PLANT RESISTANCE

Grass Species and Endophyte Effects on Survival and Development of Fall Armyworm (Lepidoptera: Noctuidae)

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ABSTRACT Grass selections including 10 zoysiagrasses, 18 paspalums, 34 Bermuda grasses, tall fescue, creeping red fescue, and perennial ryegrasses with and without endophyte were evaluated for potential resistance to fall armyworm, Spodoptera frugiperda (J. E. Smith), larvae. Laboratory evaluations assessed the degree of antibiosis among >70 grass lines to first-instar fall armyworms. When all parameters measured were considered, the trend in resistance to fall armyworm among endophyteinfected (E+) and endophyte-free (E-) cool season grasses from greatest to least was: 'Dawson' E+ > APR 1234 > 'Dawson' E- > 'Rosalin' E+ > Lp 5425, 'Rosalin' E-, ATF 480 > 'Tulsa' or: E+ slender creeping red fescue > E+ turf- type perennial ryegrass > E- slender creeping red fescue > E+ for age-type perennial ryegrass > E- for age-type perennial ryegrasses, and E+ tall fescue > E- turf-type tall fescue. Among warm season grasses larval weight gain was reduced on all zoysiagrasses. Larval weight gain also was lower on the Bermuda grasses 'Tifsport', 'Tifgreen', 97-4, 97-14, 97-22, 97-28, 97-39, 97-40, 97-54, 98-15, 98-30, and 98-45 than when larvae were fed 'Tulsa' tall fescue or the diet control. Only APR1234 and 'Dawson' creeping red fescue reduced larval survival to the same extent that was observed for zoysiagrasses. Survival on Bermuda grasses was least on 97-8. Seashore paspalums were only rarely less susceptible to fall armyworm than tall fescue, although pupal weights were consistently lower on 'Temple 1' and 'Sea Isle 1' paspalums than that on 'Tulsa' tall fescue. Genetic resistance to key grass pests can reduce insecticide use and simplify management of these cultivars.

KEY WORDS Spodoptera frugiperda, host plant resistance, turfgrass, forage, sod production, endophyte

THE FALL ARMYWORM, Spodoptera frugiperda (J.E. Smith), annually migrates northward, invading much of the continental United States and Canada (Potter and Braman 1991). Pasture grasses and turf, especially in the southeastern and Gulf states, can be severely damaged by this sporadic pest. Wiseman et al. (1982) compared 'Common' centipedegrass (*Eremochloa ophiuroides* (Munro) Hack.), 'Coastal' Bermuda grass (*Cynodon dactylon* (L.) Pers.), and carpetgrass, (*Axonopus affinis* Chase) for susceptibility to this pest. Nonpreference and antibiosis in centipedegrass were observed. Bermuda grass, centipedegrass, and zoysiagrass (*Zoysia* spp. Willd.) also were evaluated for susceptibility to fall armyworm by Chang et al. (1985, 1986), revealing a high level of antibiosis among Bermuda grass selections. Wiseman and Duncan (1996) investigated 81 *Paspalum* taxa for resistance to fall armyworm. They discovered very high levels of resistance in *Paspalum modestum* Mez and *Paspalum scrobiculatum* L. Larvae that were fed these two species were significantly smaller at 9 d than larvae that were fed other *Paspalum* spp. Larvae reared on diet containing these two grass genotypes failed to develop to pupation. High levels of resistance to fall armyworms have been identified among certain zoysiagrass cultivars (Reinert et al. 1994, 1997, 1998; Braman et al. 2000b; Reinert and Engelke 2000).

Many grasses are infected with fungal endophytes that grow intercellularly within leaves, stems, and seeds and may confer enhanced fitness to their hosts. Benefits conferred by endophytes include enhanced drought tolerance, disease resistance, and deterrence of insect and mammalian herbivory. This resistance is mediated by toxic alkaloids that are produced by the fungi. While beneficial in turfgrasses, it can be detrimental in forage grasses resulting in fescue toxicosis and ryegrass staggers in livestock. Resistance to >23 species of insects in 10 families and five orders has been noted for grasses infected with *Neotyphodium*

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spp. = Acremonium endophytes (Breen 1994). Expression of endophyte-enhanced resistance may be affected by endophyte genotype, host plant genotype, host \times endophyte interactions, endophyte concentration, allelochemical concentration, and external factors such as temperature, soil pH, and soil fertility. The use of selected strains of endophytes that are associated with either insect resistance or other stress tolerance but not livestock problems can permit the development of pasture grass cultivars with endophyte enhancement allowing persistence of grasses without negative effects on livestock.

