Antibiosis Resistance in Soybean Plant Introductions to *Dectes texanus* (Coleoptera: Cerambycidae)

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ABSTRACT No soybean cultivars exhibit resistance to larval damage by the cerambycid, *Dectes texanus* LeConte, in the United States. Selected soybean varieties and plant introductions (PIs) in maturity groups VI to VIII from the U.S. Department of Agriculture National Soybean Germplasm Collection were evaluated for *D. texanus* resistance in a series of field and laboratory experiments from 2005 through 2008. In field cage experiments, the numbers of oviposition punctures (OPs) per plant were determined as indicators of oviposition antixenosis and the ratio of OPs per live *D. texanus* larvae (OP/Lv) served as an indicator of plant antibiosis to larvae. A *D. texanus*-susceptible variety treated with the systemic insecticide fipronil was used as a positive antibiosis control. Plant introduction PI165673 had the highest OP/Lv ratio, indicating that even if oviposition was successful, an antibiosis factor in PI165673 significantly reduced egg hatch and the resulting number of live *D. texanus* larvae. Factorial analyses indicated that maturity group is not a significant factor in the expression of resistance. Thus, PI165673 appears to be a potential source of resistance to *D. texanus*. In related field studies, the preferred *D. texanus* oviposition site was localized to leaf petioles in the upper four or five nodes of the plant canopy. Histomorphological analyses of petiole cross-sections of plant introductions PI171451, PI165676, and PI165673 indicated that leaf petiole morphology may be related to reduced *D. texanus* oviposition on petioles of PI171451 and PI165676, but that resistance in PI165673 is independent of petiole morphology.

KEY WORDS soybean plant introduction, plant resistance, oviposition puncture to larvae ratio, soybean petiole morphology, vascular histochemistry

The cerambycid beetle, *Dectes texanus* LeConte (Coleoptera: Cerambycidae) is a native of North America (Bezark 2008), where it is thought to have fed originally on wild plants such as cocklebur, *Xanthium pennsylvanicum* Waller (Compositae), and common and giant ragweed, *Ambrosia artemisifolia* L. and *A. trifida* L. (Asteraceae [formerly Compositae]) (Piper 1978). During the past 50 yr, *D. texanus* has become an economic pest in soybean, *Glycine max* (L.) Merrill, and in cultivated sunflowers, *Helianthus annuus* L. in some production areas of North America (Daugherty and Jackson 1969, Patrick and White 1972).

Adult *D. texanus* can be found on soybean plants from late June through August (Hatchett et al. 1975, Sloderbeck et al. 2003, Niide et al. 2006a, Patrick and White 1972, Campbell 1980, Buschman and Sloderbeck 2010). Adults feed on the epidermis of young soybean plants for ≈10 d, and females then begin to oviposit into tender soybean tissues. The majority of *D. texanus* eggs are oviposited in soybean petiole pith (Hatchett et al. 1975), and the eggs hatch in ≈5 d (Piper 1978). Oviposition punctures are visible on the plant with close inspection.

The first three instars feed and tunnel into the petiole pith until they are large enough to tunnel through the junction with the main stem. When larvae tunnel through this junction between the leaf petiole and stem, vascular tissues are damaged and the leaf dehydrates and dies. Dead leaves in the upper soybean canopy are the first obvious sign that *D. texanus* larvae are present in plants. Larval damage that remains visible at the node when dead leaves drop from the plant is referred to as an "entry node." Larvae continue to feed and tunnel in the pith of the main stem and often in side branches as well. Heavy infestations result in multiple oviposition punctures, tunneled petioles, and larval entry nodes that suggest multiple larvae feeding in the plant; however, tunnels soon merge, and larval cannibalism reduces the number of larvae to one per plant at the end of the season.

Surviving larvae at the end of the season tunnel to the base of the plant and develop overwintering chambers (Hatchett et al. 1975, Campbell and VanDuyn 1977). In this process, larvae also move back up the

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plants several centimeters to cut off the plants from the inside, known as girdling. Girdled plants eventually fall over, or "lodge." The larvae plug the open tunnels with frass to seal the chamber against winter weather. Plant girdling causes economic damage to commercial soybean production because lodged plants require more time and care to harvest. Some plants may even be lost during harvest. Lodging damage increased dramatically in Kansas from 1985 to 2008. Increased lodging appeared to be associated with an increase in soybean planting, from 0.6 to 1.3 million hectares, and an increase in no-till cultivation of soybean in this period (Buschman and Sloderbeck 2010; Sloderbeck et al. 2003, 2008).

Host plant resistance is an essential component of integrated pest management (IPM) in crops. Host plant resistance includes three categories: antixenosis (adverse effects on insect behavior), antibiosis (adverse effects on insect physiology and survival), and tolerance (plants withstand, repair or recover from insect damage). Antixenosis and antibiosis can determine the acceptability of the plant to the insect (Painter 1951, Smith 1989) and can be mediated by plant biochemical or biophysical factors (Smith 1989, 2005). In addition, several studies indicate that insect oviposition can be affected by plant tissue thickness or structure (Brewer et al. 1986, Lundgren et al. 2008, Michaud and Grant 2009).

Several attempts have been made to develop soybean varieties with resistance to *D. texanus* infestation. Richardson (1975) and Campbell (1976) screened a wide variety of soybean genotypes for *D. texanus* resistance and identified 18 plant introductions in maturity groups V, VI, and VII with moderate resistance. These selections were based on end-of-season observations of infested plants and may have been confounded by plant maturity group and larval cannibalism. More recently, Kaczmarek et al. (2003) reported contradictory results from several years of evaluating Midwestern soybean varieties. Several attempts also have been made to determine if *D. texanus* resistance is associated with resistance to cyst nematode, *Heterodera glycines*, but results have been inconclusive (Whalen et al. 1998, Higgins et al. 2003, Niide et al. 2006b). Resistance to *D. texanus* has been difficult to document using end-of-season observations such as percentage of infested or girdled plants. Resistance to *D. texanus* has been difficult to determine because midseason larval cannibalism in plants may obfuscate differences in larval populations. Therefore, *Dectes* ratings were made earlier in the season to avoid confusing resistance assessments because of the effects of cannibalism.

