Western Corn Rootworm (Coleoptera: Chrysomelidae) Feeding on Corn and Soybean Leaves Affected by Corn Phenology

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ABSTRACT The failure of crop rotation to protect corn from larval western corn rootworm, *Diabrotica virgifera virgifera* LeConte, injury has become common in regions of Illinois and Indiana, and is apparently spreading east into Ohio and Michigan. The extensive use of a corn-soybean rotation is considered to have selected a variant of the western corn rootworm that has expanded its ovipositional range to include soybean fields. Laboratory and field observations suggest that suspected variant western corn rootworm adults have a greater acceptance for soybean foliage as an adult feeding site than that of wild type adults. We attempted to identify variant western corn rootworm populations based on their propensity to feed on soybean foliage and what factors influence the consumption of soybean foliage. Feeding on soybean and corn leaves was quantified in laboratory feeding assays. There was no significant difference in amount of soybean leaf area eaten by western corn rootworm from Illinois versus those from Nebraska or Michigan, both regions were rotation failures have not been reported. To identify what factors influence western corn rootworm feeding on soybean, we first demonstrated that western corn rootworm feeding on corn foliage was influenced by corn phenology. Corn phenology also influenced the consumption of soybean leaves; more soybean leaf area was consumed in the presence reproductive stage corn leaves than younger, vegetative stage corn leaves. A phenology effect was observed also with corn silks; soybean consumption was reduced in the presence of corn silks compared with leaves. Given that western corn rootworm acceptance for soybean increases in the presence of older corn, we propose an explanation for western corn rootworm oviposition in soybeans based on corn phenology.

KEY WORDS oviposition, crop rotation, resistance

DAMAGE TO FIRST year (rotated) corn by western corn rootworm, *Diabrotica virgifera virgifera* LeConte, has been reported in Illinois (Levine and Gray 1996), Indiana, (Sammons et al. 1997), Iowa, (Rice and Tollefson 1999), Michigan, (DiFonzo 1998), and Ohio (Onstad et al. 1999). Formerly, female western corn rootworms were thought to oviposit only in cornfields, and since the larvae can survive only on the roots of corn and a few grasses, crop rotation was a highly effective management practice (Levine and Oloumi-Sadeghi 1991). However, during the late 1980s, rootworm injury to corn following soybeans was reported in isolated areas of east central Illinois (Levine and Gray 1996, Levine and Oloumi-Sadeghi 1996). By 1995, western corn rootworm larval injury to corn following soybeans was observed throughout east central Illinois and northwestern Indiana (Levine and Gray 1996, Onstad et al. 1999).

Entomologists hypothesized that widespread adoption of corn-soybean rotation had selected a variant of the western corn rootworm that lays at least a portion of its eggs in soybean fields (Levine and Gray 1996, Sammons et al. 1997, Spencer et al. 1999). In a corn-soybean rotation, larvae from eggs oviposited and overwintering in soybean emerge in a cornfield the following spring. These first-year fields are typically not treated with a soil insecticide and can experience extensive root injury and yield reduction from western corn rootworm larval feeding (O'Neal et al. 2001). Alternatively, eggs laid in cornfields hatch the following year in a nonhost field (i.e., soybean). Thus, where corn is grown in rotation with soybeans there is an advantage for female western corn rootworms to lay eggs in soybeans. Accordingly, O'Neal et al. (1999) found greater numbers of adult western corn rootworms in soybean versus cornfields in east central Illinois, including a greater percentage of females in soybean fields than in cornfields during August (O'Neal et al. 1999), when western corn rootworm likely laid the majority of their eggs (Hein and Tollefson 1985). Interfield dispersal of western corn rootworms is common, with first-year cornfields a site of female immigration (Godfrey and Turpin 1983). While corn phenology has been shown to influence northern corn rootworm (*Diabrotica barberi* Smith & Lawrence) dispersal (Naranjo and Sawyer 1988), and

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is thought also to affect movement of western corn rootworm (Naranjo 1991), its role in western corn rootworm movement into soybeans has not been investigated.

Both Sammons et al. (1997) and Spencer et al. (1999) observed suspected variant western corn rootworm adults feeding on soybean leaves. Specifically, Sammons et al. (1997) reported that suspected variant beetles from Indiana fed more on soybean leaves in a no-choice assay than western corn rootworms from Iowa and Nebraska. They found that beetles from Nebraska did not feed at all on soybean leaves. In Illinois, Spencer et al. (1999) also reported field observations of western corn rootworms feeding on soybeans. They suggested that although a preference for soybeans is not necessary to explain rootworm oviposition in soybeans, it may be possible to identify western corn rootworms that have oviposited in soybean fields based on the presence of soybeans in their gut.

