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The nutritional ecology of *Dectes texanus* (Coleoptera: Cerambycidae): Does host choice affect the macronutrient levels in overwintering larvae?

Jodi J. Rowland¹, Kelly V. Tindall^{2,3}, Kent Fothergill², and Timothy M. Judd^{1,*}

Abstract

Dectes texanus LeConte (Coleoptera: Cerambycidae) is a stem-boring cerambycid that is an agricultural pest of soybean and cultivated sunflower. For *D. texanus*, cultivated sunflower is thought to be nutritionally superior to soybean and preferred over soybean. This study compared the macronutrient levels in overwintering larvae and the pith of the host plants to determine if soybean is an inferior host. The levels of total protein, total carbohydrates, and total lipids were measured in larvae from sunflower and soybean; larval head capsule width and larval mass also were compared. There were no differences between levels of total protein and total carbohydrates per unit mass between larvae from the 2 hosts; however, larvae from sunflower had significantly higher levels of lipids than larvae from soybean. A comparison of head capsule width indicated that larvae from soybean had significantly larger head capsule widths than those from sunflower, suggesting that soybean-fed larvae were larger or were in a later instar. Larvae from soybean and sunflower did not have significantly different masses, unlike what was found in pupae in previous studies. Soybean pith had significantly higher protein and carbohydrate levels whereas sunflower pith had a significantly higher level of lipids. The results suggest that the nutritional differences between the 2 host plants did affect the nutritional content and possibly growth or development rates in *D. texanus* before diapause.

Key Words: soybean; sunflower; nutrition; diapause

Resumen

Dectes texanus LeConte (Coleoptera: Cerambycidae) es un cerambícido barrendador del tallo que es plaga agrícola de la soja y el girasol cultivado. Para *D. texanus*, se cree que el girasol cultivado es nutricionalmente superior a la soja y preferible a la soja. Este estudio comparó los niveles de macronutrientes en la hibernación de las larvas y la médula de las plantas hospederas para determinar si la soja es un hospedero inferior. Se midieron el nivel de proteína total, el total de carbohidratos y los lípidos totales en las larvas de girasol y soja; también se compararon el ancho de la cápsula de la cabeza y la masa de las larvas. No hubo diferencias entre los niveles de proteínas totales y carbohidratos totales por unidad de masa entre las larvas de los 2 hospederos; sin embargo, las larvas que se alimentaron de girasol tenían niveles significativamente más altos de lípidos que las larvas sobre la soja. Una comparación de la anchura de la cápsula cefálica indicó que las larvas sobre la soja tuvo la cápsula de la cabeza significativamente más grande que las larvas sobre el girasol, lo que sugiere que las larvas alimentadas con soja son más grandes o fueron de un estadio de mayor edad. Las larvas sobre la soja y el girasol no tenían significativamente diferentes masas, a diferencia de lo que se encontró en pupas en estudios previos. La médula de soja tenían niveles de proteína y carbohidratos significativamente más altos, mientras que la médula girasol tenía un nivel significativamente más alto de lípidos. Los resultados sugieren que las diferencias nutricionales entre las 2 plantas hospederas afectaron el contenido nutricional y, posiblemente, las tasas de crecimiento o desarrollo de *D. texanus* antes de la diapausa.

Palabras Clave: soja; girasol; nutrición; diapausa

Typically, before insect larvae enter diapause, they must sequester enough nutrients to meet certain metabolic needs and have sufficient nutritional reserves to complete development (Hahn & Denlinger 2007). Macronutrients needed for diapause include lipids, carbohydrates, and protein (Hahn & Denlinger 2011). Lipids provide high energy content and are preferentially stored by insects (Hahn 2005; Arrese & Soulages 2010). Carbohydrates are a valuable nutrient used for an immediate energy source, and are often metabolized first (Nation 2002). Ingestion of carbohydrates in excess of immediate needs can lead to the formation of triglycerides (Cohen 2004; Hahn & Denlinger 2007, 2011). Proteins are a principal source of nitrogen (Cohen 2004) and noted for their influence on larval growth (Berenbaum & Zangerl 1994).