The objectives of this study were to develop procedures to identify soybean antibiosis or antixenosis to *D. texanus*, to screen soybean germplasm for *D. texanus* resistance, to determine the *D. texanus* vertical oviposition preference to improve sampling procedures, and to determine the relationship between soybean petiole morphology and *D. texanus* resistance in soybean.

Materials and Methods

Field Resistance Evaluations. In 2005 and 2006, 15 soybean genotypes, including six commercial varieties and nine plant introductions (PIs), were evaluated for *D. texanus* resistance. Commercial varieties included the most resistant and most susceptible varieties in maturity groups II to IV, based on the results of Buschman et al. (2005). The PIs included several identified by Richardson (1975) as resistant to *D. texanus* and others known to have resistance to various other insect pests of soybean: the Mexican bean beetle, *Epilachna varivestis* Mulsant (VanDuyn et al. 1971, 1972); bean leaf beetle, *Cerotoma trifurcata* (Forster); striped blister beetle, *Epicauta vittata* (F.) (Clark et al. 1972); banded cucumber beetle, *Diabrotica balteata* LeConte (Layton et al. 1987); the corn earworm, *Helicoverpa zea* Boddie (Smith and Brim 1979, Smith et al. 1979); and Asian soybean defoliating pests (Talekar et al. 1988).

Plants treated with fipronil (BASF Corporation, Research Triangle Park, NC), a systemic insecticide that effectively controls *D. texanus* larvae (Buschman et al. 2005), were used as a positive antibiosis control, because at the time the experiments began, no commercially available varieties exist that have *D. texanus* resistance. In 2006, the susceptible conventional variety Pioneer '93M50' received a soil treatment of the systemic insecticide fipronil (Regent 4 SC, 4.2 oz/acre) to simulate antibiosis. A 30-cm barrier (corrugated metal roofing) was installed 20.3–25.4 cm deep around the fipronil-treated plants to reduce the chances that roots of other plants would absorb the insecticide.

In 2007, the number of soybean genotypes evaluated was reduced to increase the number of plants of each line that could be evaluated. Plant introductions PI165673, PI171451, and PI165676 were selected for further research based on 2005 and 2006 results. The 2007 results suggested that the antibiosis and antixenosis observed in the three selected PIs might be associated with maturity group (MG VI-VIII); therefore, in 2008, we selected three commercial varieties with maturities similar to each PI to include in the test. The susceptible commercial variety 93M92 was also included both treated and untreated with fipronil. In 2007 and 2008, 93M92 soybean seed was treated with fipronil (Regent 500TS at 25 [2007] or 100 [2008] mg [AI]/100 kg) as a positive control for antibiosis. Untreated 93M92 served as a susceptible check. Variety seed planted in experiments was obtained from the following sources: 93M50 and '93M92,' Pioneer Hi-Bred International, Inc., Johnston, IA; 'DG32C25' and 'DG31M25,' Dyna-Gro Seed Company, Pocahontas, IA; 'NC-Roy,' North Carolina State University, Raleigh, NC; 'NEX2403K,' University of Nebraska; 'Prichard,' University of Georgia; 'R2803RR,' Renze Seeds LL, Templeton, IA; 'Santee,' Clemson University; and 'X3727NRS,' Ohlde Seed Farms Inc., Palmer, KS. Kansas Agricultural Experiment Station breeding lines were provided by the soybean breeding program at Kansas State University, and PI seed was obtained

from Dr. Randall L. Nelson, USDA–ARS (Agriculture Research Services) Soybean Germplasm Collection, Urabana, IL.

Fourteen plants from each of 15 soybean entries were planted 5 cm apart in rows 76 cm apart on 2 June 2005, and 20 May 2006, at the Kansas State University North Central Kansas Experiment Field near Scandia, KS. Entries were spaced to fit inside a commercial screen cage that could be placed over the plants later in the season. Placement of entries within each cage was a stratified random design to ensure that each entry was included in the center positions at the same frequency. Plantings included five replications in 2005 and six replications in 2006, but heavy rainstorms destroyed two replications in 2005 and one replication in 2006, yielding three and five replications, respectively, for data collection. A 1-m high trellis with horizontal cords was constructed to support procumbent PI plants to match the height of the commercial varieties. Entries were planted 31 May 2007, and 30 June 2008. In 2007, six replications were included in three screened cages, and in 2008, six replications were included in six cages.

When beetles were first noted in the field, polyester screen cages were installed over the experimental plants to keep the beetles from the plants until they were introduced into the cages. We used commercially available patio screens (in 2005 and 2006 they were Ozark Trail Polyester Screen House, 4.3 × 3.1 m, North Pole USA, Washington, MO; in 2007 and 2008 they were First-up Outdoor Shelters, 3.7 × 3.7 m, North Pole USA). Beetles were collected from surrounding soybean fields using sweep nets and a total of 550, 300, 315, and 110 beetles were released into each screen cage in 2005, 2006, 2007, and 2008, respectively. Plant height and maturity were recorded when cages were installed. Cages were left in place for 28 d (2005) or 10 d (2006) before removal. In 2007 and 2008, beetles were confined in the cages for at least 15 d before the cages were opened to release any remaining beetles. Plants in cages were not collected for another 7 d to allow eggs time to hatch. Plants from one or two replicates were collected at one time, taken to the laboratory, and processed. When possible, three plants were collected per replicate from each of the 15 entries in 2005 and 2006, and five plants were collected per replicate from each of five entries in 2007 and from eight entries in 2008.