Recent reports of injury to rotated corn in southwestern Michigan (DiFonzo 1998) suggest that variant populations are present in Michigan as predicted by Onstad et al. (1999). Our initial objective was to determine if feeding assays could identify the presence of variant western corn rootworms within regional populations. We first evaluated if western corn rootworm adults from the regions tested by Sammons et al. (1997) varied in their consumption of soybean in no-choice assays. Results from these tests led us to study western corn rootworm acceptance for soybean when in the presence of corn at different phenological stages. Finally, we investigated whether the influence of corn phenology on soybean feeding is unique for western corn rootworm from putative variant populations. Based on the results, we suggest a model that can explain western corn rootworm dispersal from corn and oviposition in soybeans.

Materials and Methods

General Assay Conditions. We measured the surface area of corn and soybean leaves fed on by western corn rootworm adults in no-choice and choice assays based on the no-choice assay of Sammons et al. (1997), in which 10 adult beetles were presented individual soybean leaves within a petri dish. In our preliminary studies, as few as one in 10 individuals fed on a soybean leaf during a 24-h period; moreover, females fed more than males. Feeding by western corn rootworm adults often occurs in groups, on both corn and soybeans. Therefore, we decided to use 10 adult female beetles in a petri dish as the experimental unit to assure measurable feeding would occur, and to allow us to compare our results to that of Sammons et al. (1997). Plant material and western corn rootworm source varied among experiments, but unless otherwise specified, the following conditions were kept constant. All beetles were kept in wire screen (30 cm by 30 cm by 30 cm) cages in an insect rearing facility (24°C and 16:8 [L:D] h) on the campus of Michigan State University. To ensure that exposure to soybean leaves in the assays was not a novel experience, beetles were provided with a potted soybean plant (V6 to R3 stage), as well as a fresh corn ears, silks, and leaves. Water was provided continuously from dental wicks placed in water-filled flasks. Beetles were taken from cages, briefly chilled on ice for easier handling, and then separated by sex based on the shape of the last abdominal sternite (White 1977). Beetles and test foliage were placed in petri dishes (15.5 cm diameter and 1 cm high) on filter paper (Whatman No. 2, Hillsboro, OR) moistened with water. Unless otherwise specified, foliage used in feeding assays was from the third fully expanded leaf from the apex of both corn and soybeans. Beetles were allowed to feed for 24 h in a growth chamber (24°C and 16:8 [L:D] h). After 24 h, beetle mortality was recorded and the leaf area consumed was digitally measured using the public domain NIH Image software (National Institutes of Health 1999). Every beetle survived the 24-h assay; therefore, leaf area consumed is reported as a mean per dish. A subsample of beetles from each assay was saved and preserved as voucher specimens in the A. J. Cook Arthropod Research Collection at Michigan State University.

No-Choice Assay. In 1999, our objective was to differentiate variant from wild type western corn rootworm using no-choice assays. We conducted no-choice assays with beetles from Illinois, Nebraska, and Michigan. Based on the findings of Sammons et al. (1997), we hypothesized that western corn rootworms from Illinois (variant) would feed on soybeans and those from Nebraska (wild type) would not. We further postulated that feeding by Michigan beetles might be an intermediate between Nebraska and Illinois, based on whether they were predominately of a variant or wild type population.

Insects. Adult western corn rootworms were collected from cornfields in Nebraska (Saunders County, 30 July 1999; 3.2 km from the collection site of Sammons et al. 1997), a region of corn production that has not reported rootworm larval injury to rotated corn. Western corn rootworms from Michigan were collected in a continuous cornfield at the Michigan State University Entomology Research Farm (East Lansing, MI), also a region where western corn rootworm injury to rotated corn has not been reported. Beetles from Illinois were collected from a rotated cornfield in Champaign County in a region frequently reporting injury to rotated corn (O'Neal et al. 2001). Beetles from Nebraska were sent to Michigan in containers with corn ears, silks, water, and arrived within 48 h of collection. Beetles from Illinois and Michigan were collected 48 h before the arrival of those from Nebraska; Illinois beetles were transported by car in cages with corn ears, silks, and water.