Some grasses used for turf in managed systems such as golf courses, recreational areas and home lawns have been characterized for their resistance to certain turfgrass pests, including the fall armyworm: e.g., see reviews, (Reinert 1982, Quisenberry 1990). Here, we examined selected warm-season Bermuda grass, paspalum, and zoysiagrass taxa for potential resistance to the fall armyworm. We also evaluated cool-season grass genotypes with and without endophyte for potential resistance to this common grass pest.

Materials and Methods

Fall Armyworm, Cool-Season Grass Taxa, and Endophyte Effects. Fescue (Festuca spp. (L.) and ryegrass (Lolium spp. (L.) genotypes with and without endophyte were maintained in a greenhouse in 15.2cm-diameter pots. Grasses included 'Dawson' E+, a slender creeping red fescue with the endophyte *Epi*chloe festucae and 'Dawson' E-; APR 1234, a turf-type perennial ryegrass with the endophyte *Neotyphodium* lolii; 'osalin' E+, a forage-type perennial ryegrass with the endophyte Neotyphodium seigelii and 'Rosalin' E-; Lp 5425, a forage-type perennial ryegrass without endophyte; ATF 480, tall fescue with the endophyte Neotyphodium coenophialum; and 'Tulsa', a turf-type tall fescue without endophyte. Daylength was 14 h, maintained using high intensity, metal halide light. Grasses were grown in granular calcinated clay (Turface, Applied Industrial Materials, Deerfield, IL). Pots were watered daily and fertilized once per week with a solution containing 250 ppm (N-P-K, Peters 20 - 20 - 20, Scotts-Sierra Horticultural Products, Maryville, OH). Grasses were sheared weekly and maintained at an 8-cm height. Separate trials were conducted in November and December 1998, and February 1999. Data were combined for analysis.

Neonate fall armyworms from a colony maintained on commercial diet (Bioserve, Frenchtown, NJ) were placed into 32-ml clear plastic cups, which in turn were held in 30-cell clear plastic trays. The fall armyworm colony was initiated from eggs supplied by the USDA/ARS Crop Protection and Management Research Unit in Tifton, GA, in 1994 and supplemented annually with new material from the USDA colony (corn strain). Larvae were fed clippings of experimental grasses (1.5 g each daily) until pupation or death of the larva. Each grass genotype was represented by 20 individual grass pots. Clippings from individual pots were combined. Larvae were confined individually, with 25 replications arranged in a completely randomized design, within environmental chambers (Percival Scientific, Perry, IA) at 24°C and a photoperiod of 15:9 (L:D) h. Larval survival to the pupal stage, larval weights at day 10, pupal weights, taken within 24 h of pupation and days to complete larval development were compared among grasses using Bonferroni's test following a significant analysis of variance (ANOVA) (SAS GLM procedure, SAS Institute 1985). Orthogonal contrasts were used to compare performance of larvae on fescue versus ryegrass and with versus without endophyte.

Fall Armyworm, Warm-Season Grass Taxa Effects. Bermudagrasses, seashore paspalums and zoysiagrasses were maintained in the greenhouse as described above. Fall armyworm evaluations were conducted using these grasses exactly as described above (n = 25 individuals per grass cultivar per trial) during March-August, 2000. Four separate trials were conducted until all grasses had been included in at least two separate trials.

Results

Fall Armyworm, Cool-Season Grass Taxa and Endophyte Effects. Grass genotype and endophyte status significantly affected development of fall armyworm at day 10 (F = 20.2; df = 7, 722; P < 0.01). Among cool-season grasses, larval weights of fall armyworms at day 10 were most reduced by feeding on APR 1234, an endophypte enhanced perennial ryegrass (Table 1). Endophyte-free 'Rosalin' perennial ryegrass as a food source resulted in significantly greater larval weight at day 10 than any other selection. Pupal weights (F = 7.4; df = 7, 472; P < 0.01) ranged from 197.7 mg on 'Rosalin' E+ to 248.0 mg on 'Dawson' E+. Development time (F = 8.74; df = 7, 474; P < 0.01) ranged from 20.9 d for larvae fed LP 5,424, an endophyte-free perennial ryegrass, to 23.1 d when larvae were fed the creeping red fescue 'Dawson' E-. Survival to the pupal stage among cool-season grasses was least when larvae were fed 'Dawson' E+ creeping red fescue, and greatest when larvae were fed 'Tulsa' tall fescue. Survival in perennial ryegrass 'Rosalin' lines enhanced with the newly described endophyte Neotyphodium x seigelii Schardl (Craven et al. 2001) was statistically similar to endophyte-free 'Rosalin'. Orthogonal contrasts were only significant for with versus without endophyte and only for larval weights (F = 35.1, df = 1, P < 0.01). This illustrates the importance of individual grass and grass by endophyte evaluations to identify the contributions of cultivar and endophyte to observed differences in biological parameters. Evaluating solely for plant genera or endophyte status in this case would lead to erroneous conclusions concerning host suitability to the armyworm.

