Antibiosis Among Selected *Paspalum* Taxa to the Fall Armyworm (Lepidoptera: Noctuidae)[1]

S. K. Braman[2], P. L. Raymer[3], M. Harrison-Dunn[4] and Shakunthala Nair

Department of Entomology, University of Georgia, Griffin, Georgia 30223-1797 USA

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Abstract Twenty-one taxa of the warm-season perennial grass, *Paspalum* spp., were evaluated for response to the fall armyworm, *Spodoptera frugiperda* (J. E. Smith), an important pest of turfgrass. In studies using excised grass clippings conducted in a growth chamber and on whole plants in a greenhouse, the most resistant taxon was *P. ionanthum* Chase (PI 404,449) as measured by larval and pupal weights, days to develop to pupal stage, and survival. *Paspalum notatum* Flüeggé var. *saurae* Parodi (PI 422,024), *P. notatum* Flüeggé (PI 310,146), *P. thunbergii* Kunth ex Steud. (PI 286,486) and *P. macrophyllum* Kunth. (PI 282,807) showed moderate resistance, whereas the turf-type *P. vaginatum* Swartz taxa were highly susceptible. Identifying resistant *Paspalum* taxa can inform plant breeding programs in development of pest-resistant grasses, a foundational integrated pest management strategy.

Key Words *Spodoptera frugiperda*, host plant resistance, seashore paspalum, *Paspalum vaginatum*, antibiosis

Fall armyworms, *Spodoptera frugiperda* (J. E. Smith), can be severely damaging to turfgrass, especially in the southeastern United States. Problems often occur in late summer or fall after migrating populations have increased during the season (Reinert and Cobb 2012). Seashore paspalum, *Paspalum vaginatum* Swartz, is a warm-season perennial grass valued for its salt tolerance (Duncan and Carrow 2000). Additionally, it is tolerant to drought, poor soils and low mowing levels, resulting in its popularity for use in golf courses and other turfgrass settings (Duncan and Carrow 2000). Previous experiments have identified a gradient in resistance among warm-season turf grasses to the fall armyworm (Braman et al. 2000, 2002). *Paspalum vaginatum* taxa, in general, were more susceptible to fall armyworm than other warm-season grasses such as centipedegrass [*Eremochloa ophiuroides* (Munro) Hack.], zoysiagrass (*Zoysia* Willd.), and some bermudagrasses (*Cynodon* Rich.). Identification and utilization of turfgrasses with resistance to the major turfgrass pests is an important component of integrated pest management strategies in turf production.

Various evaluations of pasture and turf grasses have revealed antibiosis as a mechanism of resistance against the fall armyworm (Wiseman et al. 1982, Chang et al. 1986). This was indicated by smaller size and delayed development of larvae feeding on the resistant grasses. A study using diet-incorporated plant tissue, identified

[1]Received 20 February 2013; accepted for publication 24 March 2013.

[2]Address inquiries (email: kbraman@uga.edu).

[3]Crop and Soil Sciences, University of Georgia, Griffin, GA 30223.

[4]USDA/ARS Plant Genetic Resources Conservation Unit, Griffin, GA 30223

antibiosis among some *Paspalum* species (Wiseman and Duncan 1996) when 81 *Paspalum* taxa were evaluated for potential resistance to fall armyworm. The objective of the experiments described herein was to compare the response of fall armyworm on fresh plant tissue among turf-type *Paspalum* taxa with that on other *Paspalum* species. The zoysiagrass taxon 'Cavalier' (Braman et al. 2000, Reinert and Engelke 2010) was used as a resistant control.

Materials and Methods

Paspalum vaginatum taxa were obtained from the UGA Paspalum Breeding Program whereas *Paspalum* spp. taxa were grown from seed obtained from the USDA National Plant Germplasm System (Table 1). Seeds were germinated under mist conditions and then transplanted to 15cm standard plastic pots containing Metro Mix 300 (Sun Gro Horticulture Canada Ltd.). Plants were fertilized at transplanting with a controlled-release fertilizer (Osmocote 18 - 6-12; The Scotts Company, Marysville, OH) and regularly thereafter with a water-soluble general purpose fertilizer (Peter's 20 - 20 - 20; The Scotts Company, Marysville, OH).