Plants. Soybeans used for all feeding assays (Asgrow Ag2201) were planted on 12 May 1999 at the Michigan State University Entomology Research Farm (East Lansing, MI) and maintained using conventional agronomic practices. Soybeans used in the no-choice assay were in the late R2 to early R4 stage (Sinclair and Backman 1989).

Experimental Design and Data Analysis. Beetles were offered a single soybean leaf within an 8.5 cm diameter and 1.5 cm high petri dish. No-choice assays were performed with females from each state on three separate dates: 2, 3, and 9 August 1999. Each treatment was replicated three times on each day. Results from the 3 d were combined and analyzed using analysis of variance (ANOVA) for a randomized complete block design, with assay date as the block, state of origin as the treatment and the interaction between the block and treatment included in the ANOVA. The amount of soybean leaf foliage consumed was compared across the three treatments (western corn rootworm from Illinois, Nebraska, and Michigan) using least significant difference (LSD) mean separation (SAS Institute 1996).

Corn-Soybean Choice Assays. Based on preliminary data, we observed that corn age affected western corn rootworm feeding on corn leaves, such that feeding on corn leaves decreases as the plant enters the late vegetative to reproductive stage. Overall, our results support those of Sifuentes and Painter (1964) who found that delaying the plantings of similar lines of corn by a month decreased leaf feeding by corn rootworms.

Based on these results, we inferred that corn phenology may influence western corn rootworm consumption of soybean leaves. We postulated that soybean leaf consumption would be greater in the presence of corn from a phenological stage not readily eaten by western corn rootworm adults (late vegetative to reproductive stage) than in the presence of corn from a phenological stage more readily eaten (early vegetative stage). We further postulated all postreproductive stages of corn (R1- R6, Ritchie et al. 1986) would have a similar effect on soybean consumption. We also tested western corn rootworm feeding on soybean leaves in the presence of corn silks. Because western corn rootworm feeding on corn silks is more commonly observed than feeding on leaves, we tested the hypothesis that soybean leaf feeding occurs only in presence of corn foliage and not in the presence of corn silks.

Insects. Western corn rootworm used in the corn-soybean choice assays came from a continuous cornfield on the Michigan State University Entomology Research Farm (East Lansing, MI). Adult beetles were collected by hand from corn plants the day before assay.

Plants. Corn used in the corn-soybean choice assays was planted on 29 April and 15 May, 2000. As with the corn phenology assay, a 6 by 3-cm section of corn leaf tissue cut from either side of the midrib was used in the corn-soybean choice assays. Soybean was planted on 16 April 2000. A whole soybean leaflet was taken from the third fully expanded trifoliate, below the apex of the plant. We were interested in how corn phenology influences soybean consumption, and not in comparing corn and soybean leaf consumption by western corn rootworm. Therefore, we did not attempt to offer equal mass or surface area of each leaf type.

Experimental Design and Data Analysis. Petri dishes contained a section of corn leaf from one of the two planting dates along with a full soybean leaf. Assays were conducted on three separate dates (21 July, 29 July, and 3 August 2000), to compare feeding on corn at differing phenological stages. On the first assay date, leaves came from corn in either early or late vegetative stages. On the second assay date, leaves came from corn in either the mid-vegetative or reproductive stages. The final assay date, leaves came from corn in early or late reproductive stages. On 3 August, corn silks were tested in a separate choice test. Corn silks were taken from plants in the R1 or R2 stage (Ritchie et al. 1986), representing fresh versus older silks (browning) respectively. Silks from plants in the R1 stage were selected if that plant was shedding pollen, and silks from plants in the R2 stage were selected if pollen shedding had ceased. Silks were cut from the corn-ear tip and weighed. The weight of corn silk provided was equal to the weight of the soybean leaf included in the petri dish. On 21 and 29 July, 10 replications of each choice assay were conducted, whereas on 3 August only seven replications were conducted for each of the four choice assays.

For each assay date, data were analyzed separately as a completely randomized design with type of plant material (corn or soybean) eaten as the treatment factor. ANOVA was used to test the effect of corn phenology on corn consumption, and corn phenology and organ type (silk versus leaf) on soybean consumption (SAS Institute 1996). A student *t*-test compared the amount of soybean consumption when the silks presented came from R1 versus R2 corn plants.

Regional Corn-Soybean Choice Assays. Finally, we tested whether corn phenology (early vegetative or reproductive stage) affected corn and soybean consumption of western corn rootworms from different regions. Beetles from Illinois (putative variant), Nebraska (putative wild type), and Michigan were analyzed using the corn-soybean choice assay.