The number of oviposition punctures was counted as an estimate of oviposition antixenosis, and the number of live larvae was recorded as an estimate of larval survival or antibiosis. Plants were dissected to record these measurements as early as possible to minimize *D. texanus* cannibalism to avoid confounding resistance with cannibalism. Because the number of oviposition punctures may be related to the number of surviving larvae, the ratio of oviposition punctures to live larvae was used to correct for plants that received fewer oviposition punctures.

For each plant, the following measurements were recorded for each petiole and internode: number of oviposition punctures, live larvae, eggs, entry nodes, length of main stem, and plant development stage. The ratio of oviposition punctures to live larvae (OP/Lv) was calculated. Oviposition punctures were recorded for each node or internodes so we could determine the vertical oviposition preference. Plant developmental stages were recorded as the number of fully expanded leaves (Pedersen 2004). In 2006, the plant growth stage was recorded when the cage was first installed on 12 July, but not in 2007; therefore, the plant growth stage in 2007 was estimated from plants collected 8 August. Plant maturity was recorded 53 and 79 d after seeding in 2006 and 69 d after seeding in 2007.

Petiole Morphology. Measurements of petiole vascular tissues were made on PI165673, PI171451, PI165676, and the susceptible soybean variety Pioneer '93M50' grown in 2007. Tissue samples were collected from the first, third, fifth, seventh, and ninth fully expanded trifoliates (counting from the plant apex) from a single plant from each genotype when cages were opened to release beetles on 8 August 2007. Petioles were removed from each plant and a 2-cm section was excised from the base and placed individually in small centrifuge tubes filled with 80% ethanol and stored at 5.6°C for later histochemical analyses. Preserved petioles were hand-sectioned and prepared as wet mounts on microscope slides. Sections were placed in safranin (to stain cell nuclei), fast green (to stain protein/cytoplasm), and phloroglucinol-HCl (to stain lignin) (Peterson et al. 2008, Zimmermann 1983). Prepared sections were digitally photographed using a stereoscopic zoom microscope (Nikon SMZ 1500, Nikon Instruments Inc., Melville, NY).

Captured cross-section images of dissected petioles were analyzed using ImageJ (NIH 2009). Measurements were made of petiole diameter, petiole pith diameter, mean number and diameter of vascular bundles, thickness of sclerenchyma fiber layer, total vascular bundle diameter, total intervascular perimeter, and proportion of total petiole perimeter occupied by vascular bundles.

Statistical Analyses. Data in all experiments were analyzed using SAS PROC GLM (Colette and Robinson 2000). Treatment means for numbers of oviposition punctures, live larvae, eggs, and entry nodes; length of main stem; plant development stage; and the ratio of OP/Lv, when significant, were compared using Duncan's Multiple Range Test ($\alpha = 0.05$). Treatment means for petiole diameter, petiole pith diameter, mean number, and diameter of vascular bundles, thickness of sclerenchyma fiber layer, total vascular bundle diameter, total intervascular perimeter, and proportion of total petiole perimeter occupied by vascular bundles were evaluated by one-way analysis of variance (ANOVA). When the ANOVA was significant the means were compared using LS Means ($\alpha = 0.05$).

Results

Field Resistance Evaluations. In 2005, PI171444, PI171451, and PI227687 had the fewest numbers of OPs ($F = 3.74$; df = 16, 110; $P < 0.0001$) and PI227687

Table 1. Mean ± SE number of *D. texanus* oviposition punctures (OP), eggs, and larvae, plant entry node, and OPs per larva on 15 soybean genotypes, 2005

Soybean genotype (maturity group)	OPs per nine plants	Live larvae per nine plants	Entry node per nine plants	OPs/larva ratio per nine plants
R2803RR (II)	134.0 ± 13.9abcd	6.9 ± 1.2ab	5.0 ± 1.0a	22.3 ± 2.5bc
DG31M25 (II)	96.1 ± 11.9cdef	5.4 ± 1.3abcd	4.1 ± 1.2ab	29.2 ± 11.7bc
93M50 (III)	160.0 ± 41.5ab	7.5 ± 1.9a	3.6 ± 1.2abc	24.9 ± 8.7bc
X3727NRS (III)	75.1 ± 8.9cdef	4.7 ± 0.7abcde	1.6 ± 0.6bcd	20.3 ± 5.1bc
KS4404RR (IV)	65.6 ± 18.3def	4.3 ± 1.1abcde	2.2 ± 1.0bcd	16.5 ± 1.9c
KS4704RR (IV)	69.3 ± 12.4def	4.7 ± 0.4abcde	2.7 ± 0.7abcd	15.4 ± 2.6c
PI82312 (VI)	196.0 ± 52.2a	6.4 ± 2.6abc	0.0 ± 0.0d	39.8 ± 11.9bc
PI165673 (VI)	175.0 ± 19.7a	2.3 ± 0.7de	1.3 ± 0.4cd	99.3 ± 30.2a
PI171444 (VI)	61.7 ± 18.7ef	4.1 ± 1.2abcde	1.9 ± 0.9bcd	15.3 ± 2.8c
PI171451 (VII)	49.1 ± 7.4f	2.6 ± 0.7de	1.8 ± 0.5bcd	24.4 ± 8.2bc
P228065 (VII)	131.0 ± 26.9abcde	3.7 ± 1.5bcde	1.4 ± 0.4cd	46.5 ± 15.7bc
PI229358 (VII)	85.8 ± 11.7cdef	3.2 ± 0.5cde	2.1 ± 0.6bcd	29.1 ± 4.3bc
PI323275 (VII)	85.3 ± 27.7cdef	1.4 ± 0.7e	2.0 ± 0.7bcd	3.1 ± 23.1b
PI165676 (VIII)	143.0 ± 15.5abc	2.1 ± 0.7de	1.3 ± 0.6cd	54.0 ± 9.9b
PI227687 (VIII)	61.6 ± 11.1ef	1.4 ± 0.5e	1.2 ± 0.5cd	35.0 ± 7.9bc
F value	3.30	3.30	2.23	3.86
df	16, 110	16, 110	16, 110	16, 93
P value	< 0.0001	< 0.0001	0.0080	< 0.0001