Hunter & McNeil (1997) proposed that the nutritional value of a host plant can influence growth rates and diapause time in insects. Fecundity, growth, and development time can suffer if a host does not contain the proper nutrients (Hunter & McNeil 1997; Mody et al. 2007). Many studies that examined host quality focused on host plant choice and the results of that choice; fewer examined the actual nutritional value of each host plant. Larvae forced to feed on low- or high-quality foods, such as old and young leaves, respectively, showed lower growth rates when fed on poorer diets (Rauscher 1981; Mevi-Schütz & Erhardt 2003; Bittencourt-Rodrigues & Zucoloto 2009). Studies on insects that use multiple hosts can be particularly informative when examining the effect of host plant quality on herbivorous insects (Lawrence & Bach

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1989). For example, the seed beetle *Callosobruchus maculatus* (F.) (Coleoptera: Chrysomelidae) had a significantly smaller body mass when switching from its natural host *Vigna radiata* (L.) R. Wilczek to a larger host *Vigna unguiculata* (L.) Walp. (Fabales: Fabaceae) (Messina 2004). Despite exhibiting a smaller body mass when switching hosts, *C. maculatus* had a higher survival rate and a shorter development time than when feeding on its natural host (Messina 2004). The effects seen in studies such as these could be due to differences in nutrient availability of the hosts and differences in what nutrients the larvae are able to acquire from the hosts. Thus, it is important to consider both the nutritional value of the food source and the uptake of these nutrients by the forager (Simpson & Raubenheimer 2012) when examining the effect of host plants on insect life histories.

Dectes texanus LeConte (Coleoptera: Cerambycidae) is a stem-boring cerambycid that has been identified as an agricultural pest of both soybean, *Glycine max* (L.) Merr. (Fabales: Fabaceae), and cultivated sunflower, *Helianthus annuus* L. (Asterales: Asteraceae) (Hatchett et al. 1975; Rogers 1977). Larvae feed on the pith of the host and settle near the base of the stem before undergoing diapause (Hatchett et al. 1975). *Dectes texanus* was first reported in 1968 causing severe damage and yield loss to soybean crops in southeast Missouri (Hatchett et al. 1975) and subsequently identified as one of several cerambycid pests of cultivated sunflower (Rogers 1977, 1985). The larvae girdle the base of soybean stems, creating an overwintering chamber, and this girdling behavior results in lodging due to a weakened stem (Hatchett et al. 1973, 1975; Hanks 1999). In Missouri, *D. texanus* is univoltine (Hatchett et al. 1975) and, like many cerambycids, is known to use the same host plant for feeding, mating, and oviposition (Hanks 1999). Thus, this beetle is an excellent model system to explore the interplay between plant nutritional values and development.

Cultivated sunflower is thought to be a preferred and more nutritionally valuable host plant than soybean because one of the natural hosts of *D. texanus* is wild sunflower (Michaud et al. 2007). The findings of Michaud & Grant (2005) indicate that body weight of *D. texanus* pupae developing in soybean is 40% less than of those developing in sunflower, causing these authors to suggest that soybean is a nutritionally inferior host plant. Michaud & Grant (2005) also indicated that larger females had higher reproductive vigor than those that were smaller in size, although this observation was not based on females being larger as a result of host plant. In this study, we analyzed the macronutrient contents (total protein, carbohydrates, and lipids) in *D. texanus* larvae in their overwintering state collected from both sunflower and soybean hosts and in the pith of the plants (the portion of the plants the larvae feed on). If soybean is an inferior host for *D. texanus*, as suggested by Michaud & Grant (2005), we would expect the nutrient levels in the pith of soybean to be lower and/or less well utilized by the larvae collected from soybean. Because soybean plants have a smaller diameter than sunflower (Michaud & Grant 2005), we also examined the size and mass of the overwintering larvae to ensure that differences in head capsule width and mass are not simply influenced by the stem diameter of the plant.

