



Foraging by Red Imported Fire Ants, *Solenopsis invicta* (Hymenoptera; Formicidae) on Turfgrasses

Authors: Reinert, James A., and McCoy, Joe E.

Source: Florida Entomologist, 93(2) : 248-253

Published By: Florida Entomological Society

URL: <https://doi.org/10.1653/024.093.0215>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

FORAGING BY RED IMPORTED FIRE ANTS, *SOLENOPSIS INVICTA* (HYMENOPTERA; FORMICIDAE) ON TURFGRASSES

JAMES A. REINERT AND JOE E. MCCOY

Texas AgriLife Res. & Ext. Urban Solution Center, Texas A&M System, 17360 Coit Road, Dallas, TX 75252-6599

E-mail: j-reinert@tamu.edu

ABSTRACT

Red imported fire ant, *Solenopsis invicta* Buren (Hymenoptera; Formicidae) is a major pest in urban landscapes including residential/commercial lawns, sports fields, golf courses, parks, and highway rights-of-way. Foraging preferences for various turfgrass clippings were investigated under controlled lab conditions. Among bermudagrass (*Cynodon* sp.) cultivars, clippings of 'Tifway' and 'Baby' were 7 times more preferred than clippings of 'Tifton 10' and 'GN1'. The Texas bluegrass × Kentucky bluegrass hybrid (*Poa pratensis* L. × *P. arachnifera* Torr.), TXKY 00-34-2 had 5 times more foraging ants on it than TXKY 01-59-9. Among the zoysiagrasses (*Zoysia japonica*), 'El Toro' was only 2 times more preferred than 'Crowne'. For St. Augustinegrass (*Stenotaphrum secundatum* Walt. Kuntze), 'BitterBlue' was 3.4 times more preferred than 'Floritam'. On the buffalograss cultivars (*Buchloe dactyloides* (Nutt.) Engelm.), there were 2 and 4 times more ants foraging 'Texoka' than either 'Prairie' or 'Bison', respectively. After foraging for 5 h on clippings of the 5 or 6 cultivars in each replicate, the number of ants on each grass was bermudagrass (169.3) > zoysiagrass (137.5) = bluegrass hybrids (136.8) > St. Augustinegrass (127.1) > buffalograss (34.5).

Key Words: red imported fire ant, *Solenopsis invicta*, host plant resistance, turfgrass, *Cynodon* spp., *Zoysia* spp., *Buchloe dactyloides*, *Stenotaphrum secundatum*, *Poa* spp., hybrid bluegrass

RESUMEN

La hormiga roja de fuego, *Solenopsis invicta* Buren (Hymenoptera; Formicidae) es una plaga importante en ecosistemas urbanos, incluyendo céspedes residenciales y comerciales, campos deportivos, campos de golf, parques y derechos de vía en carreteras. La preferencia para la búsqueda de alimento en varios recortes de pastos fue evaluada en condiciones controladas de laboratorio. Los recortes de variedades de bermudagrass (*Cynodon* sp.) 'Tifway' y 'Baby' mostraron 7 veces más preferencia que 'Tifton 10' y 'GN1'. Entre los híbridos de Texas bluegrass × Kentucky bluegrass (*Poa pratensis* L. × *P. arachnifera* Torr.), TXKY 00-34-2 presentó una cantidad de hormigas explorando 5 veces mayor que TXKY 01-59-9. Entre variedades de zoysiagrass (*Zoysia japonica*) 'El Toro' solo mostró 2 veces más preferencia que 'Crowne'. Para cultivares de St. Augustinegrass (*Stenotaphrum secundatum* Walt. Kuntze), 'la preferencia por BitterBlue' fue 3.4 veces mayor que 'Floritam'. Entre materiales de Buffalograss (*Buchloe dactyloides* (Nutt.) Engelm.), 'Texoka' presentó 2 y 4 veces más hormigas buscando alimento, al compararse con 'Prairie' y 'Bison' respectivamente. Después de permitir por 5 horas la exploración por alimento en recortes de los cinco o seis cultivares en cada repetición, el número de hormigas en cada césped fue: bermudagrass (169.3) > zoysiagrass (137.5) = híbridos de bluegrass (136.8) > St. Augustinegrass (127.1) > buffalograss (34.5).