For growth chamber studies, clippings from the *Paspalum* spp. and *Zoysia* sp. grasses grown and maintained in greenhouses at the UGA Griffin campus were provided daily to the fall armyworm larvae. Fall armyworm eggs from a commercial supplier (Benzon Research, Carlisle, PA) were held at 27°C until eclosion. Neonate larvae were confined individually in individual 32-ml clear plastic diet cups with snap-on paper lids (Bio-Serv, Frenchtown, NJ) containing fresh clippings of the grasses of interest. These cups were arranged in trays. Three different growth chamber trials (no-choice) were conducted, using randomized complete block design. In the first trial, 22 turfgrass taxa (Trial 1, Table 1) were included with 60 larvae per taxon (12 replications of 5 larvae each). In the second and third trials (Trials 2 and 3, Table 2), 10 turfgrass taxa were selected to represent a range in response to the fall armyworm. Thirty larvae were tested per taxon in 6 replications of 5 larvae each. Each cup within a tray was labeled with a number that corresponded to one of the turfgrass taxa selected as a treatment. The trays were randomly stacked within an environmental chamber maintained at constant temperature (24°C) and photoperiod (15:9 Light hours: Dark hours) for the duration of the study.

Daily feeding of grass clippings continued until all larvae had either successfully pupated or died. Larval survival per treatment was recorded at 8 d and at pupation. In addition to larval survival, larval weight at 15 d, pupal weight, days to develop to pupal stage and adult emergence were recorded. Larval and pupal weights, days to develop to pupal stage and survival were used to determine potential antibiosis among *Paspalum* taxa in comparison with resistant 'Cavalier' zoysiagrass.

Two greenhouse studies on whole plants (Trial 4 and 5), were performed using 10 turfgrass taxa selected to represent a range in response to the fall armyworm (Table 3). Both studies used randomized complete block design. Plants in 15cm diam plastic pots were maintained at 31°C and photoperiod (12:12 L:D) for the duration of the study. The plants were watered daily during the study. Ten larvae were placed on a plant, and 2 such plants were enclosed in a cage (BugDorm, Bioquip, Inc.) in Trial 4, whereas 3 plants were placed in a cage in Trial 5, and this was replicated twice. Thus, there were a total of 40 larvae (8 replications of 5 larvae each) per treatment in Trial 4, and 60 larvae (12 replications of 5 larvae each) in Trial 5. Larval survival per treatment,

Table 1. Developmental parameters of fall armyworm when fed grass clippings of 22 turfgrass taxa in a growth chamber study (Trial 1).

Turfgrass taxa	Mean larval weight (mg)	Mean pupal weight (mg)	Mean days to pupation	% survival to 8 d	% survival to pupation	% adult emergence
Z. matrella 'Cavalier'[z]	–	–	–	–	–	–
P. macrophyllum (PI 282,807)	–	–	–	–	–	–
P. notatum (PI 310,146)	–	–	–	–	–	–
P. notatum var. *saurae* (PI 422,024)	–	–	–	–	–	–
P. plicatulum (PI 462,290)	–	–	–	–	–	–
P. quadrifarium (PI 462,298)	–	–	–	–	–	–
P. thunbergii (PI 286,486)	5.6 e	–	–	16.7 c-e	–	–
P. dilatatum (PI 419,929)	8.4 e	99.5 e	33.8 ab	31.7 bc	30.0 b-d	28.3 cd
P. minus (PI 404,465)	8.5 e	–	–	3.3 e	–	–
P. ionanthum (PI 404,449)	10.8 e	–	–	16.7 c-e	–	–
P. vaginatum 'Aloha'	13.4 e	144.2 cd	34.6 a	43.3 b	43.3 b	43.3 bc
P. nicorae (PI 209,983)	14.6 e	88.1 ef	35.9 a	31.7 bc	21.7 c-e	20.0 d-f
P. conjugatum (PI 404,643)	25.3 de	82.9 ef	35.7 a	26.7 b-d	20.0 c-f	15.0 d-g
P. vaginatum 'Sea Spray'	25.5 de	142.0 cd	36.0 a	6.7 de	5.0 ef	5.0 fg
P. vaginatum 'Sea Isle 2000'	30.8 de	134.4 cd	30.0 c	35.0 bc	35.0 bc	33.3 cd
P. dilatatum subsp. *flavescens* (PI 477,100)	33.3 c-e	94.2 ef	31.0 bc	36.7 bc	31.7 b-d	25.0 c-e
P. vaginatum 'Salam'	36.7 c-e	129.6 d	28.6 cd	18.3 c-e	16.7 c-f	16.7 d-g