Means followed by the same letter in a column are not significantly different ($P < 0.05$), Duncan's Multiple Range test.

and PI323275 contained significantly fewer larvae ($F = 3.30$; df = 16, 110; $P < 0.0001$) (Table 1). No significant differences occurred among entries for numbers of eggs on plants. In general, varieties had greater numbers of larval entry nodes than plant introductions (0.0–2.1 per nine plants) (data not shown). Among stems of plant introductions, fewer larvae appeared to develop successfully to the stage of tunneling into the main stem or side branches. As a result, there were significant differences among entries for the OP/Lv ratio ($F = 3.86$; df = 16, 93; $P < 0.0001$) (Table 1), with PI165673 exhibiting a significantly greater ratio than all other entries.

In 2006, the mean number of OPs per plant among the remaining 12 entries differed significantly ($F = 5.32$; df = 18, 199; $P < 0.0001$) as did the numbers of live larvae ($F = 5.17$; df = 18, 199; $P < 0.0001$) (Table 2). PI82312, PI228065, and 'KS4704RR' had significantly more eggs per 15 plants than PI165676, PI165673, PI171451, 'KS4404RR', or 'NEX2403K' ($F = 3.21$; df = 18, 199; $P < 0.0001$) (Table 2). The largest number of entry nodes occurred in KS4404RR and was significantly larger than the numbers of entry nodes in fipronil-treated NEX2403K control plants ($F = 9.38$; df = 18, 199; $P < 0.0001$) (Table 2). With the exception of the NEX2403K positive control, commercial varieties had comparatively more entry nodes than plant introductions. The OP/Lv ratio varied significantly among entries ($F = 9.84$; df = 18, 186; $P < 0.0001$). Ratios in the fipronil-treated NEX2403K control plants and PI165673 plants were significantly greater than those for all other entries (Table 2).

Table 2. Mean ± SE noumber of *D. texanus* oviposition punctures (OPs), eggs, and larvae, plant entry node, and OPs per larva on 15 soybean genotypes, 2006

Soybean genotype (maturity group)	OPs per 15 plants	Live larvae per 15 plants	Eggs per 15 plants	Entry node per 15 plants	OPs/larva ratio on 15 plants
NEX2403K[a] (II)	23.7 ± 2.8d	0.4 ± 0.2e	0.3 ± 0.2c	0.0 ± 0.0de	26.8 ± 4.6a
DB32C25 (II)	27.0 ± 4.7cd	6.1 ± 1.1abcd	0.5 ± 0.2bc	3.2 ± 0.9a	4.6 ± 0.5ef
93M50 (III)	55.1 ± 8.5b	6.5 ± 0.9abcd	0.7 ± 0.3bc	1.9 ± 0.4b	9.7 ± 1.3de
X3727NRS (III)	37.3 ± 4.3bcd	9.4 ± 1.7a	0.6 ± 0.2bc	1.3 ± 0.3bcde	4.6 ± 0.4ef
KS4404RR (IV)	43.8 ± 3.2bcd	6.6 ± 0.5abcd	0.3 ± 0.1c	4.2 ± 0.7a	7.2 ± 0.7def
KS4704RR (IV)	27.9 ± 2.9bcd	8.1 ± 1.1ab	1.2 ± 0.3ab	1.7 ± 0.5bc	3.9 ± 0.4ef
PI82312 (VI)	110.0 ± 43.5a	9.3 ± 2.8a	1.8 ± 0.7a	0.6 ± 0.3cde	11.7 ± 2.5cd
PI165673 (VI)	49.3 ± 5.6bcd	3.3 ± 0.5de	0.3 ± 0.1c	1.3 ± 0.4bcd	20.5 ± 3.4b
PI171444 (VI)	25.3 ± 2.6d	5.3 ± 0.8bcd	0.9 ± 0.3bc	0.4 ± 0.1de	5.7 ± 0.7ef
PI171451 (VII)	30.5 ± 4.5bcd	4.3 ± 0.7cd	0.1 ± 0.1c	1.1 ± 0.3bcde	7.9 ± 1.1def
PI228065 (VII)	46.1 ± 9.6bcd	7.0 ± 1.2abc	1.2 ± 0.3ab	0.9 ± 0.2bcde	7.6 ± 1.0def
PI229358 (VII)	25.5 ± 2.5d	4.5 ± 0.6cd	0.5 ± 0.2bc	1.1 ± 0.5bcde	6.7 ± 0.9def
PI323275 (VII)	38.4 ± 4.3bcd	4.7 ± 0.6cd	0.9 ± 0.3bc	0.6 ± 0.3bcde	7.8 ± 0.7def
PI165676 (VIII)	53.9 ± 5.5bc	5.5 ± 0.9bcd	0.3 ± 0.1c	1.1 ± 0.4bcde	14.5 ± 2.7c
PI227687 (VIII)	47.4 ± 6.8bcd	8.5 ± 1.8ab	0.8 ± 0.3bc	0.6 ± 0.3cde	6.7 ± 0.6def
F value	5.32	5.17	3.21	9.38	9.84
df	18, 199	18, 199	18, 199	18, 199	18, 186
P value	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001

Means followed by the same letter in a column are not significantly different ($P < 0.05$), Duncan's Multiple Range test.
[a] Fipronil soil treatment (4.2 oz/acre, Regent 4SC).