Materials and Methods

MACRONUTRIENT ASSAYS WITH *D. TEXANUS* LARVAE

After harvest, on 11 Dec 2009, 40 individuals for the macronutrient analysis were collected from a field at the University of Missouri Delta Research Center Lee Farm near Portageville, Pemiscot County, Missouri (36.4061833°N, 89.6111639°W). Twenty overwintering larvae from Wal-Mart® brand commercial black oil sunflower stubble and 20

from Merschman Seed Miami®949 soybean stubble were collected. Specimens were transported to the laboratory and stored at -80 °C. Each individual was keyed (by J. J. Rowland) using Craighead (1923) to confirm that larvae were *D. texanus*. The wet mass of each individual was determined to the nearest 10 µg (Mettler AE 163) while larvae were frozen, and head capsule width was measured to the nearest 0.1 mm (Zeiss at 0.8' with micrometer). Each individual was tested for total proteins, carbohydrates, and lipids as described by Judd et al. (2010). In preparation for each assay, each individual from the sunflower and soybean hosts was homogenized separately in 300 µL of deionized water and centrifuged at 14,000 *g* for 2 min.

Protein

Protein levels were determined using the Bradford assay (Bradford 1976). For each individual, an aliquot of 50 µL was placed in a separate tube. One mL of Bradford reagent was added and the sample was mixed on a vortex at 14,000 rpm. The reaction was allowed to develop for 5 min. Absorption levels from each sample were measured using a spectrophotometer (Beckman DU 730) at 595 nm and compared with those from 0.107, 0.214, 0.428, 0.642, and 0.856 µg bovine serum standards. Results were adjusted to the total amount for each sample.

Carbohydrates

For each individual, an aliquot of 10 µL was added to 40 µL of deionized water and placed in the corresponding tubes, with the exception of 9 of the individuals sampled from sunflower, for which we used 50 µL of aliquot because they had a low mass (<0.03 g). To each tube, 12.5 µL of an 18% NaSO₄ solution and 1.25 mL of anthrone reagent were added and the tube contents were mixed on a vortex at 14,000 rpm. Samples were heated for 12 min at 100 °C and then allowed to cool to room temperature. The absorption was then measured in a Beckman DU 730 spectrophotometer at 625 nm and compared with that of 10, 25, 50, 75, and 100 µg glucose standards. Results were adjusted to the total amount of carbohydrate for each individual.

Lipids

For each individual sample, 150 µL of a 1:1 chloroform/methanol solution was added to the homogenate, mixed on a vortex at 14,000 rpm, and centrifuged at 14,000 *g* for 2 min. From each mixture, 20 µL of chloroform layer (which contained the lipids) was separated and dried in an individual tube. An exception was made for 1 individual collected from sunflower, whose large weight indicated that less sample was needed, so only 2.5 µL chloroform layer was used for that individual. To each sample, 0.2 mL of concentrated sulfuric acid was added, mixed on a vortex, and heated at 100 °C for approximately 10 min. Each mixture was combined with 3 mL phosphovanillin reagent and allowed to develop for approximately 30 min. Absorption was measured with a spectrophotometer (Beckman DU 730) at 525 nm and compared with that of 18, 45, 72, and 90 µL of corn oil standards. Results were adjusted to the total amount of lipid per individual.

MACRONUTRIENT ASSAYS WITH HOST PLANT TISSUE

To analyze the macronutrients available in the chosen host plants of *D. texanus*, the same chemical assays were used with plant material. Sixty Miami®949 soybeans and 60 Wal-Mart® brand sunflower seeds, which were the same seed stock of plants from which the larvae were collected in Portageville, were planted in the Southeast Missouri State University Biology greenhouse in 1.89 L pots (soybean) and 3.78 L pots (sunflower). Each plant was initially fertilized with Miracle-Gro® fer-

tilizer using the amount recommended by the manufacturer for each pot size in order to simulate nutrients available to field-grown plants. Only 8 of the sunflower seeds germinated, and 10 of the soybeans germinated. Two months later, the sunflower and soybean plants were harvested. Plants were split and pith material was collected and stored at -80°C . Each sample from the sunflower and soybean plants was tested for total proteins, carbohydrates, and lipids using the same assays as described for the larvae.