The authors provided the translation by Raul I. Cabrera and Carlos Campos.

Solenopsis invicta Buren, the red imported fire ant (RIFA), is an invasive and constant pest in urban/suburban landscapes in the southern United States. Their colonies may be present in any areas in which turfgrass is used; including residential/commercial lawns, golf courses, sports fields, and parks (Potter 1998; Reinert et al. 2007; Vittum, et al. 1999). They are a serious problem on roadside rights-of-way and in sod production facilities (USDA-APHIS 1999). RIFA was accidentally introduced into the southeastern United States around the 1930s from native habitats in South America (Drees 2009). It has now spread from

coast to coast and infests over 133.5 million hectares (330 million acres) across the southern half of the United States and it is predicted to continue to spread (Korzukhin et al. 2001). It has most recently spread into Mexico (2005) and infests portions of Australia (2001), New Zealand (2001), Taiwan (2004), and China (2006). Total annual cost from damages and expenditures for control for RIFA within Texas was estimated at over \$1.2 billion for 1998 and the costs continue to rise each year (Lard et al. 1999; Lard et al. 2002).

Several species of turfgrass are maintained under lawn culture across the southern states

where RIFA is well established. These turfgrasses include annual ryegrass (*Lolium multiflorum* Lam.), Bahiagrass (*Paspalum notatum* Flugge), bermudagrass (*Cynodon dactylon* (L.) Pers. and *C. transvaalensis* Burt-Davy), buffalograss (*Buchloe dactyloides* (Nutt.) Engelm.), centipedegrass (*Eremochloa ophiuroides* Munro Hack.), perennial ryegrass (*Lolium perenne* L.), Texas bluegrass (*Poa arachnifera* Torr.), bluegrass hybrids (*P. pratensis* L. × *P. arachnifera* Torr.), seashore paspalum (*P. vaginatum* Swartz), St. Augustinegrass (*Stenotaphrum secundatum* Walt. Kuntze), tall fescue (*Festuca arundinacea* Schreb.) and zoysiagrass (*Zoysia japonica* Steud. and *Z. matrella* (L.) Willd.) (Beard 2002; Christians 2007; Emmons 2008).

These lawns or landscapes are mowed often and weekly or biweekly in residential/commercial lawns and usually daily or twice-daily on golf greens and some sports fields. Leaf exudate contain sugars, mineral salts, amino acids, amides and other organic compounds (Beard 1973; Duell & Markus 1977; Taiz & Zeiger 2002). Sugars and some minerals and amino acids are attractive and consumed by the RIFA (Ricks & Vinson 1970; Vinson 1970) and are probably gathered as food from exudates of grass clippings by *S. invicta* since they are available during the night time when this ant does much of its foraging.

MATERIALS AND METHODS

Grasses for these evaluations were maintained in the greenhouse in 18-cell trays at the Texas AgriLife Research and Extension Urban Solution Center, Texas A&M System, Dallas, TX. Tray cells measured 7.5 × 7.5 cm and 4 cm deep. Plants were fertilized bi-monthly during the growing season and monthly during winter with Miracle-Gro All Purpose fertilizer 24-8-16 + B (200 ppm), Cu (700 ppm), Fe (1500 ppm), Mn (500 ppm), Mo (5 ppm), and Zn (600 ppm) (Scotts, Marysville, OH). Plants were watered and trimmed as needed throughout the test period to maintain good vegetative growth.

Laboratory studies of RIFA foraging on grass clippings were conducted over a period from Sep 2004 to Dec 2005. Cultivars evaluated included: 5 bermudagrasses ('Baby', 'GN1', 'TifSport', 'Tifton 10' and 'Tifway'); 6 Buffalograsses ('609', 'Bison', 'Density', 'Legacy', 'Prairie' and 'Texoka'); 5 Texas × Kentucky bluegrass hybrids ('Reveille', TX-KY 00-31-18, TX-KY 00-34-2, TX-KY 01-59-6, TX-KY 01-59-9 and TX-KY 00-64-21); 6 St Augustinegrass ('Bitter-Blue', 'Delmar', 'Floralawn', 'Floratam', 'Raleigh' and 'Texas Common') and 6 zoysiagrass ('Cavalier', 'Crowne', 'DeAnza', 'El Toro', 'Palisades' and 'Zeon'). Grasses were grouped by genera and exposed to foraging by ants from 5 established RIFA lab colonies.