Insects. In 2000, we used beetles from the same locations in Illinois and Nebraska, as well as Michigan beetles from our corn-soybean choice assay. Western corn rootworms from Illinois and Michigan were collected 48 h before the arrival of those from Nebraska (5 August 2000), with Illinois beetles transported by car in containers with corn ears, silks, and water.

Plants. Soybean planted for the corn-soybean choice assays was used. In 2000, corn used in the regional choice assays came from the 29 April planting used in the corn-soybean choice assay and additional planting made on 30 May, to ensure a source of vegetative stage corn.

Experimental Design and Data Analysis. On 8 August 2000, we conducted choice assays with beetles from Michigan, Illinois, and Nebraska. An intact soybean leaf was offered along with a 6 by 3-cm section of corn leaf, with 10 replications for each state. The statistical analysis followed that of the corn-soybean choice assay, with separate analyses conducted for western corn rootworms from each state.

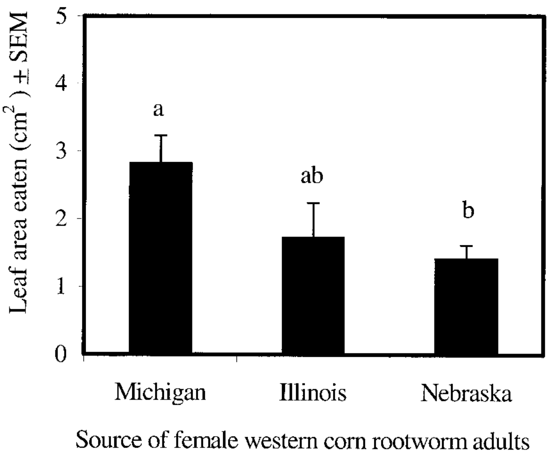

Fig. 1. Mean ± SEM soybean leaf area eaten by 10 female western corn rootworms from Michigan, Illinois, and Nebraska in a 24-h no-choice assay. Means labeled with the same letter are not significantly different (LSD, $P = 0.01$).

Results

No-Choice Assay. Beetles from each location consumed measurable amounts of soybean foliage (Fig. 1). Overall, there was a significant effect on the amount of soybean leaf area consumed due to the western corn rootworm source ($F = 6.24$, df = 2, 18; $P = 0.01$) as well as an interaction between assay date and western corn rootworm source ($F = 3.56$, df = 4, 18; $P = 0.03$). Female western corn rootworms from Michigan consumed more leaf area than beetles from Nebraska. There was no significant difference in the amount of soybean leaf area eaten between beetles from Illinois and Nebraska.

Corn-Soybean Choice Assay. There was significantly more feeding on the younger of two corn leaves (Fig. 2), when corn phenology varied from early to late vegetative stages (21 July, $F = 4.86$, df = 1, 18; $P = 0.04$), and when the corn phenology varied from vegetative to reproductive stages (29 July, $F = 4.53$, df = 1, 18; $P = 0.05$). There was no difference in amount of western corn rootworm feeding when both corn leaves were taken from plants in reproductive stages (3 August, $F = 2.08$, df = 1, 12; $P = 0.18$).

Corn phenology also influenced soybean consumption, with more soybean area eaten in the presence of the older corn leaves (Fig. 2). Western corn rootworm feeding on soybean was greater in the presence of the late versus early vegetative stage corn leaves (21 July,