STATISTICAL ANALYSES

To test for size and mass differences between the larvae collected from the 2 host plants, the head capsule width and mass measurements of individuals ($n = 20$) collected from soybean were compared with those from sunflower ($n = 20$) with a MANOVA (Proc GLM in SAS/STAT Software, SAS Institute, Inc., Cary, North Carolina). The levels of the 3 nutrients in larvae collected from both host plants were compared with a separate MANOVA. Similarly, the levels of protein, carbohydrates, and lipids per unit mass in soybean ($n = 10$) and sunflower ($n = 8$) plant pith tissue were compared with a MANOVA.

Results

LARVAL COMPARISONS

Larvae collected from soybean had significantly larger head capsule widths than those from sunflower ($F = 5.6$; $df = 1,38$; $P = 0.023$; Fig. 1A). When the mass of larvae was compared, the results were not significant ($F = 0.28$; $df = 1,38$; $P = 0.60$; Fig. 1B). The differences between the amount of protein ($F = 0.13$; $df = 1,38$; $P = 0.72$; Fig. 1C) and carbohydrate ($F = 0.24$; $df = 1,38$; $P = 0.63$; Fig. 1D) per unit mass in larvae collected from sunflower or soybean were not statistically significant. Larvae from sunflower had significantly higher lipid content per unit mass than larvae from soybean ($F = 4.14$; $df = 1,38$; $P = 0.049$; Fig. 1E).

PLANT PITH COMPARISONS

Soybean pith had significantly higher levels of protein per unit mass than sunflower ($F = 8.56$; $df = 1,17$; $P = 0.010$; Fig. 2A) and significantly higher levels of carbohydrates per unit mass than sunflower ($F = 10.72$; $df = 1,17$; $P = 0.005$; Fig. 2B). Sunflower pith had significantly higher levels of lipids present per unit mass than soybean ($F = 27.52$; $df = 1,17$; $P < 0.0001$; Fig. 2C).

Discussion

The overall findings in this study were that 1) larvae of *D. texanus* collected from soybean and sunflower did not show a difference in mass, but the head capsule widths of larvae from soybean were significantly larger than those of larvae from sunflower; 2) larvae from soybean and sunflower contained similar levels of protein and carbohydrates, but larvae from sunflower had higher lipid levels; and 3) soybean pith had significantly higher levels of protein and carbohydrates, whereas sunflower pith had a significantly higher lipid level.

Larvae from soybean in this study had larger head widths than larvae from sunflower even though soybean plants have thinner stems (Michaud & Grant 2005). Thus, the width of the plant did not seem to regulate larval size. At first glance, it may appear that our mass results contradict those of Michaud & Grant (2005), but these authors examined pupae, a stage that occurs post-diapause. The larvae in this study were collected from adjacent plots so that any large-scale envi-

