

Potassium and Nitrogen Impacts on Survival and Development of Fall Armyworm (Lepidoptera: Noctuidae)¹

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Abstract This study determined the effects of nitrogen (N) and potassium (K) plant fertilizers on the survival and development of fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae), on 'TifEagle' bermudagrass [*Cynodon dactylon* (L.) Pers. x *C. transvaalensis* Burt-Davy]. The treatments were various ratios of N:K: (1) 0:0, (2) 1:0, (3) 2:1, (4) 1:1, (5) 0:1, and (6) 1:2, where 1 = 113.4 g N or K per 92.3 m². Treatments were applied from May to October in 2018 and 2019 at biweekly intervals via foliar spraying. Neonates of *S. frugiperda* were introduced to treated plants under laboratory conditions. In 2018, survival was significantly lower in the 0:1, 1:2, 1:0, and 0:0 treatments than in the 2:1 and 1:1 treatments at 10 d and 24 d postintroduction; whereas, in 2019, survival was significantly lower in the 0:0 treatment than in the other treatments at 10 d and 24 d postintroduction. Development of *S. frugiperda* larvae was significantly faster in the 2:1 treatment than in the 1:1 treatment in both years. Our data indicate that N favors and K discourages the growth and development of *S. frugiperda* larvae on bermudagrass.

Key Words *Spodoptera frugiperda*, turfgrass, integrated pest management

The fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae), is an important pest of bermudagrass [*Cynodon dactylon* (L.), Family: Gramineae] in the central and southeastern United States (Luginbill 1928). Bermudagrass is a major pasture and turfgrass species in the southeastern United States (Burton 1991). Turfgrass was ranked 23rd in value in the 2018 Georgia Agricultural Commodity Rankings. Georgia is one of the major sod-producing states in the United States, and the turfgrass industry generates \$118.3 million USD for Georgia's economy (Georgia Farm Gate Value Report 2018). In Georgia, *S. frugiperda* does not diapause but rather overwinters in tropical regions of Florida and Texas and disperses throughout the eastern and central United States during spring and summer each year. Younger larvae consume only green leaf tissue, causing leaf skeletonization. Older larvae (fourth to sixth instars) consume the entire leaf blade and stolon. Currently, *S. frugiperda* management is accomplished primarily by using pyrethroid insecticides, although most of these insecticides are only effective against the younger larvae. Pyrethroid insecticides are known for their hazardous effects on nontarget organisms, especially beneficial insects such as

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predators and parasitoids (Cheng et al. 2018, Regan et al. 2017, Sarto et al. 2014). Nonchemical options are available as part of integrated pest management programs but are rarely utilized for *S. frugiperda* management in commercial production and maintenance.

Potassium (K) is known to increase fiber strength and quality in plants (Read et al. 2006). As an enzyme activator, K plays a vital role in various plant physiological processes, such as photosynthesis, respiration, carbohydrate metabolism, translocation, and protein synthesis (Pettigrew 2008). Insufficient available K not only contributes to nutrient imbalances (Miller 1999) but also increases susceptibility to arthropod infestation. Perrenoud (1990) reviewed more than 2,000 studies and concluded that K fertilizer application tends to reduce the incidence of diseases and insect pests in many agroecosystems. K fertilizer application in rice has been shown to improve rice tolerance to various abiotic and biotic stresses, including insect pests (Tiwari 2002). Similarly, resistance to insect pests and diseases is directly related to plant physiology, and factors influencing plant physiology may affect plant resistance or tolerance levels (Altieri and Nicholls 2003). Studies also have demonstrated that K fertilizer inputs influence the effectiveness of applied nitrogen (N); for example, the yield response was related to increased N uptake in 'Tifton 85' bermudagrass (Haby et al. 2007).

In Georgia, the available soil K is highly prone to leaching, and the soil quickly becomes K deficient (Mikkelsen 2007). Bermudagrass is highly responsive to N fertilizers but also requires a considerable amount of K fertilizer for root and shoot growth. Bermudagrass consumes considerable amounts of nutrients from the soil. For the production of every 6 tons of bermudagrass hay, approximately 136 kg of N and 114 kg of K are removed from the soil (Lee et al. 2017). Similarly, it was reported that K levels decreased from 160 to 50 ppm in 3 yr under bermudagrass production (Nelson et al. 1983). Supplementing the soil with K fertilizer is critical because it improves plant health by helping plants to develop a better root system and to withstand the stress induced by disease and highly saline soils (Wang et al. 2013). Because K does not directly yield plant growth benefits as N does, turfgrass managers are reluctant to regularly supplement grass with K (Miller and Dickens 1996). Thus, the University of Georgia recommends the application of K at twice the rate of N in the fall season to combat disease problems. However, it is not clear whether high K levels in plant tissue can help reduce *S. frugiperda* pest incidence. Little is known about how plant nutrient levels influence the ability of turfgrass to resist *S. frugiperda* feeding in bermudagrass. Previously, Leuck et al. (1974) showed that the foliar application of K could repel *S. frugiperda* larvae; however, the effects on survival and development were not well documented. Thus, the objective of the current study was to determine whether K, as a stand-alone fertilizer and in combination with N, significantly affects the survival and development of *S. frugiperda* on bermudagrass.