Table 3. Mean ± SE number of *D. texanus* oviposition punctures (OPs), eggs, and larvae; plant entry node; and OPs per larva on three soybean introductions and fipronil-treated and untreated soybean variety 93M50, 2007

Soybean genotype (maturity group)	OPs per 30 plants	Live larvae per 30 plants	Eggs per 30 plants	Entry node per 30 plants	OPs/larva ratio on 30 plants
PI165673 (VI)	25.3 ± 2.2b	0.9 ± 0.2c	0.07 ± 0.05b	0.30 ± 0.09b	23.5 ± 2.9a
PI171451 (VII)	15.6 ± 1.8c	0.9 ± 0.2c	0.03 ± 0.03b	0.27 ± 0.09b	15.1 ± 1.8b
PI165676 (VIII)	15.3 ± 2.2c	0.6 ± 0.2c	0.11 ± 0.06ab	0.37 ± 0.13b	12.7 ± 3.1b
93M50 T[a] (III)	35.8 ± 2.5a	1.7 ± 0.2b	0.27 ± 0.09a	0.57 ± 0.17b	25.4 ± 3.4a
93M50 U[b] (III)	24.8 ± 2.9b	2.3 ± 0.3a	0.00 ± 0.00b	1.92 ± 0.24a	12.8 ± 1.6b
F value	14.97	9.86	3.20	22.46	5.38
df	4, 5	4, 5	4, 5	4, 5	4, 5
P value	< 0.0001	< 0.0001	0.0151	< 0.0001	0.0007

Means followed by the same letter in a column are not significantly different ($P < 0.05$), Duncan's Multiple Range test.
[a] T, fipronil seed treatment (25 mg AI/100 kg seed, Regent 500TS).
[b] U, untreated check.

In 2007, significant differences ($F = 14.97$; df = 4, 5; $P < 0.0001$) were measured in the number of OPs with the most occurring in PI165673 and the treated 93M50 (Table 3), whereas PI171451 and PI165676 had comparatively fewer OPs, respectively. All plant introductions had significantly fewer live larvae per 30 plants than fipronil-treated and untreated 93M50 plants ($F = 9.86$; df = 4, 5; $P < 0.0001$) (Table 3). No eggs were found in untreated 93M50 plants (Table 3), but the three plant introductions received 0.03–0.11 eggs per 30 plants. The largest number of entry nodes was found in untreated 93M50 plants (Table 3), which was significantly greater than all other entries ($F = 22.46$; df = 4, 5; $P < 0.0001$). The OP/Lv ratio was significantly greater ($F = 5.38$; df = 9, 85; $P < 0.0007$) for PI165673 and fipronil-treated 93M50 than for PI171451, PI165676, and the untreated 93M50 control (Table 3).

In 2008, the largest number of OPs was again found in PI165673 and the treated 93M92, and significantly fewer OP were found on PI171451, untreated 93M92, and Prichard ($F = 3.13$; df = 7, 5; $P < 0.0044$) (Table 4). NC-Roy and untreated 93M92 had significantly more live larvae than PI165673, PI171451, PI165676, Prichard, or fipronil-treated 93M92 ($F = 3.24$; df = 7, 5; $P < 0.0034$) (Table 4), even though untreated 93M92 received very few OPs. The numbers of eggs and larval entry nodes were too small to provide useful information and no significant differences were found between genotypes. Differences in the OP/Lv ratios were highly significant ($F = 7.59$; df = 7, 5; $P < 0.0001$), with PI165673 and treated 93M92 exhibiting significantly higher ratios than all other entries except PI165676 (Table 4). Untreated 93M92 plants had a significantly smaller OP/Lv ratio than all other genotypes except PI171451.

Factorial analysis of 2008 data (Table 5) yielded *P* values indicating that maturity group had no significant effect on any infestation variable except entry node, where the numbers were too small to give meaningful results. Significant differences occurred in OP/Lv ratios ($F = 19.75$; df = 3, 1; $P < 0.0001$) between resistant and susceptible entries, but no difference ($F = 1.65$; df = 3, 1; $P = 0.1819$) was found among maturity groups. Interactions in the OP/Lv ratio were significant ($P = 0.0002$), indicating that not all the entries assumed to be resistant were truly resistant. Maturity group VII and VIII entries were not significantly different from each other (Table 4), indicating that resistance was not present across these entries; however, antibiosis in PI165673 was similar to that in the fipronil-treated plants (90–100% control) (Tables

Table 4. Mean ± SE number of *D. texanus* oviposition punctures (OPs), eggs, larvae, and soybean entry node per plant, and OPs per larva on three soybean introductions and fipronil-treated and untreated soybean variety 93M92, 2008

Soybean genotype (maturity group)	OPs per 18 plants	Live larvae per 18 plants	Eggs per 18 plants	Entry node per 18 plants	OPs/larva ratio on 18 plants
PI165673 (VI)	24.2 ± 4.0a	1.2 ± 0.3b	0.2 ± 0.1a	0.0 ± 0.0a	16.0 ± 2.2a
NC-Roy (VI)	19.1 ± 2.6ab	2.6 ± 0.5a	0.1 ± 0.1a	0.0 ± 0.0a	10.2 ± 1.7bc
PI171451 (VII)	12.0 ± 2.1b	1.5 ± 0.3b	0.2 ± 0.1a	0.0 ± 0.0a	8.2 ± 1.0cd
Santee (VII)	20.6 ± 2.8ab	1.9 ± 0.3ab	0.7 ± 0.7a	0.0 ± 0.0a	10.2 ± 1.2bc
PI165676 (VIII)	16.3 ± 3.9ab	1.2 ± 0.3b	0.1 ± 0.1a	0.0 ± 0.0a	13.0 ± 2.0ab
Prichard (VIII)	13.1 ± 2.5b	1.2 ± 0.3b	0.0 ± 0.0a	0.1 ± 0.1a	9.4 ± 1.4bc
93M92 T[a] (III)	24.2 ± 2.7a	1.4 ± 0.2b	0.6 ± 0.3a	0.7 ± 0.7a	15.7 ± 1.7a
93M92 U[b] (III)	13.6 ± 2.0b	2.7 ± 0.4a	0.2 ± 0.1a	0.2 ± 0.1a	4.6 ± 0.5d
F value	3.13	3.24	1.04	0.99	7.59
df	7, 5	7, 5	7, 5	7, 5	7, 5
P value	0.0044	0.0034	0.4091	0.4442	< 0.0001

Means followed by the same letter in a column are not significantly different ($P < 0.05$), Duncan's Multiple Range test.
[a] T, fipronil seed treatment (100 mg AI/100 kg seed, Regent 500TS).
[b] U, untreated check.

