia a los gusanos cogolleros que se alimentan del follaje en la etapa de la plántula.

Fall armyworm, *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae) is one of the most important whorl-feeding insect pests of corn production in the southeastern U.S. Corn resistance to *S. frugiperda* has been studied extensively, and a series of corn germplasm conferring *S. frugiperda* resistance has been developed at Mississippi State, MS (Brooks et al. 2007) and Tifton, GA (Wiseman et al. 1996) for corn production in the southern states. Although corn resistance to 2 whorl-feeding lepidopteran insects (i.e., fall armyworm and southwestern corn borer, *Diatraea grandiosella* Dyar (Lepidoptera: Crambidae)) has been examined previously (Abel & Adamczyk 2004; Brooks et al. 2007), multiple insect resistance to both whorl- and ear-feeding insects is not well understood. Only reports by Ni et al. (2007, 2008) have recently examined corn germplasm for multiple ear-feeding insect resistance. High levels of corn silk maysin has been considered an important phenotypic trait that confers ear-feeding corn earworm, *Helicoverpa zea* (Boddie), resistance in laboratory bioassays, but with varying levels of resistance under field conditions (Rector et al. 2002; Ni et al. 2008). However, it is still not clear whether inbred lines with varying levels of resistance to ear-feeding insects would confer whorl-feeding insect resistance.

In addition, physiological and biochemical mechanisms of whorl-feeding insect resistance in corn are not well understood. Several recent reports have examined the biochemical and physiological bases for insect resistance in both piercing-sucking and chewing insect pests on various crop plants. Oxidation and detoxification enzymes have been examined as biochemical bases for Russian wheat aphid, *Diuraphis noxia* (Mordvilko), resistance in wheat, barley and oat (Ni et al. 2001a; Ni & Quisenberry 2003), and chinch bug resistance in turf grasses (Franzen et al. 2007). Impact of both piercing-sucking and chewing insect herbivory on photosynthetic rate and photosynthesis capacity was examined to establish baseline information on the physiological basis of crop plants resistance to insect pests (Haile et al. 1999; Macedo et al. 2003; Peterson et al. 2004; Franzen et al. 2007; Macedo et al. 2007). In addition, *D. noxia*-elicited changes in photosynthetic pigments were also assessed to unravel the underlying mechanisms of aphid-elicited leaf chlorosis and photosynthetic pigment losses (Ni et al. 2001b; Ni et al. 2002; Heng-Moss et al. 2003).

Thus, we examined the possibility of identifying multiple insect resistance/susceptibility over multiple growth stages of the corn plants. We examined *S. frugiperda* resistance at whorl (V6) stage in 4 corn inbred lines from CIMMYT (CML333, CML335, CML336, and CML338) with varying levels of corn silk maysin with *S. frugiperda*-susceptible (AB24E) and resistant (Mp708) corn inbred lines as controls. Both greenhouse and field artificial infestations of the corn seedlings with *S. frugiperda* neonates were conducted. The objectives of this study were: (1) to determine *S. frugiperda* resistance in seedlings of the four CML inbred lines with varying silk maysin levels; and (2) to elucidate the physiological basis for fall armyworm resistance and/or susceptibility in these 6 corn inbred lines using photosynthetic measurement data.

MATERIALS AND METHODS

Plants and Insects

Six maize inbred lines were used, including 4 CIMMYT inbred lines (CML333, CML335, CML336, and CML338), and Mp708 and AB24E as resistant and susceptible controls, respectively, (Brooks et al. 2007; Ni et al. 2008). The silk maysin levels in CML333, CML335, CML336 were 0.17, 0, 0.07%, respectively, of its fresh silk weight (Ni et al. 2008), and the maysin level in CML338 was 0.48% of its fresh silk weight (unpublished data). All fall armyworm neonates used in this study were from a laboratory colony maintained in the Insectary in the Crop Protection and Management Unit, USDA-ARS, Tifton, Georgia.