Materials and Methods

Plant material and insects. In 2018 and 2019, experiments were conducted in the greenhouse and in environmentally controlled chambers at the University of Georgia Griffin Campus. Plugs of 'TifEagle' bermudagrass were obtained from a

turfgrass field in Griffin and were grown in 10.2×10.2 cm plastic pots in the greenhouse. The plugs were washed to remove soil and were planted in sand media. The grass pots were irrigated each day and fertilized at weekly intervals with 20:20:20 NPK at 5.9 g per L water (100 ml per pot). The plants were maintained at 25°C and ~60% relative humidity (RH) in the greenhouse. The *S. frugiperda* larvae used in the experiments were purchased from Benzon Research, Inc. (Carlisle, PA). After receiving the larvae from the rearing facility, the whole shipment box was placed in the laboratory at room temperature (21°C and ~40% RH) and was used for the experiment within a few hours.

Experimental design. In 2018 and 2019, N (urea) and K (muriate of potash) were applied at biweekly intervals from May to October. The treatments were different N:K ratios: (1) 0:0, (2) 1:0, (3) 2:1, (4) 1:1, (5) 0:1, and (6) 1:2, where 1 = 113.4 g N or K per 92.3 m². The treatments were replicated 10 times in 2018 and 14 times in 2019 in a randomized complete block design and were applied to the grass pots by foliar spraying using a CO₂-powered sprayer inside a spray chamber. After 5 mo, ~4–10 g of grass clippings were removed and transferred into a 29.6-ml clear plastic container (Frontier Agricultural Sciences, Newark, DE). The containers with fresh grass clippings were temporarily maintained in the refrigerator at 4°C to prevent desiccation before the introduction of *S. frugiperda* neonates.

Within 3 h, 3 neonates of *S. frugiperda* larvae were introduced to each container with grass clippings. After the introduction, each container was sealed using a lid and a parafilm strip around the lid to reduce desiccation. Fresh grass clippings were added to the containers at 2-d intervals. The uneaten grass clippings and frass were removed before adding fresh grass clippings to the containers. The experimental containers were maintained in an environmentally controlled chamber at 28°C, ~40% RH and a photoperiod of 16:8 h (L:D).

Evaluation. The survival and development of larvae were recorded at 2- or 3-d intervals until pupation. Dead larvae were identified as shriveled and darkened in color. To determine larval development, larval length and weight (2018 and 2019) and head capsule width (2019) were recorded. Larval length and head capsule width were measured using a Vernier caliper. Larval weight was measured using a digital balance. When there was more than 1 larva in the container, the measurements were averaged and recorded for the container. Additionally, length, width of the thorax region, and weight were recorded for pupae of the surviving larvae (in 2018, only the length and width were recorded). Foliage samples were collected for nutrient analysis when the adults emerged from all treatments. For the foliar nutrient analysis, leaf samples from 2 pots (2 replications) for each treatment were combined; thus, there were 5 samples per treatment in both years.

The grass clippings were oven-dried at 115°C for 48 h and then were transported to the Plant and Soil Testing Laboratory (University of Georgia, Athens, GA) for foliar nutrient analysis. Nutrients (Mn, Fe, Al, B, Cu, Zn, Na, Pb, Cd, Ni, Cr, Mo, P, K, Ca, and Mg) were analyzed using an inductively coupled plasma emission spectrograph (AOAC 1995, Isaac and Johnson 1985). The combustion method was used to quantify the total percent N (Colombo and Giazzi 1982).