RIFA lab colonies were established from large nearly complete field-collected colonies, transferred to the laboratory, and allowed to become acclimated for several weeks. Five colonies used in these studies were maintained in rearing chambers with a modification of the rearing procedures of Khan et al. (1967) and Kuriachan & Vinson (2000). Each rearing chamber consisted of a 27-L (59 × 43 × 15 cm) plastic box. Boxes were colonized with a medium-sized polygyne RIFA colony (the queens, eggs, and larvae were contained within a 15-cm covered Petri dishes) and provided with feeding stations consisting of cotton-stoppered test tubes of distilled water and plastic weight boats containing cotton balls saturated with 10% sugar water. Frozen crickets were also provided as needed as food in separate weight boats. A 10-cm band around the upper edge of each chamber was coated with Insect-a-Slip Insect Barrier—Fluon® (BioQuip Products, Rancho Dominguez, CA) to prevent the ants from escaping.

Foragers from the lab-reared RIFA colonies were introduced via glass travel tubes (6.0 mm ID), to a second plastic chamber (59 × 43 × 15 cm) in which the Petri dishes (9 cm diam × 20 mm deep) containing test grass clippings were randomly arranged in a circle around the turned-up end of the travel tube. Each dish was provided with 2 water-saturated 7.5-cm filter paper discs and contained a 0.25-0.50-g sample of the test grass that had been clipped from plants in the greenhouse no more than 1 h earlier. Dishes were provided with lids to help prevent desiccation of the grass samples. Glass tubes were shaped so that the ants traveling through the tube emerged as close to the center as possible in the test chamber and non-directional from the turned upwards end of the tube. Each Petri dish containing grass clippings was provided with a 5-7-mm opening facing the travel tube to allow ants to freely enter the dish (Fig. 1). We opened the Petri dish lids slightly to allow the foraging ants to more quickly find the grasses. RIFA colonies were randomly assigned to replications daily. Grasses were re-randomized for each replicate, with replicates as follows; 16 of bermudagrass, 13 of buffalograss, 12 of Texas × Kentucky bluegrass hybrids, 14 of St Augustinegrass and 12 of zoysiagrass were evaluated. After each of the 5 grass genera was evaluated individually, the most foraged and the least foraged cultivar for each grass were brought together for an evaluation of preference across the 5 genera of grasses in 2 additional tests, each with 18 replications.

Ants were introduced in the morning and allowed to forage for 5 h. Without disturbing the ants, all foragers on each grass in each of the test dishes were recorded at 1, 1.5, 2, 2.5, 3, and 4 h. Since there were far more RIFA foragers at 5 h and the experiment was being terminated, each



Fig. 1. Procedure for exposing test grasses to foraging ants from a lab colony of red imported fire ants. Fire ant colony is positioned next to the test arenas with the grass selections. Ants can pass through a glass travel tubes from the colony to the test arena to forage on selected grasses.

dish was physically removed from the test arena to a holding plastic box where the ants could be more easily counted. Notes were made during each test to record any unusual foraging behavior associated with each cultivar or genera of grass.

Data Analysis and Statistics

Transformations [$\sqrt{(n + 0.0001)}$] were used on each data set to achieve normality and homogeneity of variance before analysis (Kuehl 2000) but untransformed means are presented. Analyses of variance (ANOVA) (PROC GLM) for randomized complete block design were performed to test the differences between treatments, and means were compared at the 5% level of significance by Fisher's least-significant difference (LSD) multiple range test (SAS Institute 2008).

RESULTS AND DISCUSSION

A comparison of the foraging activity within each test on each grass indicated a high preference for bermudagrass clippings and a least pre-

ferred or non-preference for buffalograss clippings. When the final assays were taken at 5 h, the mean number of RIFA foragers on clippings of the 5 or 6 grasses in the Petri dishes within each replicate was bermudagrass (169.3) > zoysiagrass (137.5) = bluegrass hybrids (136.8) > St. Augustinegrass (127.1) > buffalograss (34.5). Most ants were observed inside the individual Petri dishes, except in tests with buffalograss. In the buffalograss foraging chambers, with a mean number of 271.7 foragers within the chamber, only 12.7% of the ants were observed foraging within the Petri dishes. With the other more preferred grasses, only a small percentage of ants were not on the grass or forming the trail back to the transport tube to the colony.