Artificial Insect Infestation and Damage Rating

Experimental plants used in the greenhouse study were infested individually with 0 or 5 *S. frugiperda* neonates for each of the inbred line entries when the plants were at the 6-leaf (V6) stage. All plants in the field experimental plots were planted in a single-row plot 3 m in length, and were infested with 15-20 *S. frugiperda* neonates/plant, with the protocol by Davis et al. (1996). The insect injury ratings were conducted 7 and 14 d after the infestation with a scale of 1-9 as described by Davis et al. (1992) and Smith et al.

(1994). Briefly, 1 = no damage or few pinholes; 2 = few short holes on several leaves; 3 = short holes on several leaves; 4 = several leaves with short holes and a few long lesions; 5 = several holes with long lesions; 6 = several leaves with lesions < 2.5 cm; 7 = long lesions common on one half of the leaves; 8 = long lesions common on one half to two thirds of leaves; and 9 = most leaves with long lesions. While insect injury was rated by individual plants in the greenhouse study, injury rating under field conditions was recorded as the mean for all plants in an experimental plot.

Plant Height, Stem Circumference, and Leaf Chlorophyll Content

Height and circumference of corn plants were measured after the injury rating to assess the impact of insect injury on plant vegetative growth in the greenhouse study. Chlorophyll content of experimental plants in both greenhouse and field experiments was measured with a SPAD-502 chlorophyll meter (Konica Minolta Sensing, Inc., Osaka, Japan) on the top expanded leaf with leaf collar of the plants. Leaf chlorophyll content (μmol m^{-2}) was calculated according to a standard curve generated for this chlorophyll meter (i.e., chlorophyll (μmol m^{-2}) = $10^{(M^{0.261})}$), where M is the chlorophyll meter reading (Markwell et al. 1995). While only chlorophyll content of the infested plants was measured for the field experiment, chlorophyll content of all experimental plants (both infested and uninfested plants) was measured in the greenhouse experiments.

Photosynthetic Measurements

Photosynthesis-related parameters were measured on the plants used in the greenhouse study. The photosynthesis rate (also known as CO_2 exchange rate) of *S. frugiperda*-infested and control plants was assessed with a LI-6400R portable photosynthesis system (LI-COR Inc., Lincoln, NE). In addition, the photosynthetic capacity of the infested and control plants was assessed with CO_2 (or A/Ci) and light response curves. Because corn is a C_4 plant, the following parameters were used for the light and CO_2 response curves. A light response curve was generated by the gas exchange rates measured at light intensities at 2000, 1500, 1000, 500, 200, 100, 50, 20, 0 μmol photons m^{-2} s^{-1}, with a constant CO_2 concentration (400 ppm), whereas the CO_2 response curve (also known as assimilation rate plotted against intercellular CO_2 concentration, or A/C_i curve) was generated by the gas exchange rates measured at CO_2 concentrations at 400, 300, 200, 100, 0, 400, 400, 600, 800 ppm, with a constant light intensity of 1500 μmol photons m^{-2} s^{-1}.

Experimental Design and Data Analysis

The field experiment utilized a randomized complete block design with 6 corn-inbred lines as the treatments. The greenhouse experiment was conducted with the individual plant as an experimental unit. The greenhouse study was a 6 × 2 factorial experiment that utilized a randomized complete block design with 3 replications (blocks). Two trials of the experiment were conducted. All insect damage ratings and plant parameters were analyzed by the PROC MIXED procedure and the means were separated by Fisher's protected LSD test (α = 0.05) (SAS Institute 2003). Both A/Ci and light response curves were established with a polynomial regression model in Sigma Plot® (version 8.02A) software (SYSTAT, Richmond, CA) at 7 and 14 d after infestation.

RESULTS AND DISCUSSION

Injury Ratings and Chlorophyll Content

Field injury ratings were significantly different among the 6 maize inbred lines at both 7 d (F = 6.1, df = 5, 17; P = 0.002) and 14 d (F = 11.6, df = 5, 17; P = 0.0001) (Figs. 1A, B). The injury ratings of CML333, CML336, and CML338 were the same as the resistant control, Mp708, and consistently lower than the susceptible control AB24E. In contrast, the injury rating of CML335 was not different from the susceptible control. Chlorophyll content measurements 14 d after infestation were significantly different among infested plants (F = 9.2, df = 5, 201; P = 0.0001). Leaf chlorophyll content in the injured CML338 and Mp708 leaves was significantly higher than AB24E and CML333 (Fig. 1C).

