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Authors: Kostromytska, Olga S., and Buss, Eileen A.

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TOMARUS SUBTROPICUS (COLEOPTERA: SCARABAEIDAE) LARVAL FEEDING HABITS

OLGA S. KOSTROMYTSKA[1] AND EILEEN A. BUSS[2]
[1]Entomology Department, Rutgers, The State University of New Jersey, 93 Lipman Drive, New Brunswick, NJ 08901

[2]Entomology and Nematology Department, University of Florida, P.O. Box 110620, Gainesville, FL 32611

ABSTRACT

The importance of soil organic matter for *Tomarus subtropicus* Blatchley larval development and survival, the amount of damage larvae could cause on turfgrasses, and potential larval host range were investigated in greenhouse experiments. First instars were reared individually in seedling trays containing sand or peat, with or without St. Augustinegrass. Survival, developmental stage, and final weight were recorded 1 month after introduction. First instars died in the pots with peat but no grass, so it appears that grass roots were critical for larval growth and development. Soil organic matter did not significantly affect grub weight gain and development, but more root loss occurred with grass grown in sand. In host range tests (2005 and 2006), first and third instars were reared on 6 species of warm season grasses and ryegrass. Grub weight gain, development, survival and grass root reduction were determined 2 months after introduction. Larval survival ranged from 62-93% if grubs were reared on warm season grasses to only 40% if reared on ryegrass. Grubs reared on warm season grasses gained weight and successfully developed into third instars, indicating that all of the tested warm season turfgrasses were suitable for larval *T. subtropicus* growth and development. Grub feeding caused significant root reduction of all grasses in our study, which ranged from 36 to 87% and differed among grass species. As result, quality ratings and clipping yields decreased for most of the turfgrasses after 5 weeks of infestation, but bahiagrass and seashore paspalum were less affected by *T. subtropicus* root feeding, compared to the other grass species.

Key Words: sugarcane grub, host range, bermudagrass, sugarcane, St. Augustinegrass, ryegrass, root reduction, soil organic matter, grub weight gain and development

RESUMEN

La importancia de materia orgánica en el suelo para el desarrollo y sobrevivencia de larvas de *Tomarus subtropicus* Blatchley, la cantidad de daño que las larvas puedan causar en el césped y el rango potencial de hospederos por las larvas fueron investigados en experimentos realizados en invernaderos. Se criaron los primeros instares individualmente en bandejas usadas para plantillas con arena o turba y con o sin el césped San Augustin. El sobrevivencia, el estadio de desarrollo y el peso final fueron anotados 1 mes después de la introducción. Los primeros instares murieron en las macetas con turbo y sin grama, esto parece indicar que las raices de grama son básicas para el crecimiento y desarrollo de las larvas. La materia orgánica del suelo no afecto el aumento en el peso y el desarrollo de las larvas, pero hubo una mayor pérdida de las raices de la grama sembrada en arena. En pruebas del rango de los hospederos (2005 y 2006), se criaron los primeros y terceros instares sobre 6 especies de grama de la estación cálida y sobre centeno. Se determinaron el aumento en el peso de las larvas, el desarrollo, la sobrevivencia reducción en las raices de la grama 2 meses despues de la introducción. El sobrevivencia de las larvas fue entre 62-93% en las larvas criadas sobre grama de la estación cálida y solo 40% en larvas criadas sobre centeno. Las larvas criadas sobre grama de la estación cálida aumentaron en peso y se desarrollaron exitosamente en instares de tercer estadio, que indica que todas las clases de grama de la estación cálida probadas fueron apropiadas para el crecimiento y desarrollo de larvas de *T. subtropicus.* En nuestro estudio, la alimentación de las larvas causó una reducción significativa de las raices de 36 a 87% y varían entre las especies de grama. Como un resulto, el indice de la calidad y el rendimiento de las cortadas de grama diminuyó para la mayoría de las clases de grama después de 5 semanas de infestación, pero el césped Bahia y el paspalum costero fueron menos afectados por la alimentación de *T. subtropicus* sobre las raices, comparados con las otras especies de grama.