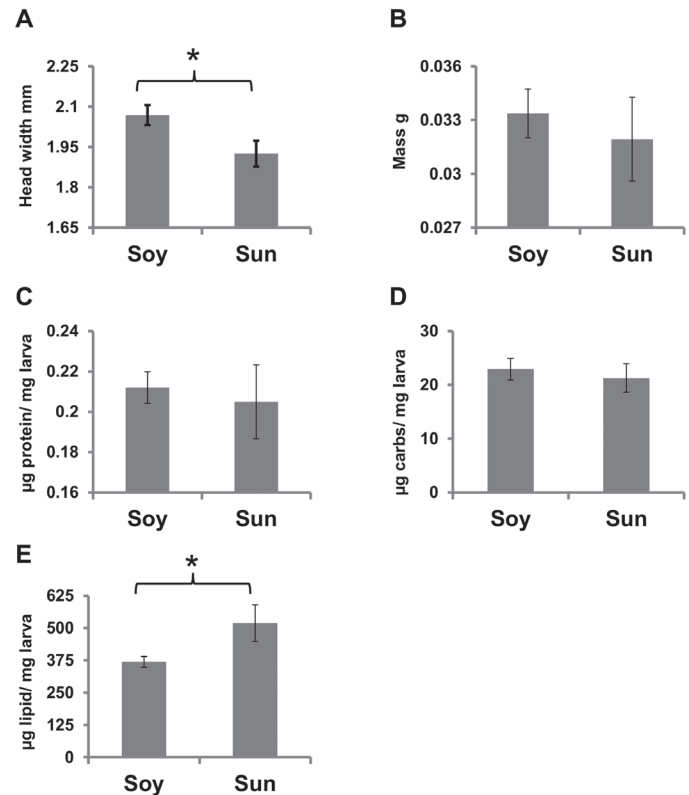


Fig. 1. The mean (\pm SE) A) head capsule width, B) wet mass, C) levels of protein per unit mass, D) levels of carbohydrates per unit mass, and E) levels of lipids per unit mass in larvae from sunflower (Sun) and soybean (Soy) plant hosts. An asterisk indicates that the levels are significantly different.

ronmental effects (temperature, rain) were eliminated as potential factors that would affect growth. Thus, the difference between the host plants is the most likely explanation for the differences between the larvae collected from the 2 host plants. The only reported head capsule widths from *D. texanus* were by Hatchett et al. (1975). These were individuals collected from giant ragweed, *Ambrosia trifida* L. (Asterales: Asteraceae), and reared in the laboratory on the artificial diet found in Hatchett et al. (1973). The measurements of the last instar by Hatchett et al. (1975) were between 1.64 and 1.74 mm which is smaller than the head capsules of the larvae collected in this study (Fig. 1A). The differences between our study and that of Hatchett et al. (1975) could be due to effects of rearing the larvae on an artificial diet outside a stem as opposed to capturing larvae from a natural food source or due to differences between populations. Therefore, it is difficult to tell if the larvae collected from soybean were at a later instar than those collected from sunflower or if the differences in diet allowed the individuals in soybean to grow larger instars. Previous studies established that not all individuals of *D. texanus* overwinter at the same instar (Hatchett et al. 1975); thus, either explanation is plausible.

One explanation for the differences found between the overwintering larvae is the nutritional differences in host plants. Nitrogenous nutrients (protein and amino acids) and energetic nutrients (carbohydrates and lipids) do not have parallel trajectories as an insect develops and approaches diapause. Energetic nutrients are generally used to produce lipid stores whereas nitrogenous nutrients are used for both growth before diapause and storage as hexamerin proteins (Hahn 2005). Insects fed on higher-lipid diets accumulate greater fat stores (Fernando-Warnakulasuriya et al. 1988; Heinrichsen & Haddad 2012). Insect larvae fed on high-protein diets (Ojeda-Avila et al. 2003; Matzkin