In addition to the injury ratings differing between uninfested and infested plants (F = 1143.6, df = 1, 199; P = 0.0001) in the greenhouse study, injury ratings were significantly different among inbred lines (F = 3.7, df = 5, 199; P = 0.0033). Injury ratings differed between the 7 d and 14 d infestation durations (F = 7.0, df = 1, 199; P = 0.0089) and the two-way and three-way interactions (P < 0.01). Thus, all injury rating data were separately presented by the s so much, once again.se a issue for your recital or not. phone:229-387-0852.infestation durations (Figs. 2A, B). When injury ratings were compared at 7 d after infestation, higher injury occurred on AB24E than on CML333, CML336, CML338, and Mp708 (Fig. 2A). This result was consistent with the field screening data. However at 14 d, injury on AB24E was not different from CML333, CML336, and CML338 (Fig. 2B). Leaf chlorophyll content was significantly different among inbred lines (F = 7.8, df = 5, 200; P = 0.0001), but not affected by either infestation type or infestation duration, or by any of the two- or three-way interactions among
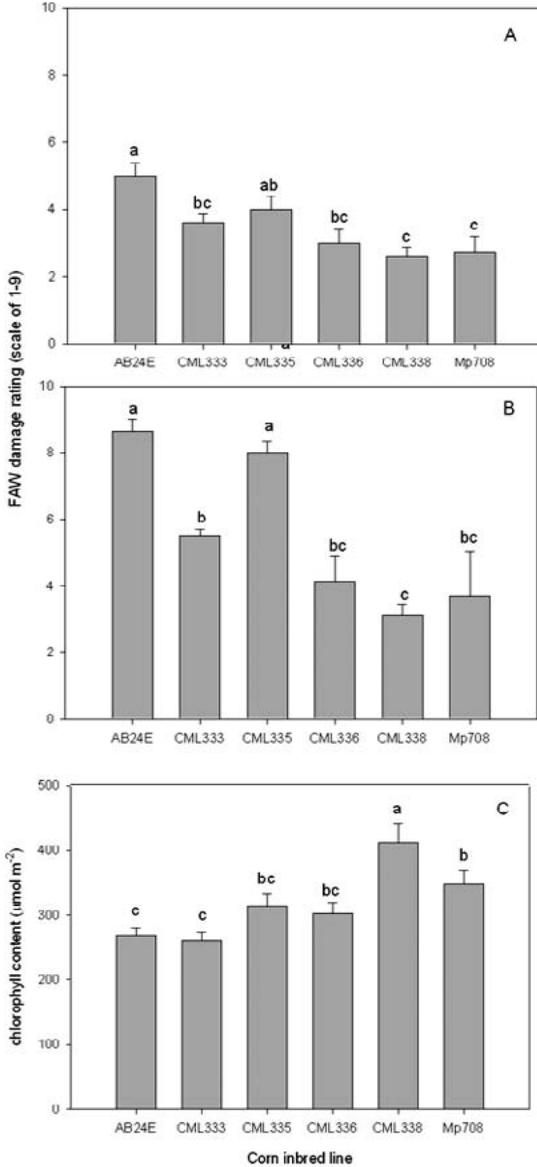
Fig. 1. Field assessment of fall armyworm resistance in the 6 selected corn inbred lines. (A) Damage rating 7 d after infestation; (B) Damage rating 14 d after infestation; (C) Leaf chlorophyll content on damaged leaves 14 d after infestation. Means followed by the same letter are not significantly different, Fisher's protected LSD test ($\alpha = 0.05$).
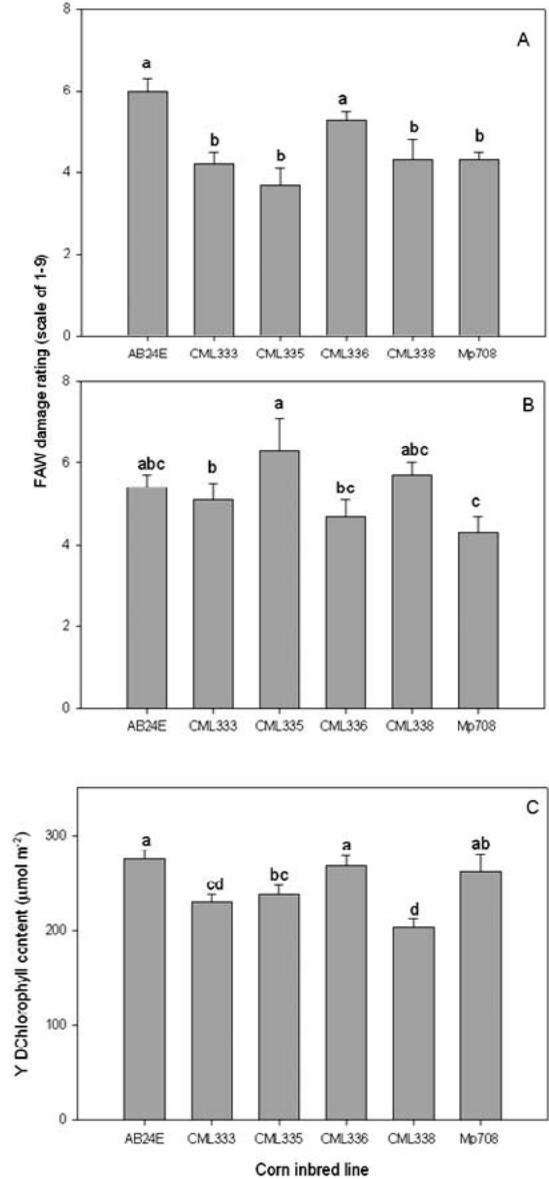