Table 1. Continued.

Turfgrass taxa	Mean larval weight (mg)	Mean pupal weight (mg)	Mean days to pupation	% survival to 8 d	% survival to pupation	% adult emergence
P. pubiflorum (PI 304,147)	37.1 c-e	74.7 f	34.9 a	21.7 b-e	11.7 d-f	6.7 e-g
P. vaginatum 'Durban'	53.2 b-d	153.7 a-c	26.9 de	73.3 a	71.7 a	66.7 a
P. vaginatum 'Sea Isle 1'	63.1 bc	149.5 b-d	26.5 d-f	70.0 a	70.0 a	66.7 a
P. vaginatum 'Sea Dwarf'	81.9 ab	171.8 a	25.6 ef	66.7 a	65.0 a	58.3 ab
P. vaginatum 'Sea Isle Supreme'	111.2 a	167.1 ab	23.6 f	76.7 a	71.7 a	68.3 a
F	12.33	19.26	17.28	12.84	12.62	11.99
df	24, 320	21, 275	21, 274	32, 231	32, 231	32, 231
P	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001

–No individuals survived for measurement; ^{Z} Selection used as a control.
Means within a column with the same letter are not significantly different ($P < 0.05$).

Table 2. Developmental parameters of fall armyworm when fed grass clippings of 10 turfgrass selections in growth chamber studies (Trials 2 and 3).

Turfgrass taxa	Mean larval weight (mg)	Meanpupal wt (mg)	Mean days to pupation	% survival to 8 days	% survival to pupation	% adult emergence
Z. matrella 'Cavalier'[z]	–	–	–	–	–	–
P. ionanthum (PI 404,449)	2.0 e	–	–	3.3 ef	–	–
P. notatum var. *saurae* (PI 422,024)	11.4 de	128.6 ab	28.0 a	15.0 d-f	15.0 cd	15.0 cd
P. quadrifarium (PI 462,298)	12.4 c-e	123.9 b	23.9 a	21.7 c-e	18.3 cd	18.3 cd
P. notatum (PI 310,146)	16.0 c-e	120.8 bc	23.2 a	36.7 bc	28.3 bc	26.7 bc
P. minus (PI 404,465)	24.6 b-e	126.6 ab	24.6 a	56.7 ab	50.0 a	50.0 a
P. macrophyllum (PI 282,807)	36.4 a-d	124.8 ab	26.8 a	21.7 c-e	15.0 cd	15.0 cd
P. thunbergii (PI 286,486)	39.2 a-c	109.5 c	26.1 a	26.7 cd	21.7 c	18.3 cd
P. vaginatum 'Seastar'	46.9 ab	137.4 a	23.0 a	50.0 ab	48.3 ab	43.3 ab
P. vaginatum 03 - 525 - 22	61.1 a	129.5 ab	21.3 a	66.7 a	65.0 a	48.3 a
F	7.94	3.70	0.6581	8.64	8.61	6.23
df	13, 157	12, 144	12, 143	14, 105	14, 105	14, 105
P	<0.0001	0.0011	0.6581	<0.0001	<0.0001	<0.0001

–No individuals survived for measurement; [z] Selection used as a control.
Means within a column with the same letter are not significantly different ($P < 0.05$).