When all parameters measured are considered, the trend in resistance to fall armyworm among cool season grasses evaluated from greatest to least appeared as follows: 'Dawson' E+ > APR 1234 > 'Dawson' E- > 'Rosalin' E+ > Lp 5425, 'Rosalin' E-, ATF 480 >

| Genotype | Endophyte | 10-day larval weight, mg | n | Pupal weight, mg | n | Days to pupation | Survival to pupal stage |
|---|------------------------------|-----------------------------|-----|--------------------------|-----|---------------------------|---------------------------|
| Festuca arundacea | | | | | | | |
| 'Tulsa' | None | $41.4 \pm 4.2c$ | 63 | $238.9 \pm 5.2 ab$ | 59 | 21.6 ± 0.1 abc | $78.7 \pm 2.7a$ |
| ATF 480 | Neotyphodium coenophialum | $53.8\pm5.1\mathrm{bc}$ | 57 | $219.9\pm6.9abc$ | 48 | $21.1\pm0.2c$ | $70.5\pm7.3ab$ |
| Festuca rubra subsp. Trichophylla | | | | | | | |
| 'Dawson' E- | None | $62.7 \pm 8.4 \mathrm{b}$ | 47 | $187.5 \pm 9.0c$ | 25 | $23.1 \pm 0.4a$ | $34.8 \pm 11.9c$ |
| 'Dawson' E+ | Epichloe festucae | $44.9\pm7.5c$ | 38 | $248.0\pm0a$ | 1 | $21.0 \pm 0c$ | $1.0\pm0\mathrm{d}$ |
| Lolium perenne | 5 | | | | | | |
| LP 5425 | None | $66.9 \pm 5.7 \mathrm{b}$ | 57 | 203.2 ± 8.0 abc | 94 | $20.9 \pm 0.2 \mathrm{c}$ | $56.5 \pm 8.7 \mathrm{b}$ |
| APR 1234 | Neotyphodium lolii | $11.9\pm1.7d$ | 36 | $215.0\pm10.5abc$ | 22 | $22.8\pm0.2ab$ | $26.0\pm12.7c$ |
| 'Rosalin' E– | | $82.5 \pm 4.2a$ | 126 | $203.2 \pm 4.8 abc$ | 38 | $21.1 \pm 0.1c$ | $63.0 \pm 3.0 ab$ |
| 'Rosalin' E+ | Neotyphodium seigelii | $63.7\pm2.3b$ | 306 | $197.7\pm2.8\mathrm{bc}$ | 193 | $21.2\pm0.1\mathrm{bc}$ | $55.0\pm4.3b$ |

Table 1. Mean \pm SE growth of fall armyworm *Spodoptera frugiperda* on endophyte-infected or endophyte-free fescue (*Festuca* spp.) and perennial ryegrass (Lolium spp.) in the laboratory (24°C)

Means followed by the name letter within a column are not significantly different (Bonferroni's test $\alpha = 0.05$).

'Tulsa' or endophyte-infected slender creeping red fescue > endophyte-infected turf- type perennial ryegrass > endophyte-free slender creeping red fescue > endophyte-infected forage-type perennial ryegrass > endophyte-free forage-type perennial ryegrasses, and endophyte-infected tall fescue > endophyte-free turftype tall fescue.

Fall Armyworm, Warm-Season Grass Taxa Effects. Larval weights at day 10 were significantly different among grass genera (F = 195.0; df = 4, 3,087; P < 0.01). Compared with the susceptible cool season grass, 'Tulsa' tall fescue and the diet control, larval weight gain at day 10 was most often reduced by feeding on zoysiagrasses (Table 2). In fact, a 15-fold difference in larval weight between zoysiagrass and artificial diet was observed. Larval weight gain also was lower on many of the Bermuda grasses = *Cynodon* than when larvae were fed fescue or the diet control (Table 2). Pupal weights (F = 36.3; df = 4, 1.975; P < 0.01) were greatest on artificial diet (277.1 mg), followed by fescue (205.2 mg). Zoysia and paspalum when fed to fall armyworms resulted in the lowest pupal weights (Table 2). Duration of development, from egg hatch to pupation, was greatly extended when larvae were fed zoysiagrasses (F = 383.25; df = 4, 1,992; P < 0.01) (Table 2). Larvae feeding on artificial diet fescue or paspalum were similar in their development times, requiring 21.2-22.6 d to pupate.