Fig. 2. Greenhouse evaluation of fall armyworm resistance on 6 selected corn inbred lines. (A) Damage rating 7 d after infestation; (B) Damage rating 14 d after infestation; (C) Leaf chlorophyll content means from the pooled data collected at 7 and 14 d after infestation. Means followed by the same letter are not significantly different, Fisher's protected LSD test ($\alpha = 0.05$).

the inbred lines, infestation types, and infestation durations ($P > 0.05$). Thus, the chlorophyll data were combined and compared only among inbred lines (Fig. 2C). In contrast to the field chlorophyll data (Fig. 1C), chlorophyll content of AB24E and Mp708 was significantly higher than CML333

and CML338. Both field and greenhouse data showed that CML333, CML336, CML338, and Mp708 were resistant to fall armyworm injury compared to AB24E, although the injury ratings varied between the field and greenhouse evaluation results.

Plant Height, Stem Circumference, and Photosynthesis Measurements

Plant height was significantly different among inbred lines ($F = 16.0$, $df = 5$, 220; $P = 0.0001$), between uninfested and injured plants ($F = 75.3$, $df = 1$, 220; $P = 0.0001$), and between 7 and 14-d infestation durations ($F = 62.0$, $df = 1$, 220; $P = 0.0001$). Plant height was significantly affected by infestation duration x infestation type interaction ($F = 9.7$, $df = 1$, 220; $P = 0.0021$). Plant height 7 d after infestation was significantly different among uninfested lines, but not among infested lines (Fig. 3 A). Plant height of uninfested AB24E, Mp708, and CML338 were significantly greater than CML333, CML335, and CML336. Larval infestation significantly reduced plant height in all entries except CML335.

Plant height 14 d after infestation was significantly affected by infestation types ($F = 36.0$, $df = 1$, 120; $P = 0.0001$), inbred lines ($F = 19.0$, $df = 5$, 122; $P = 0.0008$), and inbred line by infestation type interactions ($F = 4.7$, $df = 5$, 120; $P = 0.0005$). Furthermore, uninfested AB24E and CML338 plants were significantly taller than Mp708, CML333, CML335, and CML336 plants (Fig. 3B). In contrast, infested CML338 plants were the tallest and CML336 plants were the shortest (Fig. 3B), which suggested that CML338 was tolerant to the fall armyworm feeding injury.