Tomarus subtropicus Blatchley is a destructive turfgrass pest along Florida's Gulf and Atlantic Coasts, but is also distributed along coastal Alabama, Georgia, South Carolina, and North Caro-

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lina (Cartwright 1959). As with other grub species, *T. subtropicus* grubs directly damage turf by their root-feeding and tunneling behaviors (Ritcher 1966; Tashiro 1987; Braman & Pendley 1993). This pest is univoltine, with eggs present from late Jun to early Aug, first instars from Jul to Aug, second instars from Aug to Sep, and mostly third instars from Oct to Feb in Florida (Kostromytska & Buss 2008). *Tomarus subtropicus* attacks the roots of sugarcane (*Saccharum* spp.) (Gordon & Anderson 1981), St. Augustinegrass (*Stentaphrum secundatum* (Walt. Kuntze)) (Kostromytska & Buss 2008), and bermudagrass (*Cynodon dactylon* (L.)) (Summers 1974; Reinert 1979; Prewitt & Summers 1981), resulting in crop yield loss and large patches of dead turfgrass. Its potential to feed on and injure other warm season turfgrasses has not been assessed. *Tomarus subtropicus* grubs also feed on plant roots in ornamental plant beds, and cause plant dieback (E. Buss, personal observation).

White grub feeding habits vary depending on the species. Some species (e.g., *Cotinis nitida* L.) obtain nutrients from soils high in organic matter (Brandhorst-Hubbard et al. 2001), while others need live plant roots (e.g., *Popillia japonica* Newman, *Rhizotrogus majalis* (Razumowsky), *Cyclocephala* spp., *Phyllophaga* spp.). Some scarab species consume soil organic matter as first instars, then switch to live roots in later instars (Litsinger et al. 2002). The larval feeding habits of *T. subtropicus* have not been clearly described. *Tomarus subtropicus* females oviposit and their offspring develop in soil with a high organic matter content (e.g., muck soil in sugarcane fields) (Cherry & Coale 1994), but they also survive and develop in sandy soils with low organic matter in residential environments (Kostromytska & Buss 2008).

Because the urban landscape is a complex system with many plant species, understanding the feeding preference of key pests helps to explain pest distribution, abundance, and damage related to feeding, and can affect the management strategies used against them. We conducted no-choice tests to assess the effect of soil organic matter on *T. subtropicus* survival and development, and to determine which other warm season turfgrasses could be hosts for *T. subtropicus* grubs.

Materials and Methods

Effect of 2 Soil Types on First Instars

A no-choice test with a nutrient-poor soil (sand) and an organic soil (Black Velvet peat (Black Gold Compost Co., Oxford, Florida)) was conducted from Jul to Aug 2005 to evaluate *T. subtropicus* larval growth and survival. The roots of 'Palmetto' St. Augustinegrass plugs were washed, and grass plugs were replanted into the seedling tray cells (8 × 8 × 8 cm) with either sand or peat (48 cells for each growing media). Another 24 cells were filled with peat, but no grass. Grass was maintained in the greenhouse for 2 weeks before the experiment. Cells were arranged in a randomized complete block design.

Adult *T. subtropicus* were collected from infested St. Augustinegrass lawns in Punta Gorda (Charlotte County) and Fort Myers (Lee County), Florida, and held in the laboratory to obtain eggs and young larvae (Kostromytska 2007). Grubs (2-6 d old; mean weight: 0.028 ± 0.002 g) were randomly assigned to the following treatments: peat only, peat and grass, or sand and grass (24 replicates or cells for each). Cells of grass planted in sand or peat (24 cells of each) were uninfested controls. Individual first instars were placed in a depression (2.5 cm deep, 0.7 cm in diameter) made in the center of each cell and covered with soil. Each cell was provided 30 mL of water daily. After 1 month, cells were visually inspected, and surviving grubs were weighed. Grass roots were washed with a #10 sieve, oven-dried in paper bags for 48 h at 55°C, and root dry weights were recorded. Data were analyzed by an ANCOVA (SAS Institute 2004) with soil type as a factor, post-treatment grub weight as a dependent variable and initial grub weight as a covariate. A two-way ANOVA was also conducted with soil type and grub presence as factors and dry root weight as a dependent variable. Tukey's HSD test was conducted for mean separation.