Among individual turfgrass genotypes (Table 3), larval weights were greatly reduced by feeding on any of the zoysiagrasses (F = 19.6: df = 64, 3087; P < 0.01). Bermuda grasses with the lowest larval weights included the experimentals 97-8, 97-39, 97-40 and 97-51. Pupal weights (F = 3.7; df = 64,1915; P < 0.01) among genotypes ranged from 119.2 mg on 'Crowne' and experimental # 4375 zoysiagrasses to 203 mg on 'Tulsa' tall fescue (Table 3). Duration of larval development (F = 44.5; df = 64, 1,928; P < 0.01) was greatly extended by feeding on the zoysiagrasses 'Cavalier', 'Crowne', 'Diamond', 'Palisades', 4366, 4373, 4375, 4377, and 9601. Development on these grasses averaged as much as 44% longer than on more susceptible grasses. Bermuda grasses that extended developmental times for fall armyworms to reach the pupal stage in at least two trials included 97-8, 97-51, and 98-11. Duration of development on all seashore paspalum was similar to that on 'Tulsa' tall fescue.

Larval survival was greatly reduced by feeding on zoysiagrasses (Tables 2 and 3) where average survival among all zoysiagrass entries was 19.5%. Only APR1234 and 'Dawson' creeping red fescue in the previous study reduced larval survival to a similar extent. Larval survival on most seashore paspalums was statistically equivalent to that on an optimal artificial diet. Survival on Bermuda grasses was least on 97–8 with an average survival of 24% after three trials.

Table 2. Mean ± SE growth of Spodoptera frugiperda among turfgrass genera compared with artificial diet in the laboratory (24°C)

| Genus | 10-day larval weight, mg | Pupal weight, mg | Days to pupation | % survival to pupal stage | |
|-----------------|-----------------------------|-----------------------------|---------------------------|------------------------------|--|
| Zoysia | $6.5\pm0.3\mathrm{e}$ | $145.7\pm7.1\mathrm{d}$ | $34.8 \pm 0.7a$ | $19.5\pm2.9\mathrm{c}$ | |
| Cynodon | $35.9 \pm 0.8 \mathrm{d}$ | $182.7 \pm 2.6 \mathrm{bc}$ | $23.9 \pm 0.1 \mathrm{b}$ | $46.4 \pm 1.8 { m abc}$ | |
| Paspalum | $56.1 \pm 1.3c$ | $165.9 \pm 1.6 cd$ | $22.2 \pm 0.1 \mathrm{c}$ | $72.7 \pm 3.8 ab$ | |
| Festuca | $71.5\pm0.6\mathrm{b}$ | $205.2 \pm 5.4 \mathrm{b}$ | $22.6 \pm 0.4 bc$ | $60.0 \pm 7.6 \mathrm{ab}$ | |
| Artificial diet | $102.2\pm7.6a$ | $277.1\pm3.8a$ | $21.2\pm0.2\mathrm{c}$ | $85.0\pm5.2a$ | |

Means within a column followed by the same letter are not significantly different (Bonferroni's test $\alpha = 0.05$).

Table 3. Mean ± SE growth of fall armyworm Spodoptera frugiperda, on 65 turfgrass genotypes in the laboratory (24°C)