Statistical analysis. All analyses were conducted using SAS software (SAS Institute 2012). The survival data from 2018 and 2019 were log-transformed ($\ln [x + 1]$) and then subjected to 1-way analysis of variance (ANOVA) using the PROC GLM procedure in SAS. The length of the larvae, the width of the head capsule, and

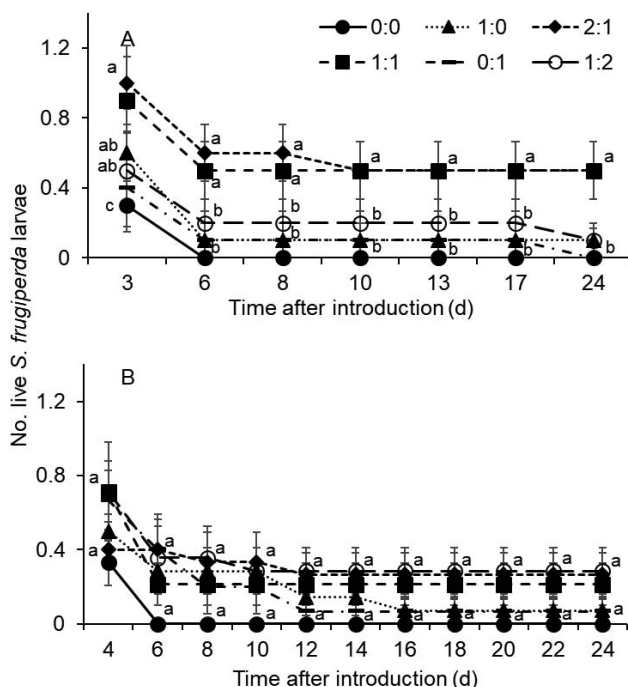


Fig. 1. Mean ($\pm$ SE) *S. frugiperda* larvae survival on various N and K ratio treatments in (A) 2018 and (B) 2019. Data points for each sample date with the same letter are not significantly different (LSD test, $\alpha = 0.05$).

the weight data were analyzed only for treatments that had at least 3 replications with live *S. frugiperda* larvae. In 2018, the data were analyzed by Student's *t* test using the PROC TTEST procedure in SAS, as only 2 treatments had live larvae; whereas, in 2019, ANOVA using the PROC GLM procedure in SAS was used after log-transformation ($\ln [x + 1]$), as there were more than 2 treatments with 1 or more live larvae. The percentage foliar nutrient data were arcsine square-root transformed before 1-way ANOVA was performed, whereas the foliar nutrient data in ppm (parts per million) were subjected to 1-way ANOVA using the PROC GLM procedure in SAS after log-transformation ($\ln [x + 1]$). Means were separated using the LSD method ($\alpha = 0.05$). Means and standard errors for the variables were calculated using the PROC MEANS procedure in SAS.

Results

Larval survival. In 2018, none of the larvae survived beyond 6 d after introduction in the 0:0 treatment where N and K were not applied (Fig. 1A). A significantly lower number of larvae survived in the 0:1, 1:2, 1:0, and 0:0 treatments than in the 2:1 and 1:1 treatments at 10 d ($F = 5.3$; $df = 5, 45$; $P < 0.001$; Fig. 1A) and 24 d ($F = 5.2$; $df = 5, 45$; $P < 0.001$; Fig. 1A) postintroduction. In 2019, the

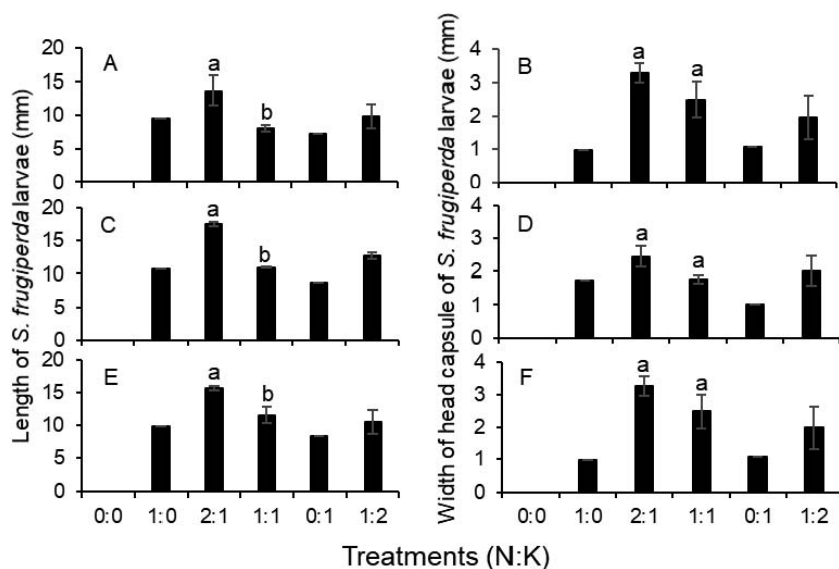


Fig. 2. Mean ($\pm$ SE) length of larvae (mm) and width of larval head capsule of surviving *S. frugiperda* larvae on various N and K treatments at (A and B) 6 d, (C and D) 8 d, and (E and F) 10 d after introduction. Bars with the same letter are not significantly different (paired *t* test, $\alpha = 0.05$). Bars without letters were not included in the analysis.

survival of larvae in the various treatments followed a similar pattern as in 2018. None of the larvae survived beyond 6 d in the 0:0 treatment (Fig. 1B). At 4 to 24 d postintroduction, the survival of larvae was not significantly different among the treatments ($P < 0.05$; Fig. 1B).