Table 3. Developmental parameters of fall armyworm feeding directly on 10 turfgrass selections in greenhouse studies (Trials 4 and 5).

Turfgrass taxa	Mean larval weight (mg)	Mean pupal wt (mg)	Mean days to pupation	% survival to 8 days	% survival to pupation	% adult emergence
Z. matrella 'Cavalier'[z]	4.3 c	–	–	2.0 e	–	–
P. notatum var. *saurae* (PI 422,024)	8.7 bc	139.9 ab	18.4 b	19.0 cd	16.0 bc	11.0 bc
P. notatum (PI 310,146)	10.7 bc	138.4 ab	17.5 bc	30.0 bc	18.0 a-c	15.0 ab
P. minus (PI 404,465)	14.1 bc	134.7 ab	18.9 b	25.0 c	18.0 a-c	11.0 bc
P. thunbergii (PI 286,486)	14.8 bc	108.4 b	18.9 b	17.0 c-e	8.0 cd	4.0 bc
P. macrophyllum (PI 282,807)	17.9 bc	124.1 ab	21.6 a	18.0 cd	7.0 cd	5.0 bc
P. ionanthum (PI 404,449)	19.1 b	–	–	8.0 de	–	–
P. vaginatum 'Seastar'	42.8 a	182.5 a	15.9 cd	47.0 a	30.0 ab	26.0 a
P. quadrifarium (PI 462,298)	53.4 a	126.9 ab	16.0 cd	15.0 c-e	13.0 cd	10.0 bc
P. vaginatum UGA-22	55.2 a	142.1 ab	15.2 d	41.0 ab	31.0 a	24.0 a
F	20.99	0.21	13.18	6.09	4.61	4.05
df	13, 270	9, 136	9, 128	14, 185	14, 185	14, 185
P	<0.0001	0.9818	<0.0001	<0.0001	<0.0001	<0.0001

–No individuals survived for measurement; [z] Selection used as a control.
Means within a column with the same letter are not significantly different ($P < 0.05$)

larval weight at 15 d, pupal weight, days to develop to pupal stage and adult emergence were recorded as in the growth chamber studies.

Statistical analyses. Data were subjected to analysis of variance (ANOVA) using the General Linear Model (GLM) procedure in SAS (SAS Institute 2003). Mean separation was by least significant difference (LSD).

Results and Discussion

Growth chamber trials. Six of the 22 turfgrass taxa used in Trial 1 did not support development to at least 8 d and these included 'Cavalier' zoysiagrass and 5 of the 13 *Paspalum* spp. taxa: *P. macrophyllum* Kunth. (PI 282,807), *P. notatum* Flüeggé (PI 310,146), *Paspalum notatum* Flüeggé var. *saurae* Parodi (PI 422,024), *P. plicatulum* Michx. (PI 462,290) and *P. quadrifarium* Lam. (PI 462,298) (Table 1). Sixteen of the 22 taxa supported growth and development of the fall armyworm, to at least 8 d.

Larval and pupal weights and days to develop to the pupal stage were significantly influenced by turfgrass selection. Survival of the initial 60 neonate larvae to 8 d ranged from 3.3% on *P. minus* (PI 404,465) to 76.7% on *P. vaginatum* 'Sea Isle Supreme'. Larvae on the *Paspalum* selection *P. thunbergii* Kunth ex Steud. (PI 286,486) had the lowest numerical larval weights, but these were statistically similar to those on *P. dilatatum* Poir. (PI 419,929), *P. minus* Fourn. (PI 404,465), *P. ionanthum* Chase (PI 404,449), *P. vaginatum* 'Aloha', *P. nicorae* Parodi (PI 209,983), *P. conjugatum* P.J. Bergius (PI 404,643), *P. vaginatum* 'Sea Spray', *P. vaginatum* 'Sea Isle 2000' and *P. dilatatum* Poir. subsp. *flavescens* Roseng. et al. (PI 477,100).