| Genotype | 10-day larval weight, mg | n | Pupal weight, mg | n | Days to pupation | % survival to the pupal stage |
|----------------|--|----|-------------------------------|----|--|-----------------------------------|
| Zoysia | | | | | | |
| Cavalier' | $4.7 \pm 0.5 t$ –w | 30 | $122.7 \pm 6.2c$ | 11 | $37.1 \pm 1.4 \text{bcd}$ | $10.0 \pm 5.8 \mathrm{fg}$ |
| Crowne' | 5.4 ± 0.5 t–w | 32 | $119.2 \pm 9.8c$ | 13 | $36.1 \pm 1.0 \text{bcd}$ | $17.3 \pm 7.4 c-g$ |
| Diamond' | $7.2 \pm 0.9 t$ –w | 35 | $138.2 \pm 5.1c$ | 14 | 34.8 ± 1.4 cde | $18.7 \pm 8.7 b-g$ |
| 'Palisades' | $4.2 \pm 0.7 u$ –w | 36 | $185.2 \pm 50.7 abc$ | 17 | 38.7 ± 1.1 ab | $17.0 \pm 7.7 \text{c-g}$ |
| 'Royal' | $3.8 \pm 0.7 u$ –w | 31 | $207.3 \pm 86.4 \mathrm{abc}$ | 8 | $21.5 \pm 3.9 \text{j-l}$ | $10.7 \pm 8.7 \mathrm{fg}$ |
| 4365' | 10.6 ± 2.1 s–w | 51 | $149.2 \pm 6.2c$ | 21 | $31.1 \pm 1.6e$ | $28.0 \pm 10.1 a$ -g |
| 4366' | $8.0 \pm 0.7 \mathrm{s-w}$ | 47 | $132.2 \pm 5.5c$ | 22 | $42.1 \pm 0.9a$ | $29.3 \pm 21.4a-g$ |
| 4373' | 8.2 ± 0.9 s–w | 34 | $149.3\pm10.4\mathrm{c}$ | 11 | $37.6 \pm 2.0 \mathrm{bc}$ | $16.0 \pm 14.0 d-g$ |
| 4375' | $3.6 \pm 0.5 v$ –w | 36 | $119.2 \pm 8.2c$ | 11 | 39.4 ± 1.9 aba | $14.7 \pm 7.4 {\rm fg}$ |
| 4377' | 7.7 ± 0.9 s–w | 46 | $144.5 \pm 5.8c$ | 25 | $33.8 \pm 0.8 de$ | $33.3 \pm 7.0a$ –g |
| 9601' | $3.3 \pm 0.9 \mathrm{w}$ | 15 | $152.4 \pm 10.3c$ | 8 | $33.5 \pm 0.8 de$ | $10.7 \pm 4.8 \text{fg}$ |
| Cynodon | | | | | | |
| Tifdwarf | $58.7 \pm 13.9 \text{b-I}$ | 63 | $171.2 \pm 5.7 bc$ | 52 | 23.0 ± 0.4 g-e | $69.3 \pm 4.8a$ -g |
| TifEagle' | $60.3 \pm 6.1 \mathrm{b-h}$ | 60 | $175.8 \pm 4.8 bc$ | 48 | 21.7 ± 0.2 i–l | $64.0 \pm 16.1 a-g$ |
| Tifgreen' | $33.7 \pm 3.3 f-u$ | 60 | $167.3 \pm 4.3 bc$ | 42 | 23.4 ± 0.3 f-l | $56.0 \pm 6.9a$ –g |
| 'TifSport' | $28.9 \pm 3.2i-w$ | 67 | $173.5 \pm 6.3 bc$ | 33 | $23.9 \pm 0.5 \text{f-l}$ | $32.0 \pm 3.2a-g$ |
| Tifway' | $47.5 \pm 6.1 \text{b-o}$ | 54 | $182.2 \pm 5.9 abc$ | 34 | $25.0 \pm 0.5 f_{-j}$ | $45.3\pm9.3\mathrm{a}\mathrm{-g}$ |
| 97-1 | $32.6 \pm 3.9 \text{f}-\text{w}$ | 50 | $169.2 \pm 7.5 bc$ | 37 | 23.3 ± 0.4 f-l | $49.3 \pm 22.2a-g$ |
| 97-3 | $40.1 \pm 4.3 err$ | 57 | $178.4 \pm 6.2 bc$ | 36 | 24.0 ± 0.4 f-l | 48.0 ± 6.1 a-g |
| 97-4 | $22.3 \pm 2.8 \text{m-w}$ | 58 | $169.0 \pm 5.0 \mathrm{bc}$ | 31 | $24.9 \pm 0.7 f_{-j}$ | 41.3 ± 7.1 a–g |
| 97-6 | $47.1 \pm 4.7b-o$ | 53 | $175.8 \pm 6.3 bc$ | 37 | 24.4 ± 0.6 f-k | $49.3 \pm 15.7 a-g$ |
| 97-7 | 28.1 ± 3.6 j–w | 57 | $190.8 \pm 5.7 \mathrm{abc}$ | 37 | $25.3 \pm 0.7 \text{f}$ -j | $49.3 \pm 9.6a$ -g |