Stem circumference was significantly different among inbred lines ($F = 13.0$, $df = 5$, 220; $P = 0.0001$), and between infestation durations ($F = 62.0$, $df = 1$, 220; $P = 0.0001$), but not affected by infestation types ($F = 0.43$, $df = 1$, 220; $P = 0.5134$). None of the two-way or three-way interactions were significant ($P > 0.05$). Thus, data of both infestation types were pooled and compared between infestation durations (Fig. 3C). Stem circumference of AB24E, Mp708, and CML335 was significantly greater than that of CML333 7 d after infestation, while 14 d after infestation stem circumference of AB24E and Mp708 was greater than that of CML333, CML335, and CML338 (Fig. 3C). The height and stem circumference of the infested plants indicated that in general, plant height was negatively affected but stem circumference was not affected by fall armyworm infestation.

Photosynthetic Rate Measurements

Survey measurement of photosynthetic rate was significantly different among inbred lines ($F = 4.8$, $df = 5$, 198; $P = 0.0003$), and between infestation types ($F = 31.0$, $df = 1$, 198; $P = 0.0001$). The photosynthetic rate of experimental plants was affected by 3 two-way interactions (i.e., inbred line by infestation type ($F = 2.3$, $df = 5$, 198; $P = 0.0486$), inbred line by infestation duration ($F = 3.2$, $df = 5$, 198; $P = 0.0092$), and infestation type
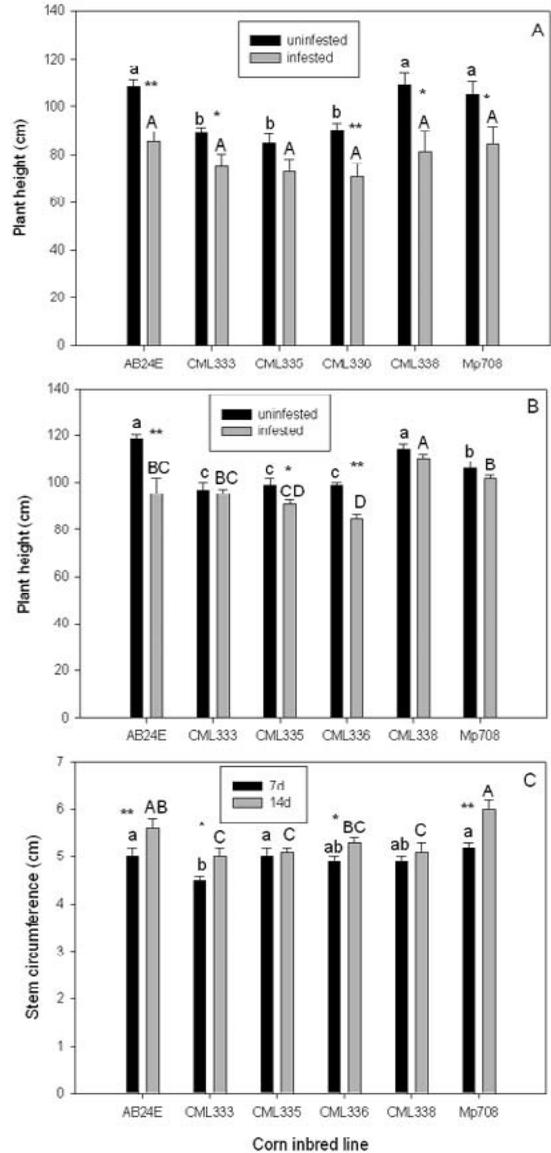

Fig. 3. Effect of fall armyworm infestation on plant growth parameters in the greenhouse study. (A) Plant height (cm) 7 d after infestation; (B) Plant height (cm) 14 d after infestation; (C) Stem circumference (cm) on uninfested and injured plants. Bars of the same type with the same letter (a-c for uninfested, or A-D for infested) are not significantly different, Fisher's protected LSD test ($\alpha = 0.05$). The * or ** between uninfested and injured plants within a germplasm entry denotes a significant difference at $\alpha = 0.05$ or $\alpha = 0.01$, respectively.