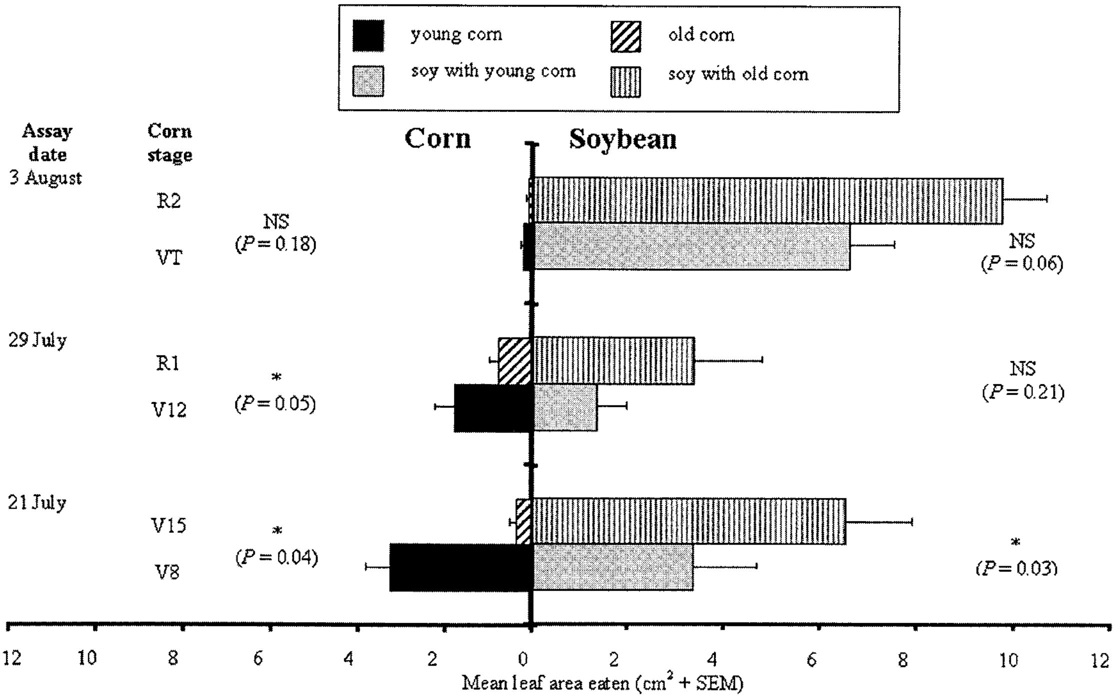

Fig. 2. Mean ± SEM corn and soybean leaf areas eaten by 10 adult female western corn rootworms. Corn and soybean leaves were offered in a choice assay. Corn leaves came from one of two planting dates, with the younger corn indicated by the black horizontal bar and the older corn indicated by the vertical strips. All soybean leaves came from the same planting date. The gray bar indicates soybean offered with the younger corn and the gray vertical strip indicates soybean offered with the older corn. Timing of the three assays was such that the phenology of the two planting dates produced a comparison of early versus late vegetative corn (21 July), late vegetative versus reproductive stage corn (29 July), and early versus late reproductive stage corn (3 August). Asterisks indicate if corn phenology affected corn or soybean consumption (*, $P < 0.05$; **, $P < 0.01$).

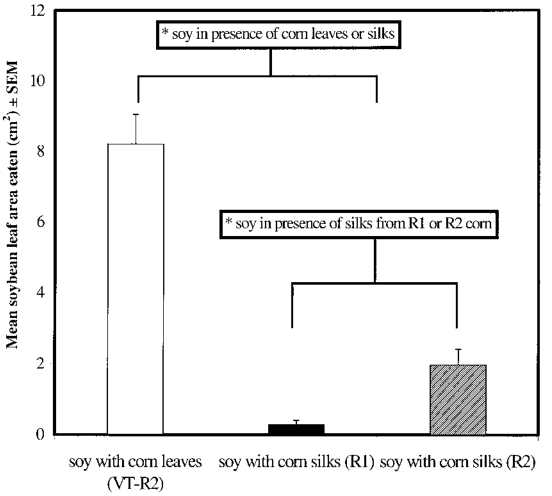

Fig. 3. Mean ± SEM soybean leaf areas eaten by 10 adult female western corn rootworms when offered with either corn leaves or silks. Silks from corn in the R2 stage were taken from plants that were no longer producing pollen, and silks from R1 corn were producing pollen.

$F = 5.26$, df = 1, 18; $P = 0.03$). This trend was present in the latter two assays, but was not significant when leaves were from late-vegetative and reproductive stage corn (29 July, $F = 1.71$, df = 1, 18; $P = 0.21$) and only marginally so when both leaves came from reproductive stage corn (3 August, $F = 4.36$, df = 1, 12; $P = 0.059$).

Western corn rootworm feeding on soybean was significantly reduced in the presence of corn silks (Fig. 3, $F = 61.56$, df = 1, 27; $P < 0.01$). However, feeding on soybean occurred in 12 of 14 replications where silks were present. Although the extent of feeding on silks was not measured, there was significant evidence of feeding on silks from both the R1 and R2 stage corn. Silks were still present in each treatment at the end of the 24-h assay. A significantly greater amount of soybean was consumed (t-test, $t = 3.7$, df = 7, $P < 0.01$) in the presence of silks from corn in the R2 stage (no pollen shed) than from corn in the R1 stage (pollen shedding).