| 97-8 | 14.7 ± 1.6 r–w | 50 | $163.8 \pm 8.3 bc$ | 18 | $26.8 \pm 0.7 f$ | $24.0 \pm 10.6a$ -g |
| 97-9 | $28.1 \pm 2.8 \text{j-w}$ | 52 | $245.7 \pm 70.9 ab$ | 40 | 23.7 ± 0.4 f-l | $50.7 \pm 8.1 a-g$ |
| 97-12 | $34.3 \pm 3.7 \text{f-t}$ | 54 | $171.9 \pm 4.5 bc$ | 42 | $23.5 \pm 0.6 \text{f-l}$ | $56.0 \pm 4.6a$ -g |
| 97-13 | $30.2 \pm 3.4 h-w$ | 56 | $175.9 \pm 6.9 \mathrm{bc}$ | 32 | $25.3 \pm 0.7 \mathrm{f}{-\mathrm{i}}$ | $42.7 \pm 13.1 a$ -g |
| 97-14 | 24.5 ± 3.4 k-w | 47 | $168.1 \pm 5.9 \mathrm{bc}$ | 32 | $24.8 \pm 0.5 f{-i}$ | $42.7 \pm 10.4a-g$ |
| 97-22 | $34.2 \pm 3.8 \text{f}-\text{t}$ | 49 | $177.0 \pm 4.7 bc$ | 29 | 23.7 ± 0.4 f-l | $38.7 \pm 9.6a - g$ |
| 97-23 | $33.9 \pm 3.2 f-u$ | 60 | 181.5 ± 5.1 abc | 44 | 24.0 ± 0.4 f-l | $58.7 \pm 7.0a-g$ |
| 97-28 | $32.0 \pm 3.5 \text{g-w}$ | 50 | $197.1 \pm 6.8 \mathrm{abc}$ | 35 | 23.3 ± 0.4 f-l | $46.7 \pm 5.8 a - g$ |
| 97-39 | $17.9 \pm 0.2 p-n$ | 60 | $197.3 \pm 6.8 \mathrm{abc}$ | 37 | $26.4 \pm 0.6 \text{f-g}$ | $50.7 \pm 12.7 a-g$ |
| 97-40 | $19.1 \pm 1.9 n-w$ | 53 | $178.4 \pm 5.4 bc$ | 30 | $24.1 \pm 0.5 f-l$ | $40.0 \pm 8.3 a - g$ |
| 97-45 | $32.5 \pm 3.1 \text{g-w}$ | 53 | $191.6 \pm 5.4 \mathrm{abc}$ | 39 | 23.7 ± 0.4 f-l | 52.0 ± 14.0 a-g |
| 97-51 | $16.8 \pm 1.8 r-w$ | 48 | $160.5 \pm 5.1 \mathrm{bc}$ | 22 | $25.9 \pm 0.9 \mathrm{f-h}$ | $30.0 \pm 7.5 a - g$ |
| 97-54 | 27.6 ± 3.9 j-w | 40 | $187.2 \pm 5.7 \mathrm{abc}$ | 29 | 23.7 ± 0.4 f-l | $38.7 \pm 13.5a-g$ |
| 98-7 | $32.8 \pm 2.9 f_{-V}$ | 63 | $183.1 \pm 6.3 abc$ | 40 | $24.1 \pm 0.5 \text{f-l}$ | $53.3 \pm 5.8a-g$ |
| 98-10 | 23.4 ± 3.1 l-w | 59 | $170.6 \pm 7.3 bc$ | 34 | $24.6 \pm 0.5 \text{f-k}$ | $45.3 \pm 7.1 a-g$ |
| 98-11 | $43.3 \pm 5.2c-q$ | 47 | $186.0 \pm 6.6 \mathrm{abc}$ | 25 | 24.6 ± 0.7 f-k | $33.3 \pm 12.7a-g$ |
| 98-15 | 27.7 ± 3.2 j-w | 62 | $186.5 \pm 5.3 \mathrm{abc}$ | 41 | $24.7 \pm 0.5 f{-i}$ | $54.7 \pm 3.5a-g$ |
| 98-16 | $39.4 \pm 4.2 err$ | 45 | $174.6 \pm 5.5 bc$ | 34 | $24.5 \pm 0.7 \text{f-l}$ | $45.3 \pm 16.7 a-g$ |
| 98-17 | $48.7 \pm 5.5 \text{b-n}$ | 49 | $170.3 \pm 5.0 \mathrm{bc}$ | 33 | $23.1 \pm 0.5 \text{f-l}$ | $44.0 \pm 16.7 a-g$ |
| 98-30 | $43.4 \pm 5.7 c-q$ | 44 | $174.6 \pm 5.8 bc$ | 31 | 24.1 ± 0.8 f-l | $41.3 \pm 19.2a-g$ |
| 98-34 | $42.7 \pm 4.8c-q$ | 53 | $179.1 \pm 4.4 bc$ | 34 | 23.7 ± 0.4 f-l | $45.3 \pm 11.8a-g$ |
| 98-35 | $41.6 \pm 4.40 - q$ | 54 | $179.3 \pm 5.8 \mathrm{bc}$ | 28 | 23.1 ± 0.5 g-l | $37.3 \pm 9.3a-g$ |
| 98-46 | $49.8 \pm 4.7 \text{b-m}$ | 58 | $190.3 \pm 5.7 \mathrm{abc}$ | 40 | 22.9 ± 0.5 g-l | $53.3 \pm 13.9a-g$ |