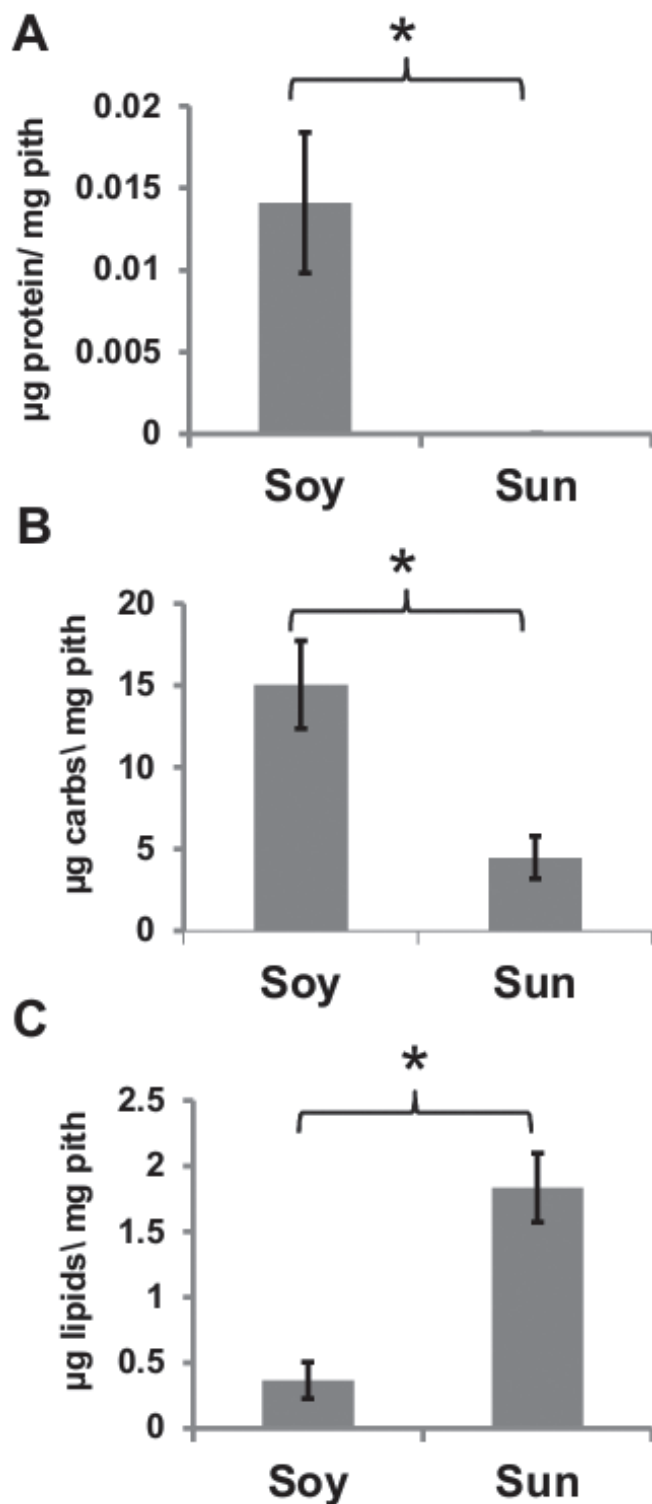


Fig. 2. Mean (\pm SE) levels of A) protein, B) carbohydrates, and C) lipids per unit mass in pith of sunflower (Sun) and soybean (Soy). An asterisk indicates that the levels are significantly different.

et al. 2011) or higher-nitrogen diets (Mattson 1980; Chen et al. 2008) tend to have faster growth rates. All else being equal, sunflower offers a high-lipid diet and soybean offers a high-protein diet. Larvae collected from sunflower, a high lipid-to-protein diet, accumulated greater lipid stores than those collected from soybean. This is what would be

expected based on previous studies. In contrast, larvae collected from soybean plants essentially had fed on a high-protein diet that would promote growth. Thus, a larger head capsule size in larvae collected from soybean might have resulted from access to a higher-protein diet, which allowed larvae to either grow larger or reach a later instar faster than individuals feeding on sunflower pith (essentially a low-protein diet). The observed difference in protein levels between larvae collected from the 2 host plants might be expected if the protein is used for growth rather than stored. Larvae collected from soybean did have lipid stores despite the low levels of lipids in the soybean pith. It is likely that some of the carbohydrates from soybean pith were converted to lipids as the larvae prepared for diapause. Some of the carbohydrates (and nitrogen) would be used for the formation of chitin in the cuticle as the larvae develop (Muthukrishnan et al. 2012). Soybean pith had higher levels of carbohydrates per unit mass than sunflower pith; thus, there was potentially enough to support both requirements.