Survival and Growth of Third Instar *T. subtropicus* Reared on Different Turfgrass Species

Six warm season and 1 cool season turfgrasses were evaluated as possible hosts for *T. subtropicus* grubs. Tested grasses included Palmetto St. Augustinegrass, 'Tifway' bermudagrass (*C. dactylon* × *transvaalensis* Burtt-Davy), 'Empire' zoysiagrass (*Z. japonica* Steud.), common centipedegrass (*Erimochloa ophiuroides* (Munro) Hack), 'Pensacola' bahiagrass (*Paspalum notatum* Flugge), 'Sea Dwarf' seashore paspalum (*Paspalum vaginatum* Swartz), and 'Gulf' annual ryegrass (*Lolium multiflorum* Lam.). Thirty plugs (15 cm diameter) of each warm season grass species were obtained from the University of Florida Plant Science Unit in Citra (Marion County), Florida, in Aug 2005. Soil was washed off the roots and the grass plugs were planted with Fafard mix #2 (Conrad Fafard, Inc., Agawam, Massachusetts) in plastic pots (15 cm diameter). Annual ryegrass was seeded at a rate of 0.05 kg/m^2. Grass was watered daily and fertilized monthly with 24.4 kg of N per ha during 2 months of establishment. Pots were arranged in a randomized complete block design in the greenhouse.

Initial grub weights were obtained, then 1 recently molted (<7 d old) third instar was put in a shallow depression on the soil of each of 15 pots

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for each turfgrass species. Grubs that failed to dig into the soil within 10 min were replaced. Larval survival, weight, and weight gain were determined after 8 weeks. Daylight was supplemented with lights to provide a photoperiod of 16:8 h (L:D) and the average ambient greenhouse temperature was ~23.4°C. Pots were watered with 150 mL of tap water every other day. Each turfgrass species was maintained at its recommended height (Turgeon 2002): 1.3 cm for seashore paspalum, 2.5 cm for bermudagrass, 5.1 cm for centipedegrass and zoysiagrass, and 7.6 cm for annual ryegrass, St. Augustinegrass and bahiagrass. To assess the amount of feeding damage, grass clippings were collected weekly and fresh weights were taken within 2 h. Clippings were then oven-dried for 48 h at 55°C, and weighed. After 8 weeks of infestation, grass roots were cut within 2 mm of the plant crown, washed with a #20 sieve, oven-dried for 48 h (55°C), and dry root weights were recorded.

Tomarus subtropicus Neonate Survival, Growth and Development on 6 Warm Season Grasses

The warm season turfgrass species noted in the previous section were tested as potential hosts for *T. subtropicus* larvae in a greenhouse experiment in 2006. Grass plugs were planted into 10-cm plastic pots with native soil (94% sand, 4% clay, 2% silt and 1.6% organic matter), and allowed 2 months to establish. First instars (1-3 d old) were weighed immediately before being individually placed in a hole (8 mm diameter, 5 cm deep) in the soil of each pot, and were covered with soil. Grass was watered daily as needed and fertilized weekly (0.6 kg of N per ha, Miracle Gro® Scotts Miracle-Gro Products Inc., Marysville, OH). Four replicates per grass species were arranged and each replicate included 6 infested and 6 uninfested control pots. Grubs were removed from the pots after 8 weeks, and larval survival, weight, and head capsule width were determined. Grass clippings were collected and processed weekly, as previously described. Grass color and density were visually assessed on a scale from 1 (yellow, sparse) to 9 (dark green, very dense) and total grass quality was calculated by averaging the two scores. After the grubs were removed, grass roots were cut to within 2 mm of the plant crown, washed with a #20 sieve, and placed in paper bags. The remaining plant parts were collectively placed into paper bags, and oven-dried for 48 h (55°C). Dry root weight and dry total plant yield were recorded.