Larval development. In 2018, only 2 treatments had more than 3 replications with live *S. frugiperda*, so only these 2 treatments were compared. The larval length was greater in the 2:1 treatment than in the 1:1 treatment at 6 d ($t = 4.4$; $df = 9$; $P = 0.002$; Fig. 2A), 8 d ($t = 2.66$; $df = 8$; $P = 0.028$; Fig. 2C), and 10 d ($t = 3.1$; $df = 8$; $P = 0.015$; Fig. 2E) postintroduction. However, the width of the larval head capsule was similar in the 2:1 and 1:1 treatments at 6 d ($t = 1.38$; $df = 8$; $P = 0.2049$; Fig. 2B), 8 d ($t = 1.38$; $df = 8$; $P = 0.2049$; Fig. 2D), and 10 d ($t = 1.38$; $df = 8$; $P = 0.2049$; Fig. 2F) postintroduction.

In 2019, the larval length was not significantly different among treatments at 8 d ($F = 2.4$; $df = 4, 7$; $P = 0.146$; Fig. 3A), 10 d ($F = 2.9$; $df = 3, 8$; $P = 0.105$; Fig. 3D), 12 d ($F = 3.25$; $df = 2, 5$; $P = 0.125$; Fig. 3G), and 14 d ($F = 3.7$; $df = 2, 5$; $P = 0.103$; Fig. 3J) postintroduction. On day 16, the larval length was significantly lower in the 1:1 treatment than in the 2:1 and 1:2 treatments ($F = 21.7$; $df = 2, 5$; $P = 0.003$; Fig. 3M). Similarly, the width of the larval head capsule was similar among treatments at 8 d ($F = 1.5$; $df = 4, 7$; $P = 0.294$; Fig. 3B), 10 d ($F = 2.2$; $df = 3, 8$; $P = 0.163$; Fig. 3E), 12 d ($F = 2.9$; $df = 2, 5$; $P = 0.146$; Fig. 3H), 14 d ($F = 2.4$; $df = 2, 5$; $P = 0.183$; Fig. 3K), and 16 d ($F = 3.2$; $df = 2, 5$; $P = 0.127$; Fig. 3N) postintroduction. The mean weight of surviving larvae was not significantly different among treatments at 8 d ($F = 2.8$;