by infestation duration ($F = 13.7$, $df = 1$, 198; $P = 0.0003$)). The three-way interaction was not significant ($P > 0.05$). In contrast to the plant height and stem circumference data, photosynthesis rate was not affected by either infestation duration or the three-way interaction of inbred line by infes-

tation type by infestation duration ($P > 0.05$). Thus, the photosynthesis rate data of both 7 and 14 d measurements were combined and presented in pairs with infestation types (Fig. 4). Photosynthetic rate of uninfested plants was not significantly different ($F = 1.7$, $df = 5$, 100; $P = 0.1414$) among inbred lines, whereas the photosynthetic rate of injured plants was different ($F = 6.3$, $df = 5$, 106; $P = 0.0001$). Mp708 had the highest photosynthetic rate, while CML335 showed the lowest photosynthetic rate (Fig. 4). Such variation in photosynthetic rate among the corn seedlings with less foliar injury suggested that the corn-inbred lines might possess different physiological mechanisms that confer varying levels of resistance. Furthermore, irrespective of resistance, insect injury significantly reduced photosynthetic rate in AB24E, CML333, CML335, and CML336, but had no effect on photosynthetic rate in CML338 and Mp708 (Fig. 4). The results suggested that the last 2 inbred lines were tolerant to fall armyworm feeding injury.

Photosynthetic Capacity Measurements

Based on the injury rating data collected from the field and greenhouse experiments, 5 inbred lines (Mp708 and AB24E controls plus 3 CIMMYT lines with low injury ratings, CML333, CML336, and CML338) were selected to assess the impact of infestation on the photosynthetic capacity of the plants. Photosynthetic capacity was assessed with CO_2 (or A/Ci) and light response curves. Insect injury significantly reduced the light-harvesting capacity of AB24E 7 d (Fig. 5A), but not 14 d after infestation, nor were
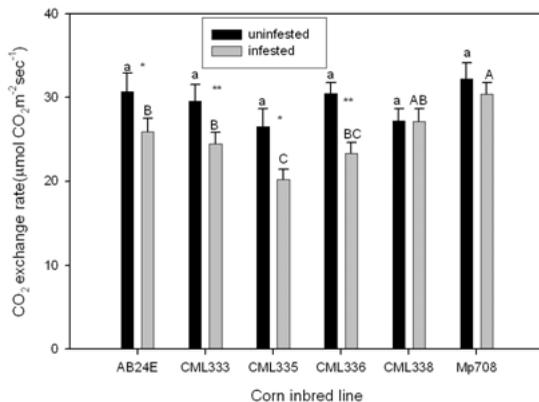

Fig. 4. Photosynthetic rates of uninfested control and fall armyworm-injured corn plants from the 6 inbred lines. Bars of the same type with the same letter (a-c for uninfested, or A-D for infested) are not significantly different, Fisher's protected LSD test ($\alpha = 0.05$). The * or ** between uninfested and injured plants within a germplasm entry denotes a significant difference at $\alpha = 0.05$ or $\alpha = 0.01$, respectively.
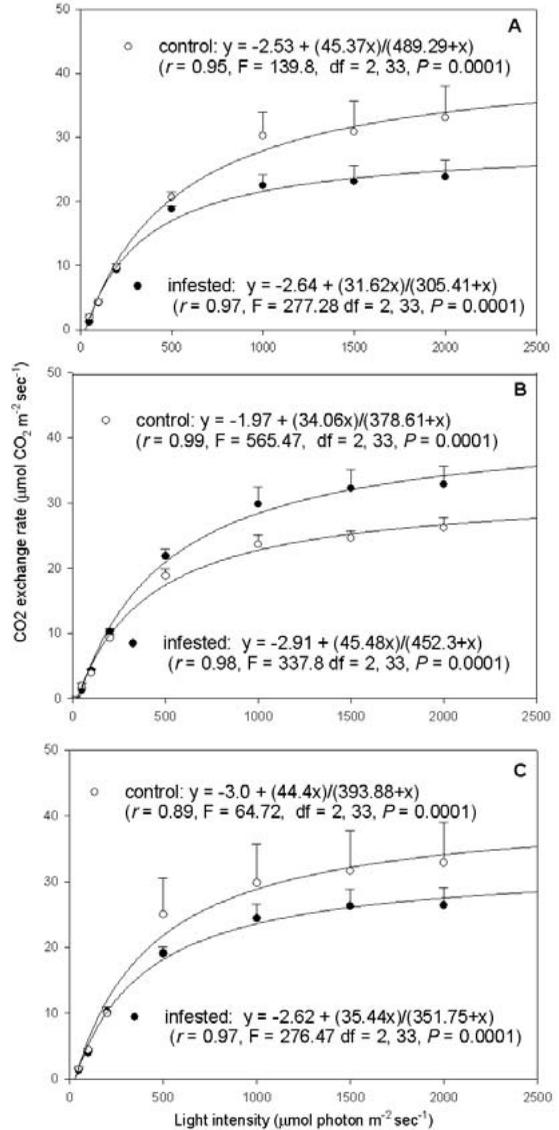