For each of the turfgrasses evaluated, a mean of <5 RIFA foragers found the grass selections within 1 h, and foragers usually did not exceed a mean of 10 until after 2.5 h of exposure. Only after 3 or 4 h of foraging did the number of ants on the highly foraged entries begin to exponentially increase to the high number of foragers recorded at 5 h. This may be a result of the time it takes the

initial foraging ants to recruit additional workers in high numbers. Also, throughout these studies, pieces of grass blades were sometimes removed from the Petri dishes and attempts were made to carry them through the travel tubes back to the colony.

Bermudagrass

Tifway and Baby (mean > 50 foragers) were the highest foraged cultivars among all 5 genera of grasses and the most preferred among the bermudagrasses, but not statistically different from TifSport when foraging counts were made at 5 h (Fig. 2). Tifton 10 and GN1 were significantly and 7 times less preferred (<15 foragers) than Tifway and Baby. Noteworthy, the number of foragers more than doubled from 4 to 5 h on all 3 cultivars Tifway, Baby, and TifSport.

Bluegrass

Among the bluegrass hybrids, TXKY 00-34-2 (mean = 48.2 foragers) was significantly more heavily foraged and had 5.1 times as many foraging ants on it as TXKY 01-59-9 (mean of 9.42 foragers) (Fig. 3). The number of foragers on TXKY 00-34-2 also doubled during the period from 4 h to 5 h. Reveille, the commercial hybrid, had an intermediate level of foragers.

Zoysiagrass

El Toro (mean = 38.1 foragers) was significantly more preferred among the zoysiagrasses but it was only 2 times more preferred than Crowne (mean = 17.5), the least preferred (Fig. 4). Foraging increased exponentially from 3 to 5 h on El Toro, similarly to the increases observed on the bermudagrasses and bluegrass hybrids. Foraging on El Toro

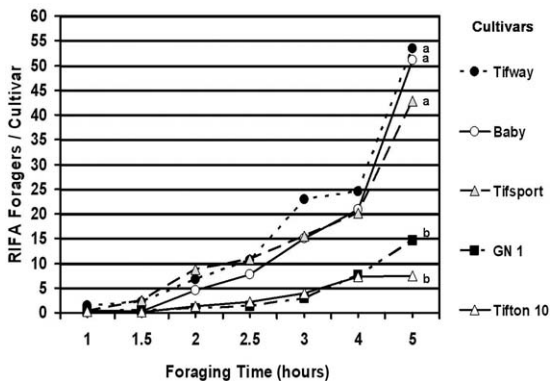


Fig. 2. Red imported fire ant foraging behavior on 5 cultivars of bermudagrass, Dallas, TX (16 replications). Mean data points at 5 h followed by the same letter are not significantly different by Fisher's protected LSD ($P \leq 0.05$).

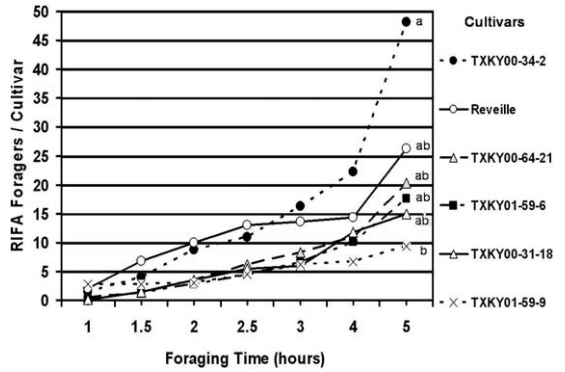


Fig. 3. Red imported fire ant foraging behavior on 6 cultivars of bluegrass hybrids, Dallas, TX (12 replications). Mean data points at 5 h followed by the same letter are not significantly different by Fisher's protected LSD ($P \leq 0.05$).

increased 1.6 times from 3 to 4 h and another 1.5 times from 4 to 5 h while foraging on the other 5 cultivars did increase but not as dramatically.