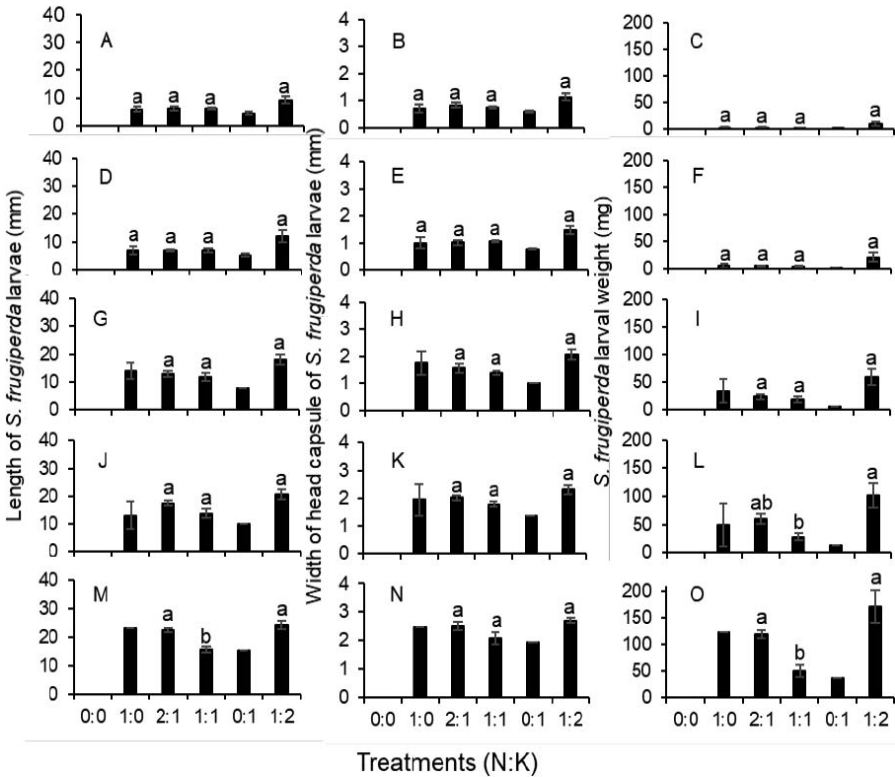


Fig. 3. Mean ($\pm$ SE) length of larvae (mm), width of larval head capsule, and larval weight (mg) of surviving *S. frugiperda* larvae on various N and K treatments at (A, B, and C, respectively) 8 d, (D, E, and F) 10 d, (G, H, and I) 12 d, (J, K, and L) 14 d, and (K, M, and N) 16 d after introduction. Bars with the same letter are not significantly different (LSD test, $\alpha = 0.05$). Bars without letters were not included in the analysis.

df=4, 7; $P=0.108$; Fig. 3C), 10 d ($F=2.6$; df=3, 8; $P=0.122$; Fig. 3F), and 12 d ($F=3.5$; df=2, 5; $P=0.111$; Fig. 3I) postintroduction. The larval weight was significantly lower in the 1:1 treatment than in the 1:2 treatments at 14 d postintroduction ($F=6.5$; df=2, 5; $P=0.041$; Fig. 3L), whereas at 16 d postintroduction, the larval weight was significantly lower in the 1:1 treatment than in the 2:1 and 1:2 treatments ($F=10.3$; df=2, 5; $P=0.0169$; Fig. 3O).

Nutrient analysis. The percentage of K in the leaves in 2018 was lower in the grass fertilized with the 0:0 and 1:0 treatments than that in the other treatments. However, it was similar in the 2:1, 1:1, 0:1, and 1:2 treatments ($F=15.2$; df=5, 20; $P<0.001$; Fig. 4A). The percentage of N in the leaves was greater in the 2:1 treatment than in the 1:1 and 1:2 treatments, followed by that in the 1:0 and 0:1 treatments. It was lowest in the 0:0 treatment ($F=8.5$; df=5, 20; $P<0.001$; Fig. 4B). In 2019, the percentage of K was significantly greater in the 1:1 treatment than in the other treatments ($F=3.1$; df=5, 20; $P=0.033$; Fig. 4C). However, the

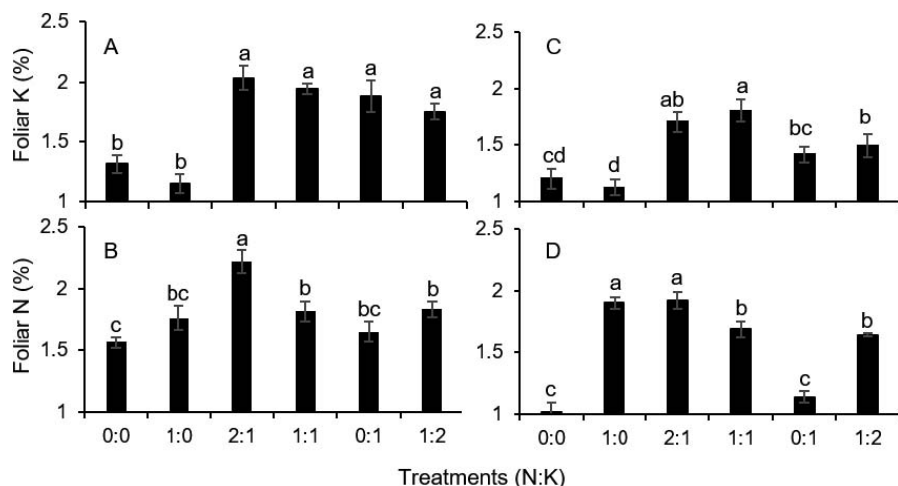


Fig. 4. Mean ($\pm$ SE) percentage of (A) K and (B) N in 2018 and (C) K and (D) N in 2019 in the foliage of treatments with various ratios of N and K after the conclusion of the experiment. Bars with the same letter are not significantly different (LSD test, $\alpha = 0.05$).

percentage of K was not significantly different between the 1:1 and 2:1 treatments or among the 2:1, 0:1, and 1:2 treatments. The grass fertilized with the 1:0 and 2:1 treatments had a greater percentage of N than the 1:1 and 1:2 treatments, followed by that in the 0:0 and 0:1 treatments ($F = 40.8$; $df = 5, 20$; $P < 0.001$; Fig. 4D).