One curious result was the little to no protein available in the sunflower pith, which raises the question as to where the larvae obtain their nitrogen. There are 2 possible sources of nitrogen that were not measured in this study. First, the pith may contain free amino acids that would not have been detected in these analyses. Second, another source of protein would be other larvae in the stem. *Dectes texanus* larvae are cannibalistic. Adult females oviposit multiple times in a single plant stem, producing a number of larvae. The larvae eat each other until only a single individual is left (Hatchett et al. 1975). Cannibalism has been reported in a number of stem-boring insects, including Coleoptera (reviewed by Richardson et al. 2010). Although there are density-dependent reasons that promote cannibalism, studies have shown that cannibalism can increase the rate of larval growth (Snyder et al. 2000; Richardson et al. 2010). In addition to other *D. texanus* larvae, other Coleoptera, Diptera, and Lepidoptera will colonize a sunflower stem (Rogers 1992). These are also potential protein sources for *D. texanus* larvae. Competition between stem borers does occur (Rathcke 1976; Rami et al. 2002) and cerambycids have been found to be aggressive towards others (Rathcke 1976). Whether or not *D. texanus* consumes other species has yet to be investigated, but the fact that it is cannibalistic and is not found overwintering with other species (K. V. Tindall & K. Fothergill, unpublished data) suggests this is a possibility.

A second factor that could have affected the growth rates is secondary metabolites. The terpenoids of sunflower and glycoellin of soybean affect palatability of these host plants to their coleopteran pests (Fischer et al. 1990; Liu et al. 1993; Michaud & Grant 2009). Hart et al. (1983) showed that phytoalexins of soybean plants had no effect on growth and survival of *Chrysodeixis includens* Walker (Lepidoptera: Noctuidae) and *Epilachna varivestis* Mulsant (Coleoptera: Coccinellidae), but there was some evidence that the phytoalexins did reduce the ability of *C. includens* to digest the plant material. The trypsin inhibitor found in soybean (Kunitz 1946, 1947) has been shown to reduce weight gain in some Lepidoptera (Hart et al. 1983; Shukle & Murdock 1983; Johnston et al. 1993; McManus & Burgess 1995; Jongsma & Bolter 1997) but has had mixed effects on Coleoptera (Jongsma & Bolter 1997; Oppert et al. 2003). In many cases, trypsin inhibitor was only effective when the dosage was well beyond the natural levels found in soybean plants (Jongsma & Bolter 1997). Terpenoids of *Helianthus* have been shown to reduce the growth rate of *Homoeosoma electellum* (Hulst) (Lepidoptera: Pyralidae) at early instars. However, the cultivated sunflower tends to have lower levels of the secondary metabolites and is more palatable to *D. texanus* than the wild sunflower (Michaud & Grant 2009). Domestication of plants does reduce the levels of secondary metabolites in some cases (Chen 2008; Chen et al. 2015).

When switching from sunflower to soybean as a host, *D. texanus* switched from a low protein-to-lipid ratio diet to a higher protein-to-

lipid ratio diet. This switch had nutritional and developmental consequences. *Dectes texanus* larvae that develop in sunflower plants will build up large lipid stores to prepare for winter. The limited levels of protein in sunflower may reduce the rate of growth and development; therefore, it seems that a portion of their nitrogen likely comes from cannibalism (and possibly predation), especially given the nature of stem ecology (Rathcke 1976). On the other hand, larvae that develop in soybean appear to have a faster rate of development or growth. These larvae end up with less lipid stores than their sunflower-dwelling counterparts. The role secondary metabolites have in limiting the ability of *D. texanus* larvae to assimilate the nutrients from their food remains to be seen, but the resulting nutritional makeup of the larvae is what one might expect based on the ratios of proteins to lipids found in the pith of the 2 host plants. How the resulting nutritional makeup of the overwintering larvae affects their survival is something that remains to be studied. Before diapause, insects generally accumulate lipid stores (Hahn & Denlinger 2011). One might predict that individuals from sunflower may have higher survivorship than those from soybean due to the greater lipid stores, or at the very least, the soybean feeders may be limited to areas with relatively mild winters. There does not seem to be any difference post diapause between individuals from the 2 host plants. Indeed, Michaud & Grant (2005) did not find any differences in fecundity between individuals reared on soybean and individuals reared on sunflower. They only found a difference in the number of ovipunctures.

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