Larvae did not survive to the pupal stage on the *Paspalum* spp. taxa *P. ionanthum* (PI 404,449), *P. minus* (PI 404,465) and *P. thunbergii* (PI 286,486). Among the taxa supporting larval development beyond 8d, survival to pupation ranged from 5% on *P. vaginatum* 'Sea Spray' to 71.7% on *P. vaginatum* 'Sea Isle Supreme' and *P. vaginatum* 'Durban'. The lowest numerical pupal weight was observed on *P. pubiflorum* Rupr. ex Fourn. (PI 304,147), which was statistically similar to those on *P. conjugatum* (PI 404,643), *P. nicorae* (PI 209,983) and *P. dilatatum* subsp. *flavescens* (PI 477,100). Larvae on *P. vaginatum* 'Sea Spray' took the greatest number of days to reach pupal stage, but this duration was statistically similar for larvae on *P. nicorae* (PI 209,983), *P. conjugatum* (PI 404,643), *P. pubiflorum* (PI 304,147), *P. vaginatum* 'Aloha' and *P. dilatatum* (PI 419,929). The lowest percentage of adult emergence was observed on *P. vaginatum* 'Sea Spray', which was statistically similar to those on *P. pubiflorum* (PI 304,147) and PI 404,643 (*P. conjugatum*), *P. vaginatum* 'Salam', *P. nicorae* (PI 209,983) and *P. dilatatum* subsp. *flavescens* (PI 477,100).

The taxa *P. vaginatum* 'Sea Isle Supreme', *P. vaginatum* 'Sea Dwarf', *P. vaginatum* 'Sea Isle 1' and *P. vaginatum* 'Durban' were highly susceptible to the fall armyworm, as indicated by high larval and pupal weights, shorter time to pupation and high percentage of adult emergence (Table 1).

In growth chamber trials with the 10 selected taxa (Table 2 shows averages over Trials 2 and 3), lowest numerical larval weights at 8 d were observed on *P. ionanthum* (PI 404,449), and these were statistically similar to those on *P. notatum* var. *saurae* (PI 422,024), *P. quadrifarium* (PI 462,298), *P. notatum* (PI 310,146) and *P. minus* (PI 404,465). Percentage of larval survival ranged from 3.33% on *P. ionanthum* (PI 404,449) to 66.67% on *P. vaginatum* UGA-22. Although larval weights were low on *P. minus* (PI 404,465), the survival of these larvae was high, and similar to that on the highly susceptible *P. vaginatum* UGA-22. Larvae did not survive to pupation on

P. ionanthum (PI 404,449). Pupal weights were significantly low on *P. notatum* (PI 310,146) and *P. thunbergii* (PI 286,486) than the other taxa, which were statistically similar with respect to pupal weights. Highest percentage of adult emergence was on *P. minus* (PI 404,465) and this was similar to that on the highly susceptible *P. vaginatum* UGA-22 and *P. vaginatum* 'Seastar', indicating the suitability of these taxa to the fall armyworm. Larvae did not survive and develop on 'Cavalier' zoysiagrass in these trials.

Greenhouse trials. In the greenhouse trials on whole plants (Table 3 shows averages over Trials 4 and 5), developmental parameters were not always consistent with those obtained on grass-clipping studies in the growth chamber. Although 2% of the larvae survived to 8 d in the second greenhouse trial on 'Cavalier' zoysiagrass, none of the larvae survived to pupation. The larval weights on this taxon were similar to those on all the others except the *P. vaginatum* taxa UGA-22 and 'Seastar', and *P. quadrifarium* (PI 462,298). Larvae on *P. ionanthum* (PI 404,449) did not survive to pupation. Lowest pupal weights were observed on *P. thunbergii* (PI 286,486), which was significantly lower than those on *P. vaginatum* 'Seastar', but similar to those on all the other taxa. Larvae on *P. macrophyllum* (PI 282,807) took the longest time to reach pupation, whereas those on the *P. vaginatum* taxa UGA-22 and 'Seastar' and *P. quadrifarium* (PI 462,298) took the shortest. *Paspalum vaginatum* 'Seastar' and *P. vaginatum* UGA-22 appeared to be suitable (susceptible) hosts, as indicated by high larval and pupal weights, fewer days and higher survival to pupation, and to adult emergence, although differences with other taxa were not always significant. The least suitable (resistant) hosts among *Paspalum* spp. taxa was PI 404,449 (*P. ionanthum*), because larvae did not survive to pupation on this taxon in both trials.