Table 5. Factorial analysis of mean ± SE number of *D. texanus* oviposition punctures(Ops), eggs, larvae, and soybean entry nodes per plant; and OPs per larva on three soybean introductions, three soybean varieties, and fipronil-treated and untreated soybean variety 93M92, 2008

Comparisons	OPs	Live larvae	Eggs	Entry node	OPs/larva
Maturity group					
(III)	18.4 ± 1.9a	2.1 ± 0.3a	0.4 ± 0.2a	0.11 ± 0.05a	10.2 ± 1.3a
(VI)	21.7 ± 2.4a	1.9 ± 0.3a	0.1 ± 0.1a	0.00 ± 0.00b	12.4 ± 1.4a
(VII)	16.3 ± 1.9a	1.7 ± 0.2a	0.4 ± 0.3a	0.00 ± 0.00b	9.2 ± 0.8a
(VIII)	14.7 ± 2.3a	1.2 ± 0.2a	0.1 ± 0.0a	0.03 ± 0.03b	11.0 ± 1.2a
Resistant[a]	18.9 ± 1.7a	1.4 ± 0.1b	0.3 ± 0.1a	0.00 ± 0.00b	13.0 ± 0.9a
Susceptible	16.5 ± 1.3a	2.1 ± 0.2a	0.2 ± 0.2a	0.07 ± 0.03a	8.6 ± 0.7b
Probabilities for:					
Maturity group	0.0978	0.0912	0.4071	0.0227	0.1819
Resistance	0.2628	0.0027	0.8875	0.0207	< 0.0001
Interaction	0.0126	0.1593	0.3166	0.0287	0.0002

Means followed by the same letter in a column are not significantly different ($P < 0.05$), Duncan's Multiple Range test.

[a] Plant introductions and fipronil-treated 93M92 were considered resistant; conventional varieties and fipronil-untreated 93M92 were considered susceptible.

3 and 4), and PI171451 also expressed some antixenosis-based resistance.

Oviposition Site Choice. In general, PIs developed more nodes than commercial varieties in 2006 and 2007. In 2006, the mean developmental stage for PIs ranged from 8.5 to 10.1 nodes during preliminary measurements, but the range increased from 16.3 to 22.5 nodes at the first dissection, depending on the entry (Niide 2009) (Table 6). Commercial varieties averaged 8.1 to 9.7 nodes during preliminary measurements, and the range increased from 14.5 to 18.3 nodes at the first dissection, depending on variety. In 2007, differences in the mean developmental stage for PIs at the first dissection ranged from 18.3 to 20.6 nodes whereas the commercial varieties averaged 18.2 to 19.0 nodes (Niide 2009) (Table 7).

In 2006, the estimated developmental stage at the time of the first cage installation (58 d after seeding) ranged from 10.1 to 12.5 nodes for PIs and 9.7 to 11.3 nodes for commercial varieties. At the second cage installation (66 d after seeding), the estimated developmental stage for PIs ranged from 12.5 to 16.3 nodes and from 12.1 to 13.9 nodes for Kansas varieties. In 2007, the estimated developmental stage at the time of the first cage installation

Table 6. *D. texanus* oviposition punctures in growth nodes of plants of 15 soybean genotypes, based on node position relative to the top fully expanded leaf when caged, 2006

Nodes	No. oviposition punctures								
	PI 165673	PI 165676	PI 82312	PI 171444	PI 171451	PI 227687	PI 228065	PI 229358	PI 323275
At caging									
−5	0.8	1.5	2.6	0.9	1.1	0.5	0.6	0.7	0.2
−4	2.4	1.3	3.1	1.5	1.2	0.9	1.8	1.5	0.4
−3	3.5	3.6	6	1.8	2.8	2.1	3.5	1.9	2.1
−2	6.8	4.1	9	1.6	1.9	2.5	2.8	2	2.3
−1	7	3.7	5.2	1.4	1.7	2.2	2.5	2.8	2.7
Second cage installed									
1	6.8	3.5	5.8	1.1	2.1	3	2.2	1.7	2.9
2	4.3	3.5	4	1.5	3.4	3.7	3	2.4	3.1
3	2.6	3.7	4.4	1.8	2.5	1.9	2.2	3.1	3.6
4	1.5	3.9	2.9	2.3	2.4	3.4	2.4	1.6	2.5
5	3.4	2.3	1.9	1.4	1.4	4	1.9	1.7	1.6
Total	45.5	38.9	50.1	19.6	23.8	33.5	30.3	22.8	25.9

Nodes	93M50	NEX2403K	DB32C25	A3727NRS	KS4704	KS4404	Total punctures	% total
At caging								
−5[a]	0.1		0.8	0.1	0.1	0.3	10.3	2.3
−4	0.8	1.2	0.7	0.4	0.4	1	18.6	4.2
−3	1.4	1.6	1.1	0.9	0.3	2.6	35.2	7.9
−2	2.5	2.1	1.5	2.1	1.7	2.8	45.7	10.2
−1	2.3	2.6	2.3	1.7	2.1		44.8	10.0
Second cage installed								
1	3.5	2.7	1.5	2.7	1.7	3.7	44.9	10.0
2	5.1	2.7	1.5	2.1	2.3	3.9	46.5	10.4
3	4.5	3.6	2.3	3.4	2.4	3.9	45.9	10.3
4	3.8	2.1	1.7	2.1	2.4	2.8	37.8	8.4
5	3.7	2.1	2.3	2.1	2.3	2.9	35	7.8
Total	39.2	22.5	18.8	23.6	20.2	32.8	447.5	96.7

Shaded areas mean.