Regional Choice Assay. Feeding on corn by beetles from Michigan ($F = 76.23$, df = 1, 18; $P < 0.01$), Illinois ($F = 76.47$, df = 1, 18; $P < 0.01$), and Nebraska ($F = 83.58$, df = 1, 18; $P < 0.01$) was affected by corn phenology (Fig. 4). Beetles from each state ate more of the younger than older corn leaf. Feeding on soybean leaves was greater in the presence of older corn than younger corn for beetles from Illinois ($F = 48.10$, df = 1, 18; $P < 0.01$) and Michigan ($F = 48.10$, df = 1, 18; $P < 0.01$). Though Nebraska beetles also consumed more soybean in the presence of older corn, this affect was not significant ($F = 3.30$, df = 1, 18; $P = 0.09$).

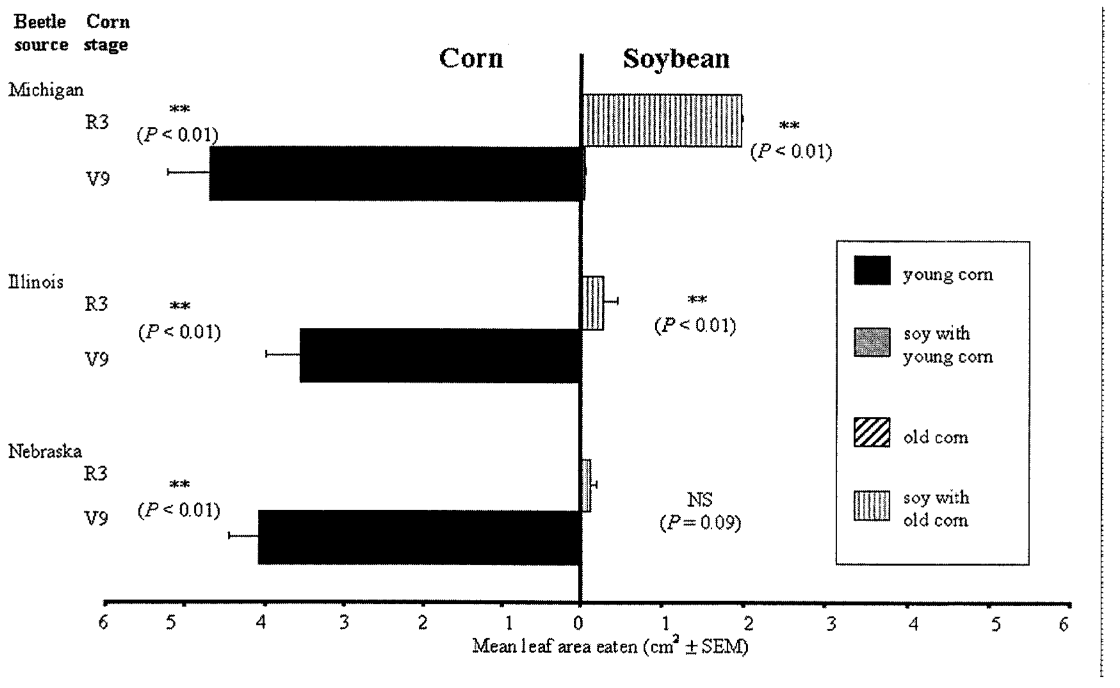

Fig. 4. Mean ± SEM corn and soybean leaf areas eaten by 10 adult female western corn rootworms from Illinois, Nebraska, and Michigan. Leaves were offered in a choice assay, with soybean leaves from the same planting date with either reproductive stage (R3) or vegetative stage (V9) corn leaves. The black horizontal bar indicates leaves from vegetative stage corn and the vertical strips indicate the reproductive stage. The gray bar indicates soybean offered with the vegetative stage corn and the gray vertical strip indicates soybean offered with reproductive stage corn. Asterisks indicate if corn phenology affected corn or soybean consumption (*, $P < 0.05$).

Discussion

No-Choice Assays. Unlike Sammons et al. (1997), in our tests western corn rootworm from Nebraska readily fed on soybean leaves and beetles from Illinois (putative variant western corn rootworm) did not consume a statistically greater amount of soybean foliage than beetles from Nebraska (wild type western corn rootworm). Rather, we consistently observed that western corn rootworm consumed soybean foliage regardless of source population. Feeding on soybean occurred in both no-choice and choice assays, even when corn silks, considered highly attractive to western corn rootworm, were offered (Fig. 3). Feeding on soybeans by western corn rootworms is also not unique to the confines of a petri dish. We observed beetles from all three populations feeding on soybeans in holding cages and by Michigan populations in the field. Western corn rootworms in Illinois (Spencer et al. 1999), and Nebraska (L. Mienke, personal communication) have also been observed to feed on soybean plants in the field. These observations suggest that adult feeding on soybeans is not unique to western corn rootworms taken from areas where oviposition in soybeans is common.