Fig. 5. Light response curves of uninfested and the fall armyworm-injured plants 7 d after infestation. (A) AB24E (susceptible control); (B) CML333 (with moderate level of silk maysin, 0.17% of fresh silk weight); and (C) CML336 (with low level of silk maysin, 0.07% of fresh silk weight).

the A/Ci curves of AB24E affected 7 or 14 d after infestation. Thus, the reduction of photosynthetic rate in AB24E might be the result of the reduction of light-harvesting capacity (or the light reaction) of the photosynthesis process, but not the carbon assimilation (or the dark reaction) process. In contrast, CML333 showed an increase in photosynthetic rate in injured plants at high light intensity (> 1000 photons m^{-2} s^{-1}) 7d after infestation (Fig. 5B). There was no difference in A/Ci curves 7

or 14 d after infestation. Although CML336 showed significantly lower injury ratings than AB24E, the A/Ci and light response curves were very similar between AB24E and CML336 (Fig. 5C).

The reduction of photosynthetic capacity in the inbred lines with low injury ratings might indicate that plants reduced their growth and increased their biosynthesis of secondary metabolites to defend against insect herbivory. Thus CML333 and CML336 might possess antibiotic resistance to insect feeding. Significant reduction in photosynthetic rate in injured susceptible plants with high injury ratings (i.e., AB24E, and CML335), and CML333, CML 335, and CML336 seedlings was similar to the previous findings in *D. noxia*-injured wheat leaves (Haile et al. 1999), and common smut (*Ustilago maydis* L.)-infected maize leaves (Horst et al. 2006). It is intriguing that a significant photosynthetic rate reduction occurred in insect-susceptible, and some but not all insect-resistant crop plants. Thus, the findings suggested that photosynthesis might not be di-

rectly related to these insect-resistant inbred lines with reduced photosynthetic rate, as shown by the susceptible inbred AB24E.