St. Augustinegrass

Differences in foraging among the cultivars of St. Augustinegrass were not as dramatic as among the cultivars of bermudagrass, bluegrass, or zoysiagrass. BitterBlue (mean = 32.0) was significantly preferred and 3.4 times greater than on Floratam (mean = 9.3), the least preferred (Fig 5). Foraging on BitterBlue increased 2.1 times from 3 to 4 h but only 1.7 times during the last period from 4 to 5 h.

Buffalograss

The amount of foraging on the aforementioned turfgrasses was 3.7 to 4.9 times greater than on

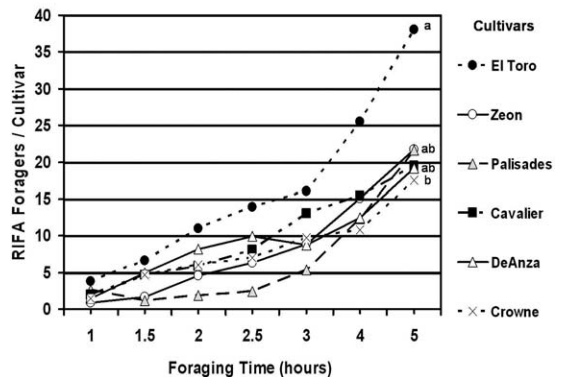


Fig. 4. Red imported fire ant foraging behavior on 6 cultivars of zoysiagrass, Dallas, TX (12 replications). Mean data points at 5 h followed by the same letter are not significantly different by Fisher's protected LSD ($P \leq 0.05$).

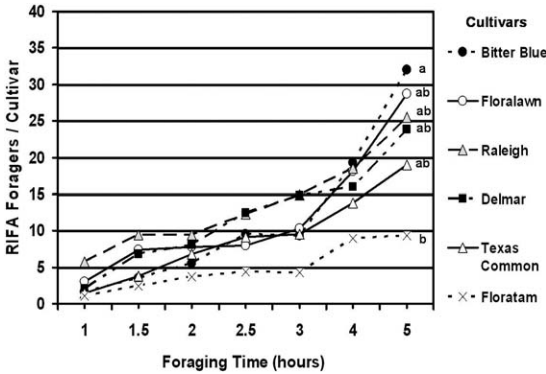


Fig. 5. Red imported fire ant foraging behavior on 6 cultivars of St. Augustinegrass, Dallas, TX (14 replications). Mean data points at 5 h followed by the same letter are not significantly different by Fisher's protected LSD ($P \leq 0.05$).

the buffalograss cultivars. However, among the buffalograss cultivars, Texoka (mean = 25.9 foragers) was significantly preferred over either Prairie or Bison (3.5 and 2.0, respectively) (Fig. 6). Like the other grasses tested, there was a dramatic and exponential increase in foraging activity from the 3-h observation to the 5-h reading for the 3 most preferred cultivars. This increase was 4.3, 6.6, and 6.1 fold for Density, 609 and Texoka, respectively.

Comparison of High and Low Foraged Cultivars among the Tested Grasses

When the cultivars that ranked highest and were most preferred for each genus of grass were compared, there was very little separation in for-

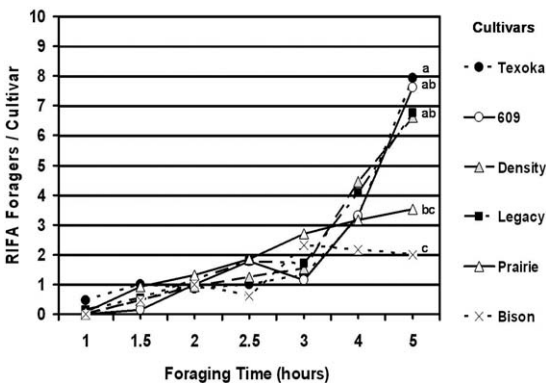


Fig. 6. Red imported fire ant foraging behavior on 5 cultivars of buffalograss, Dallas, TX (13 replications). Mean data points at 5 h followed by the same letter are not significantly different by Fisher's protected LSD ($P \leq 0.05$).

aging activity until the period from 4 to 5 h. At the 5-h-reading, Texoka buffalograss (mean = 25.9) was 5.5 times more preferred and significantly different from BitterBlue St. Augustinegrass (mean = 4.7), the least preferred (Fig. 7). The other 3 test grasses were not significantly different from either Texoka or BitterBlue.