Corn-Soybean Choice Assays. After establishing that leaves from corn in an early vegetative stage elicited greater western corn rootworm feeding than those from corn in a reproductive stage, we examined if this finding might influence western corn rootworm feeding on soybeans. As predicted, we observed greater western corn rootworm consumption of soybean foliage in the presence of phenologically older versus younger corn. We refer to this phenomenon as a phenological affect.

It is well known that western corn rootworms prefer to feed on floral parts (Krysan 1986) of corn when they are present. We investigated whether western corn rootworms would feed on soybeans in the presence of corn silks, and if the phenological effect observed with corn leaves could be produced with silks. Though western corn rootworm fed less on soybean leaves when silks instead of corn leaves were present, feeding on soybean leaves still occurred (Fig. 3). In addition, a phenological effect was present when the silks came from older plants (i.e., more soybean leaf area was eaten).

Regional Choice-Assays. In 2000, we again compared western corn rootworms from Michigan, Illinois, and Nebraska in choice tests with old and young corn. Beetles from all three states fed more on younger corn (Fig. 4). Consistent with our previous three assays (Fig. 2), Michigan beetles consumption of soybean was influenced by corn phenology. Illinois and Nebraska beetles feeding on soybeans was decidedly lower than that of Michigan beetles, though both tended to feed more on soybean in the presence of older corn leaves. Therefore, we conclude that the influence of corn phenology on soybean feeding is not unique to beetles from Michigan. However, only Illinois and Michigan beetles fed significantly more on soybean when the alternative was older corn. Nebraska beetles followed the same trend, though the relationship was not statistically significant.

A Model for Western Corn Rootworm Oviposition in Soybeans. Sammons et al. (1997) hypothesized that corn residue accumulated on the soil surface due to reduced tillage might attract western corn rootworms into soybean fields. However, olfactometer results were not consistent with this hypothesis, and they concluded that corn residue was not responsible for attracting western corn rootworms (Sammons et al. 1997). They suggested that injury to rotated corn was due to a variant western corn rootworm that has a preference for soybean environments, but did not suggest a mechanism for such a preference. Spencer et al. (1999) investigated if suspected variant western corn rootworm adults prefer soybeans to corn in a flight chamber. Overall, a greater percentage of females were collected on corn than soybean. This occurred even though corn tassels and silks, both sources of volatile attractants (Metcalf 1986), were removed from corn used in their flight chamber studies. Spencer et al. (1999) concluded that suspected variant western corn rootworm do not have an attraction for soybean plants.

Regarding western corn rootworm ovipositional habitats, all the cues necessary to induce western corn rootworm oviposition in soybeans are apparently present. Field and laboratory studies have consistently demonstrated that damp particulate substrate is sufficient to induce western corn rootworm oviposition. Gustin (1979) observed more than a four-fold increase in oviposition in corn plots with high (24.9% moisture) versus low (16.2% moisture) soil moisture. Kirk et al. (1969) demonstrated in the laboratory that damp covered soil with a large particle size (12.5–25.0 mm) is sufficient to induce females to oviposit. Of these factors, moisture had the greatest influence (Kirk et al. 1969). Kirk et al. (1969) concluded that South Dakota western corn rootworms had no inherent attraction to corn as an oviposition site. More recently, Siegfried and Mullin (1990) observed that caged western corn rootworm from Pennsylvania would oviposit in the absence of corn. They also concluded that oviposition does not appear to be regulated by cues on or near a host plant and suggest that adult feeding and oviposition are separate behaviors. Thus, it appears that given appropriate soil moisture, western corn rootworm oviposition is as likely in a soybean field as a cornfield.