[a] Negative nodes added after cage installed.

Table 7. *D. texanus* oviposition punctures in growth nodes of plants of five soybean genotypes, based on node position relative to the top fully expanded leaf when caged, 2007

Nodes	No. oviposition punctures						
	PI165673	PI165676	PI171451	93M50 T[a]	93M50 U[b]	Total punctures	% total
At caging							
−5[c]	0.6	0	0	0	0.1	0.7	0.7
−4	0.3	0.1	0.3	0.1	0.2	1	1.1
−3	0.7	0.3	0.3	0.1	0.6	2	2.1
−2	1	0.6	0.4	0.5	0.9	3.4	3.6
−1	1.2	1	0.6	1.9	1.6	6.3	6.7
Cage installed							
1	2.2	3	1.4	2.9	2.1	11.6	12.3
2	2.4	2.6	2.9	4	3.4	15.3	16.3
3	3.6	1.7	2.2	3.5	3.9	14.9	15.9
4	2.4	0.7	2.1	2.6	3.8	11.6	12.3
5	3.6	0.5	0.9	2	3.4	10.4	11.1
Total	21.5	12.6	13.8	20.1	26	94	100.0

Shaded areas mean.
[a] T, fipronil seed treatment (100 mg AI/100 kg seed, Regent 500TS).
[b] U, untreated check.
[c] Negative nodes added after cage installed.

(54 d after seeding) ranged from 12.6 to 14.3 nodes for PIs and from 12.6 to 13.3 nodes for 93M50. PI165673 had at least one more node than the other PIs, and fipronil-treated 93M50 plants appeared to have slightly more nodes than untreated plants.

In 2006, the number of days to develop a new node ranged from 2.1 to 3.4 d for PIs and from 3.0 to 5.4 d for commercial varieties. Fipronil-treated NEX2403K had the lowest rate of development. In 2007, the time to develop a new node averaged 3.7 d for PI165673, 3.9 d for PI171451, 4.0 d for fipronil-treated 93M50, and 4.2 d for PI165676 and for untreated 93M50 plants.

Oviposition puncture data were arranged relative to the top fully expanded leaf at the time of cage installation, and were used to calculate the percentage of total punctures per leaf. In 2006, 50.9% of the total punctures occurred on petioles on nodes 3 through −2 (Table 6), and in 2007, 67.9% of the total punctures occurred on petioles on nodes 1 through 5 (Table 7). These results indicate that the majority of OPs occur on five petioles that can be excised without adversely affecting test plants.

Petiole Morphology. No significant differences were found in petiole diameter, petiole pith diameter, the number of vascular bundles, or the thickness of the sclerenchyma layer in the petioles of soybean plant introductions (data not shown). Plant introductions PI165673 and 171451 had significantly thicker vascular bundles than the susceptible 93M50 control ($F = 5.59$; df = 3, 4; $P = 0.0123$), but PI165676 and PI171451 each had a significantly greater total vascular bundle diameter ($F = 4.57$; df = 3, 4; $P = 0.0235$) and a significantly greater amount of pith perimeter occupied by vascular bundles ($F = 5.93$; df = 3, 4; $P = 0.0101$) than 93M50. No difference was measured between the proportion of the petiole perimeter of PI165673 and 93M50 (Table 8). The petiole diameter of leaves of PI165673, PI171451, and 93M50 plants at lower levels of the main stem increased, reaching a maximum at the third or fifth nodes below the plant apex (Fig. 1); however, the petiole diameter of PI165676 did not follow this pattern, and in some cases decreased or remained constant.

Just as differences in numbers of OPs varied significantly among different leaf positions (Tables 6 and 7), the number of OPs increased with decreasing leaf position from the plant apex, and in most cases reached a maximum at position five or seven (Fig. 1). The number of petioles changed with plant growth during *D. texanus* infestation, however, and older leaves were exposed to oviposition for a longer period of time. The number of OPs was probably more closely related to the number of petioles present on infested plants rather than to petiole morphology.

Table 8. Mean ± SE petiole vascular bundle diam, total diam of all vascular bundles and proportion of total petiole area occupied by vascular bundles [VB/(VB + IVA)] in three soybean plant introductions and 93M50

Soybean genotype	Mean vascular bundle diam (mm)	Total diam of all vascular bundles (mm)	VB/(VB + IVA)[a] (mm)
PI165673	0.505 ± 0.048a	8.294 ± 0.883ab	0.719 ± 0.032bc
PI165676	0.478 ± 0.031ab	8.904 ± 0.232a	0.800 ± 0.016a
PI171451	0.562 ± 0.052a	9.460 ± 1.012a	0.753 ± 0.039ab
93M50	0.401 ± 0.052b	6.696 ± 1.018b	0.663 ± 0.043c
F	5.59	4.57	5.93
df	3,4	3,4	3,4
P value	0.0123	0.0235	0.0101

Means followed by the same letter in a column are not significantly different LSM ($P < 0.05$).
[a] VB, vascular bundle diam; IVA, total intervascular area.