In 2018, the percentage of Ca in the leaves was significantly greater in the 1:0 treatment than in the 1:2 treatment (Table 1). Similarly, the percentage of Mg in the leaves was significantly greater in the 1:0 treatment than in the 2:1, 0:1, and 1:2 treatments. The percentage of P in the leaves was significantly greater in the 0:0 and 0:1 treatments than in the 1:2 treatment. The concentrations of Al and Zn in the leaves were significantly greater in the 1:0 treatment than in the 0:0 treatment. However, S, B, Cr, Cu, and Mn were present in the leaves at similar quantities in all the treatments (Table 1). The concentration of Na in the leaves was significantly greater for in the 1:0 treatment and the 0:0 treatment than in the 1:1, 0:1, and 1:2 treatments and was the highest in the 1:0 treatment.

In 2019, the foliar nutrient analysis showed that the percentage of Ca was not significantly different among treatments (Table 1). The percentage of Mg was significantly greater in the 1:0 treatment than in the 1:2 treatment. The percentage of P was significantly greater in the 2:1 treatment than in the 1:2 and 1:0 treatments. The percentage of S was greater in the 1:1 treatment than in the 0:1 and 0:0 treatments. The concentrations of nutrients such as Al, B, and Mn were not significantly different among treatments. The Fe content was significantly greater in the 2:1 and 1:2 treatments than in the 0:0 treatment. Similarly, Cu was present at higher concentrations in the 1:0 and 2:1 treatments than in the 0:0 treatment. The concentration of Na was significantly greater in the 1:0, 2:1, and 1:1 treatments than in the 0:0, 0:1, and 1:2 treatments and was the highest in the 1:0 treatment. The

Table 1. Mean ($\pm$ SE) percentage or parts per million (ppm) of foliar nutrients in ‘TifEagle’ bermudagrass after foliar spraying of urea and muriate of potash from May to October 2018 and 2019.

Element	0:0	1:0	2:1	1:1
2018				
Ca	0.613 $\pm$ 0.022ab	0.702 $\pm$ 0.039a	0.595 $\pm$ 0.031ab	0.591 $\pm$ 0.044ab
Mg	0.184 $\pm$ 0.006ab	0.232 $\pm$ 0.009a	0.172 $\pm$ 0.008b	0.184 $\pm$ 0.015ab
P	0.219 $\pm$ 0.011a	0.195 $\pm$ 0.011ab	0.167 $\pm$ 0.016ab	0.183 $\pm$ 0.014ab
S	0.387 $\pm$ 0.015a	0.433 $\pm$ 0.011a	0.431 $\pm$ 0.017a	0.397 $\pm$ 0.017a
Al	13.9 $\pm$ 1.4b	30.4 $\pm$ 8.1a	17.8 $\pm$ 1.9ab	21.9 $\pm$ 1.9ab
B	2.9 $\pm$ 0.5a	4.1 $\pm$ 0.2a	3.4 $\pm$ 0.3a	3.9 $\pm$ 0.8a
Cr	1.29 $\pm$ 0.09a	1.83 $\pm$ 0.34a	1.37 $\pm$ 0.14a	1.62 $\pm$ 0.14a
Cu	10.2 $\pm$ 1.8a	8.7 $\pm$ 0.7a	6.3 $\pm$ 0.4a	8.0 $\pm$ 0.6a
Mn	65.0 $\pm$ 7.4a	86.8 $\pm$ 7.6a	80.7 $\pm$ 10.2a	78.2 $\pm$ 9.0a
Na	1443.9 $\pm$ 139.1b	2527.8 $\pm$ 298.8a	1099.9 $\pm$ 129.1bc	893.3 $\pm$ 111.3c
Zn	39.4 $\pm$ 1.6b	54.9 $\pm$ 4.9a	47.2 $\pm$ 1.5ab	43.7 $\pm$ 2.3ab
2019				
Ca	0.398 $\pm$ 0.044a	0.46 $\pm$ 0.023a	0.366 $\pm$ 0.027a	0.403 $\pm$ 0.005a
Mg	0.115 $\pm$ 0.014ab	0.137 $\pm$ 0.004a	0.113 $\pm$ 0.006ab	0.129 $\pm$ 0.006ab
P	0.157 $\pm$ 0.011ab	0.111 $\pm$ 0.004c	0.173 $\pm$ 0.011a	0.162 $\pm$ 0.009ab
S	0.215 $\pm$ 0.015c	0.278 $\pm$ 0.003ab	0.266 $\pm$ 0.008abc	0.318 $\pm$ 0.016a
Al	14.2 $\pm$ 2.2a	30.2 $\pm$ 10.5a	20.04 $\pm$ 2.8a	23.2 $\pm$ 4.6a
B	3.8 $\pm$ 0.6a	4.3 $\pm$ 0.25a	4.3 $\pm$ 0.25a	4.6 $\pm$ 0.22a
Fe	29 $\pm$ 2.03b	57.8 $\pm$ 8.52ab	104.1 $\pm$ 48.05a	50.81 $\pm$ 2.56ab
Cu	19.6 $\pm$ 2.15c	38.1 $\pm$ 4.38a	35.1 $\pm$ 4.01a	20.8 $\pm$ 0.88bc
Mn	37 $\pm$ 3.61a	36.6 $\pm$ 2.01a	49.6 $\pm$ 2.46a	41.5 $\pm$ 2.98a
Na	379.5 $\pm$ 37.5c	759.0 $\pm$ 27.7a	557.2 $\pm$ 43.1b	529.7 $\pm$ 22b
Zn	31.3 $\pm$ 4.15b	50.9 $\pm$ 4.65a	57.7 $\pm$ 3.67a	51.8 $\pm$ 3.65a