Given the potential for indiscriminate ovipositional behavior of western corn rootworm and a lack of attraction to soybeans, understanding adult dispersal from cornfields becomes key in explaining injury to rotated corn. Western corn rootworms, especially females with mature eggs, have been observed to move out of the cornfields from which they emerge and enter rotated cornfields (Godfrey and Turpin 1983). Also, later-planted (phenologically young) corn can function as a trap crop drawing in large numbers of adult corn rootworm late in the season as surrounding fields mature (Naranjo and Sawyer 1988, Hill and Mayo 1974). These observations suggest western corn rootworm adults commonly move in and between cornfields to find plants of a phenological stage acceptable for feeding. Our studies demonstrate that western corn rootworm feed little on late vegetative or reproductive stage corn foliage and, in its presence, chose to feed on soybean foliage. While silks briefly offer a preferred food source, a preference for silks does not preclude soybean feeding. Thus, where corn is planted during a short period of time in the spring and is mostly of a phenologically similar stage, western corn rootworms are presented with the following scenario. As corn matures and becomes a less acceptable food, western corn rootworms will likely disperse. In areas of strict corn-soybean rotation, they will either encounter corn in a stage as unattractive as the field from which they left or, alternatively, encounter a soybean field.

The larger numbers of western corn rootworms found in soybean than cornfields, as observed by O'Neal et al. (1999), may thus be due primarily to dispersal from cornfields whose phenology no longer makes the crop an attractive feeding site. The response of western corn rootworm to corn phenology may be particularly strong in areas of extensive corn and soybean rotation, especially where corn is planted with a high degree of synchrony. A prediction from the corn phenology model is that oviposition in soybeans is not unique to western corn rootworm from any particular geographic area. Rather, any corn-soybean landscape with highly synchronized planting resulting in phenologically similar corn, should encourage western corn rootworm dispersal into soybeans. An additional prediction of the corn phenology model is that successful oviposition in a corn-soybean rotated landscape is possible without an attraction to or a preference to feed on soybeans. This may help explain the occurrence of damage to first-year corn in northeastern Iowa (Rice and Tollefson 1999), an area well outside the predicted range of the variant western corn rootworm (Onstad et al. 1999).

Although the corn phenology model does not require a genetic component, there is a pattern of spread in damage to first-year corn originating in east central Illinois that is consistent with the diffusion of a genetic change in regional western corn rootworm populations (Onstad et al. 1999). We refer to this as the genetic variation model. Western corn rootworm that oviposit in soybean will have a selective advantage as their offspring have a higher probability of survival, and thus, selection could produce a variant. However, no genetic differences between such beetles and the wild type have yet been detected. Sammons et al. (1997) suggested that a variant would have an increased affinity for soybeans. Spencer et al. (1999) refuted this, suggesting that survival in a corn-soybean rotated landscape does not require an attraction to soybeans, but rather a reduced fidelity to corn. By combining this refined genetic variation model from Spencer et al. (1999) with the corn phenology model, we suggest that a decreased fidelity to corn, mediated by corn phenology, is likely the primary behavior selected for in a corn-soybean rotated landscape. We suggest that in areas of extensive corn-soybean rotation, especially with highly synchronous planting (as is common in east central Illinois) a corn phenology effect may have increased western corn rootworm dispersal and consequent incidental oviposition in soybeans. An increased acceptance of soybean, for either feeding or oviposition, could be a secondary adaptation, if present at all.

In conclusion, adult western corn rootworm feeding on soybeans per se is not a reliable predictor of potential oviposition in soybeans, as this behavior was not unique to western corn rootworm from areas where corn-soybean rotation fails to protect corn from western corn rootworm larval injury. Rather, we found that western corn rootworm feeding on corn leaves is highly influenced by the phenological stage of the plant, and that reduced acceptability of corn influences western corn rootworm feeding on soybeans. We suggest that in regions of extensive corn-soybean rotation, corn phenology is responsible for the greater occurrence of western corn rootworm in soybeans, and postulate that oviposition occurs coincidentally while adults visit soybean fields. Given that the affect of corn phenology on soybean feeding was not unique to western corn rootworm from areas where corn-soybean rotation has failed to protect corn, the predictions of a corn phenology model for western corn rootworm dispersal and oviposition in soybean fields does not require the assumption of a genetic variant. However, the advanced development of corn when adult western corn rootworms emerge in a corn-soybean landscape would increase wild type western corn rootworm oviposition in soybeans as less time is spent in the aging corn. Over time, these conditions would select for a variant western corn rootworm with a decreased fidelity to corn. To identify a variant that is resistant to a corn-soybean rotation, we suggest examining physiological (i.e., time to adult emergence) or behavioral differences (i.e., sensitivity to corn phenology) that would produce a greater response to corn phenology in a variant than the wild type.

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