| 98-49 | $43.2 \pm 5.3c-q$ | 55 | $188.5 \pm 5.7 \mathrm{abc}$ | 41 | 23.4 ± 0.3 f-l | $54.7 \pm 10.4a$ -g |
| Paspalum | | | | | | |
| Sullivan 2' | $57.4 \pm 5.8 \text{b-j}$ | 43 | $173.0 \pm 7.1 bc$ | 31 | 22.1 ± 0.4 h-l | $88.0 \pm 12.0 \mathrm{a}$ |
| 'Prince' | $53.9 \pm 4.3 \text{b-k}$ | 45 | $177.6 \pm 5.5 bc$ | 26 | $21.7 \pm 0.3i-l$ | $76.0 \pm 4.0a-f$ |
| 'Wailua' | 50.1 ± 3.4 b-m | 44 | $159.7 \pm 7.9 \mathrm{bc}$ | 29 | $22.8\pm0.5\mathrm{g-l}$ | $43.0 \pm 33.0a$ -g |
| 'Kaihuna' | $50.4 \pm 4.4 \text{b-m}$ | 39 | $176.3 \pm 4.5 bc$ | 25 | $22.0 \pm 0.3i-l$ | $74.0 \pm 6.0a-f$ |
| Woerner' | $75.4 \pm 7.5 \mathrm{b}$ | 39 | $153.4 \pm 5.6c$ | 24 | 20.9 ± 0.3 k–l | $66.0\pm6.0\mathrm{a}\text{-g}$ |
| 'Cloister' | $37.8 \pm 3.8 \text{f}-\text{s}$ | 44 | $163.3 \pm 10.8 \mathrm{bc}$ | 22 | $22.4\pm0.4\mathrm{h{-}l}$ | $62.0\pm2.0\mathrm{a}\text{-g}$ |
| Q36315 | $61.8 \pm 5.1 \text{b-g}$ | 42 | $149.7 \pm 5.7 c$ | 29 | 22.7 ± 0.4 g–l | 85.0 ± 5.0 a-c |
| Salam' | $54.8 \pm 5.2 \text{b-j}$ | 44 | $162.3 \pm 5.4 bc$ | 27 | $21.8 \pm 0.3i-l$ | $76.0 \pm 4.0a-f$ |
| Adalayd' | $45.5 \pm 3.9 \text{b-p}$ | 43 | $173.1 \pm 7.7 bc$ | 28 | $23.3 \pm 0.5 \text{f-l}$ | $76.0\pm4.0\mathrm{a}\text{-f}$ |
| Sea Isle 2000' | $62.8 \pm 3.8 \text{b-f}$ | 40 | $158.7 \pm 6.9 \mathrm{bc}$ | 26 | $23.3 \pm 0.5 \text{f-l}$ | 84.0 ± 16.0 a–d |
| Sea Isle 1' | $68.4\pm6.5\mathrm{b}{-\mathrm{e}}$ | 44 | $155.1\pm5.0\mathrm{bc}$ | 27 | 20.5 ± 0.4 l | $78.0\pm2.0\mathrm{a}\text{-f}$ |
| 561-79 | 49.9 ± 5.1 b-m | 38 | $174.5 \pm 5.6 \mathrm{bc}$ | 26 | 21.6 ± 0.3 i–l | $73.0 \pm 3.0a$ –f |
| HI 101 | $45.4 \pm 3.8b-p$ | 44 | $156.7 \pm 5.9 \mathrm{bc}$ | 30 | 23.3 ± 0.4 f-l | $84.0\pm4.0\mathrm{a-d}$ |
| K8 | $72.3 \pm 6.9 \mathrm{b-c}$ | 41 | $177.4 \pm 6.7 \mathrm{bc}$ | 30 | $22.5\pm0.3h\text{-l}$ | $90.0\pm10.0a$ |
| HI 32 | $53.4 \pm 4.5 \text{b-l}$ | 39 | $187.1 \pm 8.8 \mathrm{abc}$ | 27 | 21.8 ± 0.4 i–l | $81.0\pm9.0ad$ |
| HI 26 | $45.9 \pm 5.0 \text{b-p}$ | 38 | $182.7 \pm 5.4 \mathrm{abc}$ | 28 | 21.7 ± 0.4 i–l | $80.0\pm9.0\mathrm{a-e}$ |
| Hyb 7 | $54.8 \pm 4.9 \text{b}-\hat{\text{k}}$ | 36 | $156.1 \pm 7.0 \mathrm{bc}$ | 27 | $22.4\pm0.4\mathrm{h{-}l}$ | $81.0\pm9.0ad$ |
| Temple 1 | $71.4 \pm 7.0 \text{b-d}$ | 43 | $149.9\pm4.0\mathrm{c}$ | 30 | 21.8 ± 0.4 i–l | $87.0\pm3.0ab$ |
| Festuca | | | | | | |
| Tulsa' | $60.4\pm5.3\mathrm{bhh}$ | 74 | $203.0\pm4.8 abc$ | 46 | 22.9 ± 0.4 g–l | $60.0\pm7.6\mathrm{a}\text{-g}$ |
| | | 99 | $271.9 \pm 3.2a$ | 84 | 21.5 ± 0.2 j-l | $85.0 \pm 5.2 \mathrm{abc}$ |