Means for Ca, Mg, P, and S are expressed as the total percentage concentration (of dry weight), whereas those for Al, B, Na, Cu, Fe, Mn, and Zn are in ppm. Means in the same row followed by different letters are significantly different ($P < 0.05$; LSD test). Analyses of variance were performed on the arcsine square root-transformed percentage data and log ($x + 1$) transformed ppm data. Cr data are only shown for 2018 and Fe data are only shown for 2019 because they were below detectable levels. Other elements, such as Ni, Mo, Pb, and Cd, were below detectable levels and hence are not presented.

Table 1. Extended.

0:1	1:2	<i>F</i>	df1, df2	<i>P</i>
0.591 ± 0.062ab	0.463 ± 0.028b	3.3	5, 20	0.023
0.169 ± 0.015b	0.138 ± 0.006b	7.5	5, 20	< 0.001
0.212 ± 0.017a	0.150 ± 0.009b	4.8	5, 20	0.005
0.360 ± 0.028a	0.347 ± 0.018a	3.2	5, 20	0.029
21.2 ± 2.2ab	20.7 ± 1.4ab	3.1	5, 20	0.029
3.1 ± 0.4a	2.5 ± 0.1a	1.9	5, 20	0.128
1.37 ± 0.17a	1.09 ± 0.02a	1.9	5, 20	0.128
7.6 ± 0.9a	6.7 ± 0.5a	2.4	5, 20	0.078
89.9 ± 7.8a	72.9 ± 6.0a	1.5	5, 20	0.226
820.6 ± 85.2c	706.9 ± 24.3c	21.5	5, 20	< 0.001
40.2 ± 3.4b	38.3 ± 2.7b	4	5, 20	0.011
0.408 ± 0.023a	0.347 ± 0.029a	1.72	5, 20	0.175
0.114 ± 0.004ab	0.096 ± 0.009b	2.79	5, 20	0.045
0.141 ± 0.005abc	0.127 ± 0.011bc	5.31	5, 20	0.002
0.25 ± 0.011bc	0.263 ± 0.021abc	5.56	5, 20	0.002
21.4 ± 2.3a	17.8 ± 1.7a	1.37	5, 20	0.278
3.7 ± 3a	4.0 ± 0.21a	1.22	5, 20	0.335
51.6 ± 2.59ab	58.8 ± 4.74a	4.39	5, 20	0.007
31.4 ± 2.84ab	25.7 ± 2.86abc	7.27	5, 20	0.0005
35.1 ± 2.95a	43.6 ± 5.58a	1.95	5, 20	0.13
364.2 ± 17.1c	373.7 ± 18.4c	19.02	5, 20	< 0.001
58.8 ± 5.06a	44.5 ± 3.06ab	6.11	5, 20	0.001

concentration of Zn was significantly greater in the 1:0, 2:1, 1:1, and 0:1 treatments than in the 0:0 treatment (Table 1).