Statistical Analysis

The correlation between initial and final grub weights was tested before analysis. If the 2 variables were significantly correlated, the ANCOVA GLM procedure (SAS Institute 2004) was used to analyze the effect of turf species on grub final weight with a correction for initial weight for all experiments. Percent of root reduction was calculated as averaged root weights of controls minus root weights of infested plants and divided by averaged weights in controls. Analysis of variance (GLM procedure, SAS Institute 2004) was used to determine the effect of turf species on the percentage of grub survival and development, and effect of grub presence on dry root weight. Proportion data were arcsine square root transformed before analysis. Clipping weights and grass quality ratings were analyzed by a repeated measure analysis (SAS Institute 2004) with time as a repeated within-group factor and grub presence as a between-group factor. Means were separated by Tukey's HSD.

Results and Discussion

Effect of 2 Soil Types on First Instars

Tomarus subtropicus grubs fed on live St. Augustinegrass roots, regardless of soil type, in this test. Two grubs (8%) that were reared on peat without grass survived, but they remained first instars, and all other grubs in this treatment died. All grubs provided with St. Augustinegrass roots, regardless of soil type, were second instars when the test was evaluated. Grub survival to the second instar when reared on peat with grass was 83%, and 75% when reared on sand with grass. *Tomarus subtropicus* body weights were statistically similar when grubs were reared on grass grown in peat (0.87 ± 0.07 g) or grass grown in sand (0.74 ± 0.08 g).

Grub feeding significantly reduced St. Augustinegrass dry root weight compared to uninfested cells, regardless of soil type ($F = 156.66$; $df = 1, 85$; $P < 0.0001$). Uninfested pots had statistically similar dry St. Augustinegrass root weights (1.24 ± 0.06 g in peat; 1.17 ± 0.06 g in sand). The final dry root weight of infested grass grown in sand (0.31 ± 0.05 g) was significantly lower than in infested grass grown in peat (0.59 ± 0.05 g) ($F = 4.59$; $df = 1, 85$; $P = 0.03$), indicating that more root herbivory may have occurred in the pots with sand.

Peat, like muck soil, is an organic soil, consisting of poorly decomposed animal and plant remnants (Brown 2009) with organic matter content ranging from 40 to 80% (Andriesse 1988; Litaor et al. 2005; Kechavarzi et al. 2010) which can provide nutrients (e.g., carbon, nitrogen, sulfur, and phosphorous) to plants and soil fauna (Andriesse 1988; Killham 1994). Although the nutrient content of the soils or turfgrass were not measured in our test (fertilization and irrigation were consistent across all treatments), it is possible that the peat provided additional nutrients to the grass, which could lead to either more efficient grub

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feeding or increased compensatory plant growth (Radcliffe 1970; Brown and Gauge 1990; Steinger & Müller-Schärer 1992; Sparling et al. 2006). In addition, grubs may, while feeding on grass roots, acquire additional nutrients when ingesting soil with greater organic matter content (Seastedt 1985; Brown & Gange 1990), and thus cause less root damage. The tendency for insects to consume more of a nutritionally inferior food to overcome the lack of needed nutrients has been documented for many taxa (King 1977; Yang & Joern 1994; Obermaier & Zwolfer 1999; Berner et al. 2005).

Survival and Growth of Third Instar *T. subtropicus* Reared on Different Turfgrass Species