The cultivars that were least preferred for each of the grasses were also compared. TXKY 01-59-9 bluegrass hybrid (mean = 27.7) was most preferred and had 4.3 times more RIFA foragers than Floratam St. Augustinegrass (mean = 6.5) the least preferred, but there were no statistical significances due to excessive variance (Fig. 8). The excessive variation may help to support why each of these grasses was also least-preferred for each genus of grass. The means for these grasses did however begin to separate much earlier at the 2-h reading. However, foraging levels for the replicates of the high- and for the low-foraged grasses (means = 12.0 and 15.3, respectively) were very similar for the 2 groups of grasses.

Most of the separation among cultivars occurred during the period from 4 to 5 h in the tests which may be a factor of the time it takes a forager to locate a new food source and then recruit additional ants to the location. The differences in preference for certain cultivars may be due to availability of various sugars, mineral salts, amino acids, amides, and other organic compounds in the various cultivars of grass (Beard 1973; Duell & Markus 1977; Goatley & Lewis 1966; Taiz & Zeiger 2002). These plant components may be important food elements in RIFA's diet (Ricks & Vinson 1970; Vinson 1970) and these relationships need to be investigated further. Resistance to many different species of chewing and sucking insects has been documented in certain cultivars for turfgrass and

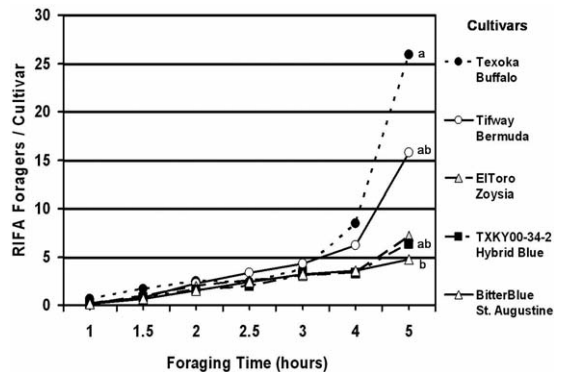


Fig. 7. Red imported fire ant foraging behavior on the 5 high foraged grass cultivars, Dallas, TX (18 replications). Mean data points at 5 h followed by the same letter are not significantly different by Fisher's protected LSD ($P \leq 0.05$).

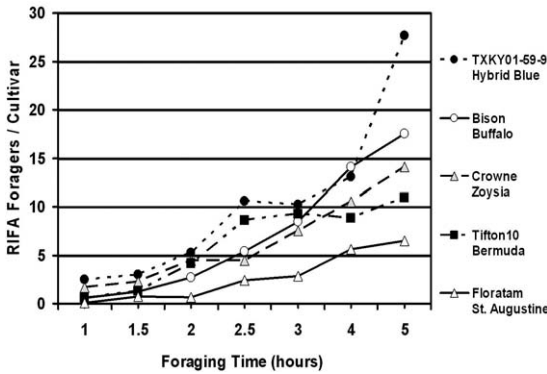


Fig. 8. Red imported fire ant foraging behavior on the 5 least foraged grass cultivars, Dallas, TX (18 replications). Mean data points at 5 h were not significantly different by Fisher's protected LSD ($P \leq 0.05$).

these are summarized by Reinert et al. (2004). The present research represents another way to measure host preference among cultivars of grass.

Within each genus, there was a major difference between the most foraged cultivar and the least preferred. The differences between most- and least-preferred for bermudagrass, bluegrass hybrids, zoysiagrass, St. Augustinegrass, and buffalograss were 7.1, 5.1, 2.1, 3.4 and 4.0 times, respectively, and they were significantly different for each genus of grass.

The buffalograsses were not preferred (average < 6 ants per Petri dish) when tested as a group, but when both the most and least preferred buffalograss cultivars were tested in the presence of other grass species, they attracted larger numbers of ants (>20 ants per Petri dish), possibly because the ants were attracted to the other grass species and once in the vicinity they found the buffalograss to be attractive and provide a good food source as well.