Discussion

Past research has demonstrated the effects of crop nutrition on inherent plant resistance mechanisms and on the biological development of the insect pests

feeding on the plants (Amtmann et al. 2008, Leuck et al. 1974, Rashid et al. 2016). The majority of studies have shown that N supports (Altieri and Nicholls 2003, Scriber 1984) and K prevents the herbivory of insect pests (Amtmann et al. 2008). The results of the current study showed that N supported the development of *S. frugiperda* larvae, whereas K discouraged their development. In 2018, both the 2:1 and 1:1 treatments had a similar percentage of K in the plant tissues, but the percentage of N was greater in the 2:1 treatment (Fig. 2A, C, E), and *S. frugiperda* larval development was faster in the 2:1 treatment than in the 1:1 treatment. Similarly, in 2019, a greater percentage of K and lower N levels in the plant tissues were observed in the 1:1 treatment than in the 2:1 treatment (Figs. 3L, O, 4C, and D), and the development of *S. frugiperda* larvae was slower in the 1:1 treatment compared with that in the 2:1 treatment. The evidence from the 2018 and 2019 data suggests that K does not favor the survival and development of *S. frugiperda* larvae and that maintaining a higher level of K in plant tissues may help to reduce feeding damage from *S. frugiperda* larvae in bermudagrass. Previously, Wiseman et al. (1973) found that neonates of *S. frugiperda* larvae preferred corn foliage treated only with N fertilizer over corn foliage treated with P, K, and a combination of P and K. Additionally, larval mortality increased and weight gain was reduced when *S. frugiperda* larvae were fed on foliage treated with K.

The data show that the survival of *S. frugiperda* larvae was reduced to less than 1 after 6 d postintroduction. Although it is not exactly clear why the bermudagrass in the current study elicited high larval mortality in *S. frugiperda*, there are several possible reasons. In the current study, only 2 nutrients were applied to the bermudagrass in different ratios. Previously, increased survival of *S. frugiperda* larvae was observed on 'TifEagle' bermudagrass when all macronutrients were applied at the same level (Braman et al. 2000, 2003). In Braman et al. (2000), bermudagrass was fertilized with 250 mg/L of 20:20:20 NPK in laboratory studies, and 460.5 kg/ha of 13:13:13 NPK was applied in a field study (Braman et al. 2003). In another study, the survival and development of *S. frugiperda* were enhanced on millet plants treated with all 3 macronutrients (N, P, and K) compared with those on millet treated with 1 or 2 nutrients (Leuck 1972). These studies suggest that the lower survival of *S. frugiperda* larvae observed in the current study could be related to the absence of all 3 macronutrients and the low levels of N fertilizer applied to the bermudagrass. Another reason could be related to the sand medium used in the current study, which can minimize the availability of other essential nutrients to the plant tissue. One principal constituent of sand is silica (Si), which can alter the plant's resistance response to herbivorous insects through a myriad of direct and indirect pathways (Reynolds et al. 2009). Elevated levels of Si in plant tissues increase the hardness and abrasiveness of epidermal cells, leading to reduced digestibility for insects feeding on them (Panda and Khush 1995). In other studies, reduced consumption was noted on plant tissues with high levels of Si, which led to high mortality rates, reduced larval growth, and reduced adult fecundity (Chu and Horng 1991, Djamin and Pathak 1967, Horng and Chu 1990, Salim and Saxena 1992). Thus, the high Si content in the grass tissues could be another factor causing the high mortality of *S. frugiperda* larvae in the current study.

The results show that the micronutrient levels varied in plant tissues that received various ratios of N and K. In previous studies, various soil micronutrients, such as S, B, Mg, Mn, Al, and Fe, were associated with the development and

reproduction of spotted alfalfa aphid, *Therioaphis maculata* (Buckton) (Kindler and Staples 1970), whitebacked planthopper, *Sogatella furcifera* (Horváth) (Salim and Saxena 1992), and hemlock woolly adelgid, *Adelges tsugae* (Annand) (Hemiptera: Adelgidae) (Joseph et al. 2011). In this study, sand was used as the growth medium, and no other micronutrients were applied. All the micronutrients found in the plant tissue were present before the experiment began. It is not clear from the data whether those varying levels of certain micronutrients influenced the survival or development of *S. frugiperda* larvae.

In summary, the results show that high levels of K in bermudagrass can affect the development of *S. frugiperda* under controlled conditions. However, the survival and development of *S. frugiperda* larvae tend to improve with high levels of N in the foliage. More research is warranted to establish optimized K and N levels that favor grass growth but reduce susceptibility to *S. frugiperda* larval survival and development under field conditions. Additionally, varying levels of essential micronutrients were observed in the grass tissues that received the various N and K treatments, which suggests that future studies are needed to determine how micronutrients influence the availability of N and K and ultimately affect the survival and development of *S. frugiperda* larvae. The current study showed that optimized N and K application could become an important tool in integrated pest management programs for *S. frugiperda*.

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