Third instar initial weights (1.97 ± 0.08 g) were statistically similar among treatments (F = 0.71; df = 6, 76; P = 0.64). However, initial and final grub weights were significantly correlated (Pearson's r = 0.37, P = 0.001) and were included as covariates in the analysis. Final grub weight differed statistically among grasses (Table 1). Third instar weights when reared on ryegrass (1.96 ± 0.2 g) and bermudagrass (2.1 ± 0.2 g) were significantly lower than grub weights on any of the other grasses tested (F = 8.51; df = 6, 76; P < 0.0001). However, 66.7% of the grubs survived on bermudagrass and only 40% survived on ryegrass. Analysis of grass dry root weight with and without grubs indicated that there was a significant root reduction in all pots with warm season grasses, but not in the pots with ryegrass (Fig. 1). These data suggest that ryegrass was a poor larval host for *T. subtropicus*. Annual ryegrass was the only C_3 grass included in the test. C_3 grasses typically are more beneficial nutritionally to herbivores than C_4 grasses (Barbehenn & Bernays 1992), however physical properties could be a key factor for herbivore host selection (Scheirs et al. 2001). Suitability of annual ryegrass as a host for *T. subtropicus* larvae may be affected by the physical structure of the grass root system. Numerous ryegrass fine roots created a dense mesh through the entire pot, which may have reduced grub movement. At evaluation, live grubs in ryegrass pots were in soil chambers that were located near pot walls and not more than 5 cm deep. In contrast, the other grasses had thick main roots from which roots branched closer to the pot walls and bottom, and grubs were often found in the center of the pots at different depths.

Grass leaf growth changed differently among grass species over time (summarized statistics are in Table 2). For St. Augustinegrass, the main effect of grub presence and the interaction of grub feeding with time were significant. On

TABLE 1. LARVAL *T. SUBTROPICUS* SURVIVAL AND GROWTH ON DIFFERENT GRASS SPECIES AND ASSOCIATED ROOT REDUCTION IN 2005 AND 2006.

Grass species	% Grub survival	Initial grub weight (g ± SEM)[1]	Final grub weight (g ± SEM)[2]	Proportional weight gain[3]	Root reduction (% ± SEM)[4]
2005					
Bahiagrass	93.3 ± 6.7	1.8 ± 0.2a	3.05 ± 0.2b	1.8 ± 0.1a	27.4 ± 8.8bc
Bermudagrass	66.7 ± 6.7	1.7 ± 0.2a	2.10 ± 0.2a	1.1 ± 0.3ab	64.9 ± 3.2a
Centipedegrass	66.7 ± 24.0	1.9 ± 0.3a	3.43 ± 0.2b	2.1 ± 0.3a	60.5 ± 4.9a
Ryegrass	40.0 ± 0.0	2.2 ± 0.7a	1.96 ± 0.2a	1.0 ± 0.1b	17.2 ± 4.9c
Seashore paspalum	86.7 ± 6.7	2.1 ± 0.2a	3.57 ± 0.2b	1.8 ± 0.1a	49.1 ± 9.1ab
St. Augustinegrass	66.7 ± 6.7	2.2 ± 0.2a	3.18 ± 0.1b	1.4 ± 0.1a	52.2 ± 7.7ab
Zoysiagrass	86.7 ± 6.7	2.0 ± 0.1a	3.04 ± 0.1b	1.8 ± 0.2a	55.3 ± 6.4ab
2006					
Bahiagrass	79.3 ± 7.9	0.028 ± 0.002a	2.62 ± 0.2abc	103.7 ± 11.2abc	48.1 ± 4.6bc
Bermudagrass	66.8 ± 6.7	0.034 ± 0.003a	2.20 ± 0.2c	69.6 ± 8.3c	87.5 ± 4.6a
Centipedegrass	91.5 ± 4.9	0.030 ± 0.002a	2.43 ± 0.2bc	87.6 ± 0.7bc	36.3 ± 4.2c
Seashore paspalum	62.5 ± 10.5	0.031 ± 0.003a	3.35 ± 0.2a	126.2 ± 15.6a	60.8 ± 4.6ab
St. Augustinegrass	87.3 ± 4.3	0.033 ± 0.002a	2.62 ± 0.2abc	92.2 ± 7.9abc	65.0 ± 6.8ab
Zoysiagrass	70.8 ± 7.9	0.030 ± 0.002a	3.13 ± 0.1ab	114.3 ± 8.7ab	80.9 ± 2.8a

[1]Initial grub weight was not significantly different among treatments at α = 0.05 (2005: F = 1.64; df = 6, 69; P = 0.15 and 2006: F = 1.84; df = 5, 143; P = 0.11).

[2]Means within columns with different letters are statistically different at α = 0.05 (2005: F = 8.51; df = 6, 76; P < 0.0001 and 2006: F = 5.04; df = 5, 109; P = 0.0004).