Means within a column followed by the same letter are not significantly different (Bonferroni's test $\alpha = 0.05$).

Discussion

Insect pests have demonstrated the ability to overcome single genetic sources of plant resistance. Endophytes provide a source of heterogeneity to enhance already resistant lines and delay the breakdown of observed resistance. Our observations of fall armyworm response to 'Dawson' E- and 'Dawson' E+, for example, suggested the enhanced potential resistance by incorporation of a desirable endophyte into an existing cultivar. Endophyte infection status in our study gave mixed results depending on host and endophyte type, endophyte concentration and growth parameter measured. Bultman and Conard (1998) also report mixed results on fall armyworm growth when fed endophyte-infected or endophyte-free tall fescue; infection in their study negatively affected pupal mass, accelerated development time, positively affected larval mass and did not affect survival. They also found that the adverse effect of endophyte was most pronounced when plants received low fertilizer applications. Pupal weight differences under high fertilizer were negligible. In contrast, Breen (1993) found no differences in consumption, weight, survival or development times were detected in fall armyworms fed tall fescue infected with endophyte compared with endophyte-free tall fescue. Fall armyworms fed endophyte-infected Chewing's fescue (F. rubra L. subs. commutata Gaud) demonstrated dramatic differences in all parameters measured compared with endophyte-free controls.

Bultman and Ganey (1995) determined that endophyte infection reduced larval and pupal weights and extended development of fall armyworm on perennial ryegrass infected with *N. lolii* especially when it had been previously damaged, inducing additional resistance. Mycelial concentration varies within the plant. Older leaves tend to have a higher concentration than younger leaves. Adverse effects on fall armyworm growth in our study became more apparent with each trial as plants aged. Fall armyworm neonates significantly preferred and fed more on older, uninfected tall fescue leaves, compared with similar-aged, infected counterparts (Hardy et al. 1986). Similarly, survival and larval weights were more adversely affected with increasing leaf age.

Data presented here comparing resistance of warm season grasses to fall armyworm were consistent with previous studies (Braman et al. 2000b) and identified additional plant genotypes that demonstrate potential resistance to this pest. Potential cross-resistance to multiple pests also has been shown among combined studies. 'Cavalier' zoysiagrass, for example, is apparently resistant to fall armyworm (Braman et al. 2000b), moderately resistant to mole crickets (Braman et al. 1994), susceptible to zoysiagrass mite, Eriophyes zoysiae Baker, Kono and O'Neill (Reinert et al. 1993), and moderately resistant to twolined spittlebugs (Shortman et al. 2002). 'Crowne' is moderately resistant to zovsiagrass mite and fall armyworm, but is relatively susceptible to tawny mole cricket and twolined spittlebug. 'Diamond' which demonstrated moderate

resistance to fall armyworm and tawny mole cricket is also moderately resistant to twolined spittlebug. Paspalum selections that demonstrated some antibiotic effects on fall armyworms compared with all paspalum selections in previous studies included 561-79, PI-509021 and PI 509022 although all were susceptible to this pest (Braman et al. 2000b). 'Glenn Oaks Adalayd' paspalum was least tolerant of tawny mole cricket. Scapteriscus vicinus (Scudder), injury, while 561-79 and HI-1 were more tolerant although none of these were highly resistant to mole crickets (Braman et al. 2000a). Insects cause major economic damage to turf Bermuda grasses each year. Significant progress has been made in incorporating tawny mole cricket resistance in 'TifSport' (Braman et al. 2000a, Hanna et al. 1997). Among Bermuda grasses, this study shows that armyworm survival was lowest on 'TifSport' compared with other commercial cultivars in the experiment. Even more important is that new experimental cultivars show significantly improved resistance to tawny mole crickets (Braman et al. 2000a, and unpublished). The lowest survival of armyworms on Bermuda grasses in this study was on experimental Bermuda grass entry 97-8. Genetic resistance to major insect pests in turfgrass can reduce pesticide use and simplify management of these cultivars.

Lengthened developmental times on many grass entries evaluated suggest the possibility of synergism of host plant resistance with conservation of parasitoids and predators. Compatibility with biological control needs to be further examined within this system. Breen (1994) reported no differences in survival of the parasitoid Lysiphlebus testaceipes (Cresson) parasitizing bird-cherry oat aphid, Rhopalosiphum padi (L.), on endophyte-infected perennial ryegrass. Bultman and Ganey (1995), however, reported preliminary findings that a fall armyworm parasitoid experienced reduced mass when parasitizing fall armyworms fed endophyte-infected grass. Intermediate levels of resistance demonstrated by several entries in our trials offer the potential for synergy with parasitoids and predators by extending the exposure time of vulnerable stages of the pest to natural enemies as a result of longer larval development times. Effects of endophyte infection in cool season grasses and antibiosis among warm season grasses on the third trophic level should be further elucidated.

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