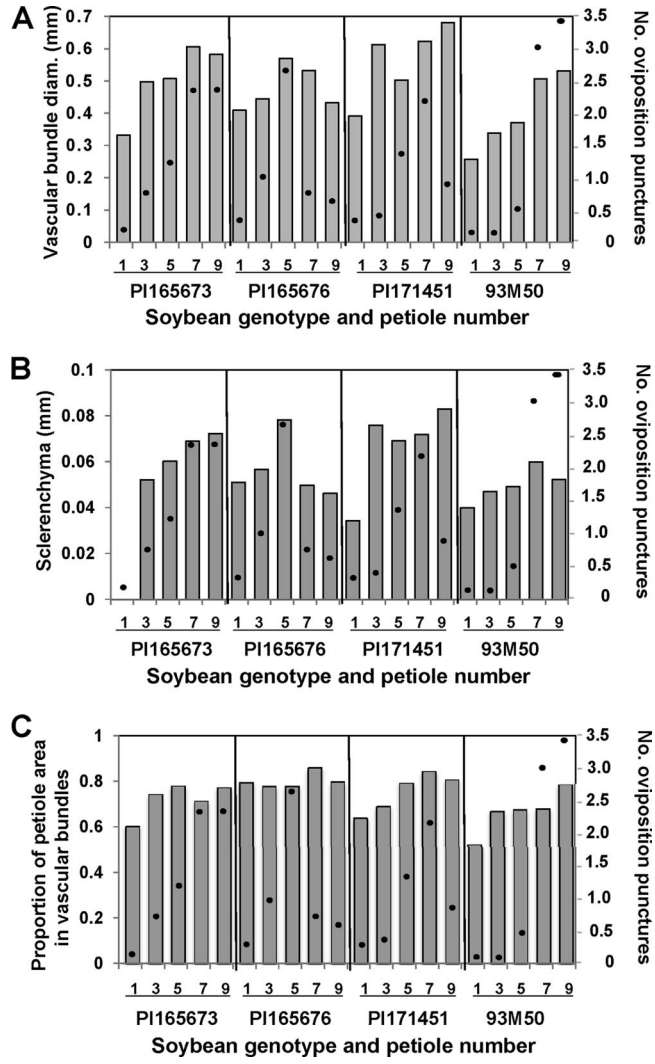

Fig. 1. Mean numbers of oviposition punctures (dots) relative to petiole parameters for the first, third, fifth, seventh, and ninth petioles of soybean genotypes PI165673, PI165676, PI171451, and 93M50. (A) petiole vascular bundle diameter (mm), (B) sclerenchyma thickness (mm), (C) proportion of total petiole area occupied by vascular bundles = [Total diameter of the vascular bundles/sum of the diameter of vascular bundles plus inter-vascular regions].

Discussion

In all 4 yr, PI165673 had the greatest level of antibiosis (highest OP/Lv ratio) against *D. texanus* compared with all other PIs and varieties evaluated (Table 1–4). Interestingly, PI165673 exhibited the lowest level of antixenosis (highest number of OPs) in 2007 and 2008 (Table 3 and 4) and the second-highest level of antixenosis in 2005 (Table 1). PI165676 exhibited moderate antibiosis, with an OP/Lv ratio similar to PI165673 in 2005 and 2008. PI171451 had significant antixenotic effects (lower numbers of OPs) relative to the susceptible control in 2007 and 2008. Although PI171451 is resistant to larval Coleopteran and Lepidopteran soybean foliar feeders, the *D. texanus* OP/Lv ratio was not close to that of PI165673. Thus, PI165673, PI165676, and PI171451 may be useful as parents for creating *D. texanus*-resistant genotypes in soybean breeding programs.

The OP/Lv ratio was a better determinant of antibiosis than variables such as numbers of larvae, eggs, or entry nodes. Susceptible 93M50 and 93M92 plants treated with fipronil successfully functioned as positive controls, because both exhibited OP/Lv ratios no different than those for PI165673. The residual activity of fipronil appeared to remain effective during the entire larval feeding period. The large field cages used to confine adult *D. texanus* on tested plants consistently maintained adult oviposition pressure and provided similar plant resistance responses in each of the 4 yr of study.

Results of oviposition preference experiments clearly indicated that *D. texanus* oviposit near the top

of the growing plant (Tables 6 and 7) where peak oviposition occurs on nodes −2 through 5. Beetle life was short in the cages, because the number of OPs decreased quickly for nodes that appeared while the plants were caged. The preferred oviposition site was more variable in 2006 (Table 6) and more difficult to interpret, because plants were caged twice and beetles were added twice. Nevertheless, preferred oviposition sites were usually very close to the highest fully expanded leaves present at cage installation. Very little oviposition occurred below nodes five and six when the first cage was installed; thus, we conclude that *D. texanus* oviposition occurs on soybean leaf petioles in the upper nodes of the plant canopy. Our conclusion is supported by behavioral observations of Hatchett et al. (1975), who reported that adults feed on tender plant stems, leaf petioles, and leaves.

In most cases, the proportion of total vascular bundle width to total intervascular area width reached a maximum for petioles on the fifth or seventh nodes (Table 8). Oviposition punctures were usually found on the side or bottom of petioles between the vascular ridges. Notably, the intervascular spaces appear to be larger in these areas and the vascular bundles appear to be larger under the five well-developed primary vascular bundles spaced around the petiole periphery. We hypothesized that resistant PIs should have a high proportion of total vascular bundle width to total intervascular area width, based on the assumption that plants with lower ratios (or a higher proportion of intervascular space) would allow beetles to penetrate pith during oviposition more easily. This hypothesis is not supported by our results, because the highest proportion of intervascular space occurred in both the susceptible 93M50 control and in PI165673 (Table 8). Nevertheless, PI165673 exhibited the most antibiosis (highest OP/Lv ratio) even though it had the highest number of OPs (Table 3).

In conclusion, although soybean leaf petiole morphology may be related to *D. texanus* oviposition, our data do not support the contention that *D. texanus* resistance is related to petiole morphology; however, Hatchett et al. (1975) reported that not all OPs contain eggs, and many OPs recorded may have been unsuccessful oviposition attempts, because it was difficult to determine egg deposition after larval tunneling through petioles. PI165673, a highly antibiotic genotype, had comparatively thin vascular bundles, suggesting that antibiosis reduces the number of live *D. texanus* larvae in this soybean plant introduction. Additional experiments are necessary to determine the genetics of larval antibiosis in PI165673 and to identify additional sources of *D. texanus* resistance in soybean.

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