[3]Proportions were calculated by dividing the final weights by initial weights. Means within columns with different letters are statistically different at α = 0.05 (2005: F = 3.89; df = 6, 76; P = 0.002 and 2006: F = 3.95; df = 5, 109; P = 0.0026).

[4]Means within columns with different letters are statistically different at α = 0.05 (2005: F = 6.32; df = 6, 105; P < 0.0001 and 2006: F = 16.52; df = 5, 111; P < 0.0001).

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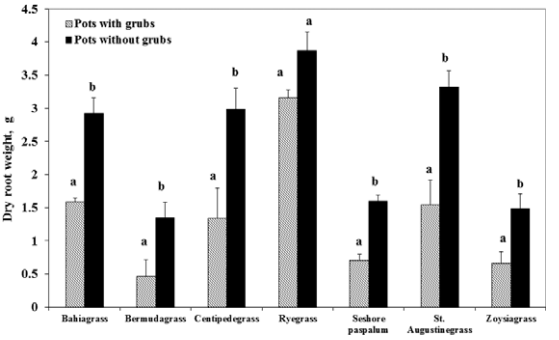

Fig. 1. Reduction of root mass caused by third instar *T. subtropicus* feeding, 2005. Means marked with different letter are different at a = 0.05 (F = 39.51; df = 1, 130; P < 0.0001)

average, clippings collected from the infested pots weighed less than clippings from uninfested control pots, and this difference increased over time. For bahiagrass, bermudagrass, and centipedegrass the main effect of grub presence was significant, whereas the interaction between grub presence and time was not significant. Clipping yield of these grasses changed significantly over time in all pots, but uninfested pots on average yielded more clippings. For zoysiagrass, the main effect of grub presence was not significant although the main effects of time and the interaction of time and grub presence were significant. Thus, decrease in clipping weight over time was more pronounced in the pots with grubs. Only the main effect of time was significant for ryegrass and seashore paspalum, so grass growth changed over time, but variation of clipping yield was not related to grub presence.

Tomarus subtropicus Neonate Survival, Growth, and Development on 6 Warm Season Grasses

On average, 76.3% of grubs survived across treatments and 70.8% of all (94% of survivors) grubs reached the third instar (Table 1). Percentage survival, percent of grubs that reached the third instar, and head capsule width did not differ among the grasses (F = 1.64; df = 5, 23; P = 0.20; F = 2.17; df = 5, 23; P = 0.10; and F = 1.73; df = 5, 109; P = 0.13).

Mean initial first instar weight (0.031 ± 0.01 g) did not correlate with mean grub final weight (2.75 ± 0.86 g) (r = 0.11, P = 0.22), and was not included in the analysis as a covariate. Final grub weight and proportional weight gain differed among grasses. Similar to the result obtained in the 2005-experiment, grubs feeding on bermudagrass gained less weight (weight gain about 70 times initial weight) when compared to grubs reared on seashore paspalum (weight gain about 126 times initial weight) and zoysiagrass (weight gain about 114 times) (Table 1).

Similar to the 2005-experiment, bermudagrass appeared to be a poorer host for *T. subtropicus* compared to the other warm season grasses. However, *T. subtropicus* larvae are reported to damage bermudagrass (Reinert 1979), so despite the slower grub growth, this grass may still be an acceptable host. Reduced grub growth may be influenced by a smaller root mass in bermudagrass (grubs consumed on average 87.5% of root mass).

TABLE 2. STATISTICS SHOWING EFFECTS OF TIME, GRUB FEEDING, AND THEIR INTERACTION ON CLIPPING YIELD DURING AN 8-WEEK PERIOD IN 2005 AND 2006.