In contrast, A/Ci and light response curves of CML338 were different from AB24E, CML333, and CML336. The A/Ci curves 7 and 14 d after infestation showed that injured plants increased photosynthetic rate in response to the change in CO_2 levels compared with control plants (Figs. 6A, B), which suggested that plants were tolerant to insect feeding by compensatory growth. In addition, the light response curves of CML338 showed no difference 7 or 14 d after infestation (Figs. 6C, D), which indicated that injury had no effect on the light-harvesting capacity of CML388 seedlings. This was opposite to the findings of CML333 and CML336 as shown in Figs. 5A and B. Using the combination of the photosynthetic survey data (Fig. 4) and the A/Ci and light response curve data (Figs. 5 and 6), we conclude that CML338 seedlings were tolerant to injury, but the resistance in CML333 and CML336 might not be directly related to plant photosynthesis.
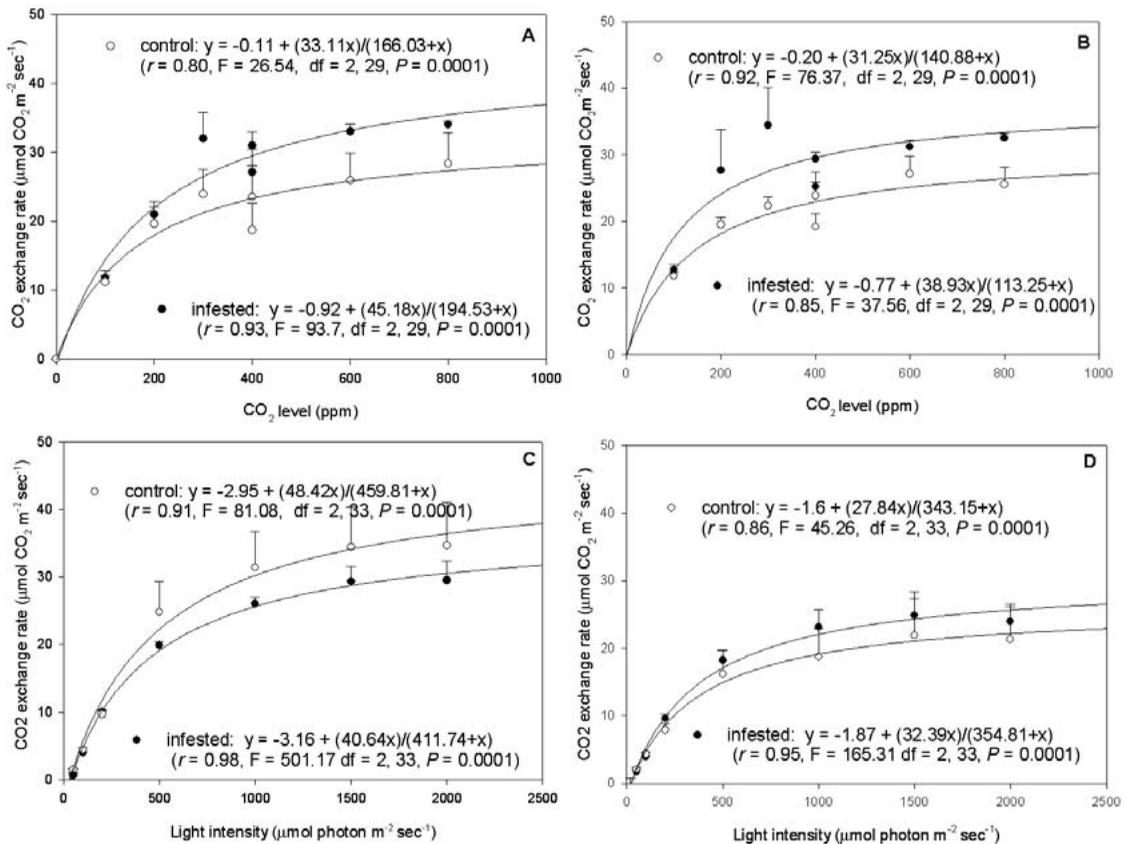

Fig. 6. Photosynthetic capacity measurement of the inbred line CML338 (with high level of silk maysin, 0.48% of fresh silk weight). A/Ci (or CO_2 response) curves recorded 7 (A) and 14 d (B) on uninfested (empty circle) and fall armyworm-injured plants (filled circle), respectively; and light response curves recorded 7 (C) and 14 d (D) on uninfested and fall armyworm-injured plants, respectively.

The correlation between insect resistance and plant secondary metabolites (e.g., chlorogenic acids) needs to be further examined. Furthermore, neither the A/Ci nor light response curves of Mp708 were different between uninfested and injured plants 7 or 14 d after infestation, which indicated that Mp708 might be tolerant to the injury as well.

In summary, the current study showed that the inbred lines CML333 (with moderate silk maysin), CML336 (with low silk maysin) and CML338 (with high silk maysin) were resistant to fall armyworm feeding at the seedling stage, and CML335 (without silk maysin) was susceptible. The findings indicate that multiple insect resistance across multiple growth stages of corn plants is promising, and merits further detailed reciprocal examinations between plant growth stages. Fall armyworm resistance in CML333 and CML336 was not directly related to photosynthesis, because the reduction in photosynthetic rate is similar to the susceptible control. At the same time, CML338 and Mp708 were categorized as tolerant to insect herbivory because uninfested and injured plants showed no differences in either survey measurements of photosynthetic rate, light response curves, or photosynthetic rate in the A/Ci curves.

Acknowledgments

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