REFERENCES CITED

- BEARD, J. B. 1973. Turfgrass Science and Culture. Printice-Hall Int., Inc., London, 658 p.
- BEARD, J. B. 2002. Turfgrass Management for Golf Courses. Ann Arbor Press, Chelsea, MI, 793 p.
- CHRISTIANS, N. 2007. Fundamentals of Turfgrass Management. John Wiley & Sons, 368 pp.
- DREES, B. M. 2009. Red imported fire ant management, impact of educational programs and considerations for recent incursions. *Int. Turfgrass Soc. Res. J.* 11: 631-637.
- DUELL, R. W., AND MARKUS, D. K. 1977. Guttation deposits on turfgrass. *Agron. J.* 69: 891-896.
- EMMONS, R. D. 2008. Turfgrass Science and Management. Thomson Delmar Learning, Albany, NY, 567 pp.
- GOATLEY, J. L., AND LEWIS, R. W. 1966. Composition of guttation fluid from rye, wheat and barley seedlings. *Plant Physiol.* 41: 373-375.
- KHAN, A. R., GREEN, H. B., AND BRAZZEL, J. R. 1967. Laboratory rearing of the imported fire ant. *J. Econ. Entomol.* 60: 915-917.
- KORZUKHIN, M. D., PORTER, S. D., THOMPSON, L. C., AND WILEY, S. 2001. Modeling temperature-dependent range limits for the red imported fire ant (Hymenoptera: Formicidae: *Solenopsis invicta*) in the United States. *Environ. Entomol.* 30: 645-6655.
- KUEHL, R. O. 2000. Design of Experiments: Statistical Principles of Research Design and Analysis. Duxbury Press, Albany, NY, 666 pp.
- KURIACHAN, I., AND VINSON, S. B. 2000. A queen's worker attractiveness influences her movement in polygynous colonies of the red imported fire ant (Hymenoptera: Formicidae) in response to adverse temperatures. *Environ. Entomol.* 29: 943-949.
- LARD, C.F., HALL, C. R., SALIN, V., VINSON, S. B., CLEERE, K. H., AND PURSWELL, S. 1999. The Economic Impact of the Red Imported Fire Ant on the Home-escape, Landscape, and the Urbanscape of Selected Metroplexes of Texas: A Part of the Texas Fire Ant Initiative 1997-1999. Texas A&M Univ., AGEC, p. 1-63.
- LARD, C. F., HALL, C. R., AND SALIN, V. 2002. Economic assessments of red imported fire ant on Texas' urban and agricultural sectors. *Southwestern Entomol. Suppl.* 25: 123-137
- POTTER, D. A. 1998. Biting and stinging pests in the turfgrass environment, Ch. 12, pp. 235-252 *In* Destructive Turfgrass Insects; Biology, Diagnosis and Control. Ann Arbor Press, Inc., Chelsea, MI, 344 pp.
- REINERT, J. A., MCCOY, J., DREES, B. M., SCHOFIELD, K., AND HEITHOLT, J. J. 2007. Fire ant management in urban landscapes with broadcast treatments. *Proc. SNA Res. Conf.* 52: 34-40.
- REINERT, J. A., ENGELKE, M. C., AND READ, J. C. 2004. Host resistance to insects and mites, a review—A major IPM strategy in turfgrass culture. 1st Int. Soc. Hort. Sci. Conf. Turfgrass Manage. Sci. Sports Fields. Athens, Greece. *Acta Hort.* 661: 463-486.
- RICKS, B. L. AND VINSON, S. B. 1970. Feeding acceptability of certain insects and various water-soluble compounds to varieties of the imported fire ant. *J. Econ. Entomol.* 145-148.
- SAS INSTITUTE. 2008. SAS system for Windows, release 9.1. SAS Institute, Cary, NC.
- TAIZ, L., AND ZEIGER, E. 2002. Water balance of plants, Ch. 4, pp. 47-65 *In* Plant Physiology, Third Ed. Sinauer Assoc., Inc., Publ., Sunderland, MS, 690 pp.
- USDA-APHIS. 1999. Imported fire ant-quarantine treatment for nursery stock and other regulated articles. USDA-APHIS Program Aid No. 1653, 19 p.
- VINSON, S. B. 1970. Gustatory response of the imported fire ant to various electrolytes. *Ann. Entomol. Soc. America* 63: 932-935.
- VITTUM, P. J., VILLANI, M. G., AND TASHIRO, H. 1999. Hymenopteran pests: family Formicidae, pp. 255-269 *In* Turfgrass Insects of the United States and Canada. Cornell Univ. Press 422 pp.