	Grub feeding			Time			Time*Grub		
Grass species	F	*df*	P	F	*df*	P	F	*df*	P
2005									
Bahiagrass	8.50	1, 27	<0.01	2.48	7, 21	0.05	1.05	7, 21	0.43
Bermudagrass	11.22	1, 23	<0.01	44.49	7, 17	<0.01	1.96	7, 17	0.12
Centipedegrass	12.80	1, 23	<0.01	3.20	7, 17	0.02	1.6	7, 17	0.20
Seashore paspalum	3.07	1, 19	0.10	20.12	7, 13	<0.01	2.57	7, 13	0.07
St. Augustinegrass	0.09	1, 27	0.76	2.92	7, 21	0.03	0.67	7, 21	0.74
Zoysiagrass	9.47	1, 23	<0.01	1.99	7, 17	0.11	2.69	7, 17	0.05
2006									
Bahiagrass	1.56	1, 41	0.22	5.43	7, 35	<0.01	1.99	7, 35	0.08
Bermudagrass	8.10	1, 38	<0.01	5.38	7, 32	<0.01	2.47	7, 32	0.04
Centipedegrass	4.66	1, 44	0.04	6.09	7, 38	<0.01	0.36	7, 38	0.92
Seashore paspalum	0.30	1, 39	0.59	6.88	7, 33	<0.01	0.68	7, 33	0.69
St. Augustinegrass	1.49	1, 44	0.01	5.38	7, 32	<0.01	2.47	7, 32	0.04
Zoysiagrass	4.61	1, 46	0.04	9.48	7, 34	<0.01	1.29	7, 34	0.28

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Grub movement was also limited, so grubs could not migrate in search of food after the previous source had been exhausted.

Grub feeding caused significant root reduction of all grasses in our study ($F = 70.61$; $df = 6, 287$; $P < 0.0001$) (Fig. 2). The percent of root reduction ranged from 36 to 87% and differed among grasses ($F = 16.52$; $df = 5, 111$; $P < 0.01$) (Table 1). However, the total plant yield was reduced only for bahiagrass and bermudagrass ($F = 22.81$; $df = 11, 287$; $P = 0.001$) (Fig. 3). Root loss does not necessarily reduce aboveground plant growth, and in some cases, minor root damage can lead to increased or compensatory foliage growth (Humphries 1958; Seastedt et al. 1988; Brown & Gange 1990; Bardgett et al. 1999; Blossey & Hunt-Joshi 2003).

Measurements of grass yield over time demonstrated that tested grasses responded differently to *T. subtropicus* herbivory (statistics are summarized in Table 2). Centipede and zoysiagrass tended to yield fewer leaf clippings if infested with grubs, and clipping weights varied over time (the main effects of infestation and time on clipping yield were significant), but effect of grub feeding was not significantly stronger with time (interaction was not significant). The interaction of the 2 factors was significant for bermudagrass and St. Augustinegrass, so grub feeding decreased clipping yield beginning week 5. Grub feeding did not affect clipping yield in pots of bahiagrass and seashore paspalum.

Grub feeding reduced the quality ratings for St. Augustinegrass, bermudagrass, zoysiagrass and centipedegrass, but not for bahiagrass and seashore paspalum (statistics are summarized in Table 3). Differences in grass quality were apparent 4 weeks (St. Augustinegrass, bermudagrass), 6 weeks (zoysiagrass), and 8 weeks (centipedegrass) after grubs were introduced. Grass crowns could be pulled easily from the pots with grubs, but grass remained green in all pots.

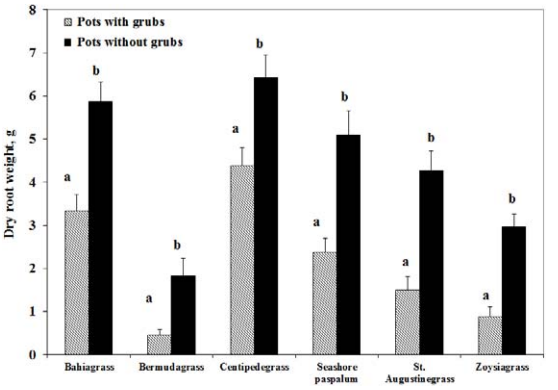

Fig. 2. Reduction of root mass caused by larval *T. subtropicus* feeding, 2006. Means marked with different letters are different at $\alpha = 0.05$ ($F = 70.61$; $df = 1, 287$; $P < 0.0001$)