Our studies compare the performance of fall armyworm on turf -type *Paspalum* taxa with that on other *Paspalum* species measured through studies on excised grass clippings in a growth chamber and on whole plants in a greenhouse (Table 4). Whereas many of the tested taxa supported growth and development of fall armyworm larvae in at least one experiment, PI 404,449 (*P. ionanthum*) showed consistent low susceptibility in growth chamber, excised-clipping and greenhouse, whole-plant studies. The taxa PI 310,146 (*P. notatum*), PI 422,024 (*P. notatum* var. *saurae*), PI-282807 (*P. macrophyllum*) and PI 286,486 (*P. thunbergii*) showed low susceptibility in growth chamber, excised-clipping studies, but low susceptibility was not as marked in greenhouse trials. Feeding on these taxa resulted in low larval and pupal weights, and longer time to reach the pupal stage, indicating antibiosis to some degree. *Paspalum vaginatum* 'Seastar' and *P. vaginatum* UGA-22 appeared to be the most suitable (susceptible) hosts, as shown by larval and pupal weights and days to develop to pupal stage. The zoysiagrass selection 'Cavalier' was resistant to fall armyworm, consistent with earlier reports (Braman et al. 2000, Reinert and Engelke 2010). Low input requirement of *P. vaginatum* has resulted in increased interest in the development of various taxa and selections that require assessment of their pest resistance. Our results are consistent with those from earlier studies (Braman et al. 2000) and also demonstrate resistance in additional species.

Significant morphological variability exists within *P. vaginatum* (Duncan and Carrow 2000) and, likewise, the degree of fall armyworm resistance may also vary among individuals within species. Therefore, information on pest susceptibility of various taxa within the species would help breeding efforts to develop of pest-resistant taxa and simplify management. Managed turf demands high levels of aesthetic perfection, and breeding objectives are often driven by this demand, whereas pest management is usually achieved by the use of effective chemical pesticides. However, concern for

Table 4. Response of fall armyworm on *Paspalum* taxa.

Response	Growth chamber study (22 taxa)	Growth chamber studies (10 taxa)	Greenhouse studies (10 taxa)
Larvae did not survive to 8d	*P. macrophyllum* *P. notatum* *P. notatum* var. *saurae* *P. plicatulum* *P. quadrifarium*	–	–
Larvae survived to 8d, but not to pupation	*P. ionanthum* *P. thunbergii* *P. minus*	*P. ionanthum*	*P. ionanthum*
Larvae survived to pupation and adults emerged, but low weights and survival rates	*P. nicorae* *P. dilatatum* *P. conjugatum* *P. pubiflorum* *P. dilatatum* subsp. *flavescens* *P. vaginatum* 'Aloha', *P. vaginatum* 'Sea Spray' *P. vaginatum* 'Sea Isle 2000' *P. vaginatum* 'Salam'	*P. notatum* var. *saurae* *P. quadrifarium* *P. notatum P. minus* *P. thunbergii* *P. macrophyllum*	*P. notatum* var. *saurae* *P. quadrifarium* *P. notatum P. minus* *P. thunbergii* *P. macrophyllum*
Larvae survived to pupation and adults emerged, high weights and survival rates	*P. vaginatum* 'Sea Isle 1' *P. vaginatum* 'Sea Dwarf' *P. vaginatum* 'Sea Isle Supreme' *P. vaginatum* 'Durban'	*P. vaginatum* UGA-22 *P. vaginatum* 'Seastar'	*P. vaginatum* UGA-22 *P. vaginatum* 'Seastar'

environmental stewardship and development of insecticide resistance provide impetus for incorporating pest resistance into breeding objectives, along with other desirable horticultural and agronomic traits.

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