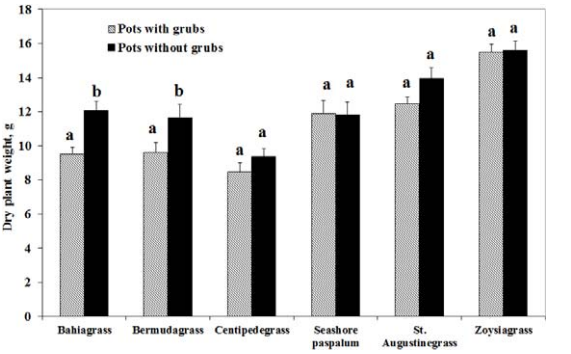

Fig. 3. Effect of grub feeding on total plant yield by warm season grasses, 2006. Means marked with different letter are different at a = 0.05 ($F = 5.51$; $df = 1, 253$; $P = 0.02$)

Our study demonstrated that *T. subtropicus* can successfully survive and develop on bahiagrass, bermudagrass, centipedegrass, zoysiagrass and seashore paspalum, and confirmed that St. Augustinegrass was an adequate host (Reinert 1979), regardless of soil organic content. Quality ratings and clipping yields decreased for most of the turfgrasses after 5 weeks of infestation, but bahiagrass and seashore paspalum were less affected by *T. subtropicus* root feeding, compared to the other grass species. It was previously reported that 3 grubs per 0.1 m^2 could severely damage bermudagrass (Reinert 1979), but the grasses in our study could tolerate approximately 5 and 12 third instar grubs per 0.1 m^2 in 2005 and 2006, respectively, despite >50% root reduction.

Environmental conditions (temperature, photoperiod, herbivore aboveground grazing or mowing, fertilization, and irrigation practices) can significantly affect plant tolerance to root herbivory in addition to plants characteristics and insect density (Ladd & Buriff 1979; Seastedt et al. 1988; Brown & Gange 1990; Potter et al. 1992; Crutchfield et al. 1995; Crutchfield & Potter 1995; Braman & Raymer 2006). For instance, 4 Japanese beetle (*Popillia japonica* Newman) grubs per 15-cm pot (~20 grubs per 0.1 m^2) significantly reduced *Poa pratensis* L. clipping yield in a greenhouse study (Ladd & Buriff 1979), but clipping yield from other field and greenhouse tests was unaffected by 60-90% root reduction from 40-60 grubs per 0.1 m^2 and 24-30 grubs per 0.1 m^2, respectively (Potter et al. 1992; Crutchfield & Potter 1995).

During our experiment, grass was regularly irrigated, and although the roots were dramatically reduced and crowns could be easily removed from infested pots, the foliage remained green. Most third instar-feeding in the field occurs during the

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TABLE 3. STATISTICS SHOWING EFFECT OF TIME, GRUB FEEDING, AND THEIR INTERACTION ON TURFGRASS QUALITY IN 2006.

	Grub feeding			Time			Time*Grub		
Grass species	F	*df*	P	F	*df*	P	F	*df*	P
Bahiagrass	0.6	1, 44	0.44	3.90	7, 40	0.15	0.95	7, 40	0.43
Bermudagrass	9.08	1, 44	<0.01	17.07	7, 40	<0.01	5.54	7, 40	<0.01
Centipedegrass	5.71	1, 44	0.02	13.51	7, 40	<0.01	8.66	7, 40	<0.01
Seashore paspalum	0.04	1, 44	0.83	4.61	7, 40	0.01	0.37	7, 40	0.70
St. Augustinegrass	9.08	1, 44	<0.01	17.07	7, 40	<0.01	5.54	7, 40	<0.01
Zoysiagrass	32.23	1, 44	<0.01	14.08	7, 40	<0.01	9.82	7, 40	<0.01

fall (Kostromytska 2007), which coincides with reduced rainfall and slower warm season turfgrass growth. Thus, drought and/or other environmental stresses during this time, in addition to root damage by grubs, may more quickly overwhelm the grass.

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