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Short-horned grasshopper subfamilies feed at different rates on big bluestem and switchgrass cultivars

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Abstract: Grasshopper species belonging to subfamilies Melanoplineae, Gomphocerinae and Oedipodinae were tested for their feeding rate on three types of grass. All grasshopper species were offered Shawnee and Kanlow cultivars of switchgrass, *Panicum virgatum* L. and big bluestem, *Andropogon gerardii* Vitman. The grasshoppers, *Melanoplus femurrubrum* and *Melanoplus differentialis* were also tested for their feeding on turgid or wilted leaves of the Shawnee cultivar of switchgrass. We found that *M. differentialis* consumed more switchgrass compared to big bluestem while *M. femurrubrum* and *Arphia xanthoptera* consumed the most Shawnee switchgrass. The *M. differentialis* consumed more turgid grass compared to wilted switchgrass. The feeding performances show differences among grasshopper species even in the same subfamily and suggest that Melanoplineae grasshoppers may become destructive pests of switchgrass planted for biofuel production.

Key words: grasshopper; switchgrass; biofuel; leaf consumption; insect herbivore

Introduction

In the central Great Plains, introduced cool season grasses and crop residues provide most of the fall and spring grazing (Krueger & Curtis 1979), while summer cattle grazing demands high quality perennial grasses. A number of warm season grasses, including switchgrass (*Panicum virgatum* L.), big bluestem (*Andropogon gerardii* Vitman), indiagrass [*Sorghastrum nutans* (L.) Nash] and little bluestem [*Schizachyrium scoparium* (Michx.) Nash] provide summer forage. Switchgrass and big bluestem, are native to the central Great Plains (Mitchell et al. 1997) have determinate growth and have a single growth flush in summer.

Switchgrass can adapt to a variety of environmental conditions and is geographically widespread (Parrish & Fike 2005). It has been recognized to be useful not only for wildlife but also in maintaining stream banks and as a buffer strip (Parrish & Fike 2005). Switchgrass can be grown on soils with moderate fertility and could be a suitable alternative pasture crop in areas facing regular droughts. Switchgrass also represents an emerging bioenergy crop and has been divided into upland and lowland cultivars based on habitat, genetics and morphological characteristics (Porter 1966). Low-

land cultivars have the ability to establish in flooded conditions while upland cultivars require moderate soil moisture conditions (Hefley 1937). Besides water requirements, the cultivars differ in nitrogen needs for their growth (Vogel 2004) while soil pH, carbon and other soil parameters also vary to some extent between these cultivars (McLaughlin et al. 1999).

To use switchgrass widely for feed-stock and biomass energy development, information about its productivity and potential pests (McLaughlin & Walsh 1998) is required. Much work has focused on improving biomass yield and weed control (Parrish & Fike 2005) for switchgrass and like other warm season grasses that have higher photosynthetic rates at high temperatures switchgrass is characterized by efficient use of nitrogen (Waller & Lewis 1979) and phosphorus (Morris et al. 1982) making it a potentially desirable for large scale production. Creating a monoculture of any plant species can cause development of serious economic pests of that crop (Andow 1991). However, very few studies of herbivory by insects on switchgrass have been conducted (Parrish & Fike 2005).

More than 100 species of short-horned grasshoppers have been reported in Nebraska (Brust et al. 2008) with about eight occurring in high enough densities

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to potentially be serious pests in rangeland. Although most grasshopper species feed on a variety of plants (Joern 1983), species tested to date show plant species preferences when choices are available (Joern 1979). However, grasshopper selection among individual plants and plant tissues of a single species has been less-studied (Lewis 1984).

In this study, we quantified feeding by the amount of tissue consumed by *Melanoplus femurrubrum* (De Geer, 1773), *Melanoplus differentialis* (Thomas, 1865), *Arphia xanthoptera* (Burmeister, 1838), *Eritettix simplex* (Scudder, 1869) and *Psoloessa delicatula* (Scudder, 1876). These species were offered switchgrass cultivars (Kanlow and Shawnee) and big bluestem. We also tested feeding by *M. femurrubrum* and *M. differentialis* on healthy or wilted Shawnee switchgrass.

Material and methods

Feeding performance among switchgrass cultivars and big bluestem

We quantified the feeding performance of five grasshopper species belonging to subfamilies Melanoplineae (*M. femurrubrum*, *M. differentialis*), Gomphocerinae (*A. xanthoptera*, *E. simplex*) and Oedipodinae (*P. delicatula*). The grasshopper species, *M. femurrubrum*, *M. differentialis* and *A. xanthoptera* were collected from the University of Nebraska-Lincoln NE and Holmes Lake recreation area, approximately 14 km south of the University of Nebraska-Lincoln. The species, *E. simplex* and *P. delicatula* were collected near Chadron, Nebraska. The grasshoppers were kept in a greenhouse at the University of Nebraska at 25 °C prior to starting the trials. Adults were starved for two days before the experiment. The switchgrass cultivars and big bluestem were collected from the Agricultural Research and Development Center (ARDC) at Mead, NE, about 50 km north of Lincoln, NE. Healthy switchgrass and big bluestem were dug up along with roots and transferred to pots filled with soil. Grasshoppers were provided Shawnee (upland cultivar), Kanlow (lowland cultivar) switchgrass or big bluestem. Sections of each grass were cut to 15 cm long sections from the blade tip, weighed to the nearest 0.01 g and individually placed into a water pick. Single grasshoppers of each species were placed into a mesh enclosure that contained a pot filled with sand and the water pick containing one type of grass (Whipple et al. 2009). There were 24 replicates of *M. femurrubrum*, seven of *M. differentialis*, six of *A. xanthoptera* and 10 for *E. simplex* and *P. delicatula* for each grass. Grasshoppers were allowed to feed on these grasses for three days. A total of six pots were also prepared, two for each grass type but without grasshoppers to serve as controls. At the end we quantified the amount of feeding for each grass by each grasshopper species. Two-way analysis of variance and pairwise multiple comparison tests (Holm-Sidak method) were performed using SigmaPlot (Systat Software, San Jose, CA).

Feeding preference for turgid and wilted switchgrass

Adult *M. femurrubrum* and *M. differentialis* were collected in late August of 2011 using a sweep net from fields of the University of Nebraska-Lincoln, NE. The grasshoppers were kept in a greenhouse at the University of Nebraska at 25 °C prior to starting the trials. Adults were starved for two days before the experiment.

Samples of the switchgrass cultivar Shawnee were collected from the Agricultural Research and Development Center (ARDC) at Mead, NE, about 50 km north of Lincoln, NE. Healthy green plants of approximately the same size were dug up along with roots using a shovel and transferred to plastic pots. These pots were then transferred to the greenhouse and maintained with sufficient water to prevent dehydration. The pots used for the wilted condition were not given water for two days before the experiment.

Individually caged grasshoppers were offered a choice between adjacent dry and turgid leaves for three days. Leaf sections of approximately 15 cm were weighed to the nearest 0.01 g and placed into a small plastic pot. The turgid leaves were supplied with water to maintain the water level for tissue while no water was supplied for wilted sections. Both turgid and wilted grasses were kept together within the pot covered with mesh cloth. Eight replicates for each grasshopper species were made. After three days, the plants were removed and reweighed. Clippings that had fallen to the bottom of container were identified by texture and appearance and were weighed and included in the totals of mass remaining after feeding. For mass change associated with the water uptake or loss, four pots, two for each condition, were prepared in the same manner as the experimental groups, but without a grasshopper. Gain in mass was interpreted as water uptake by the leaves. A two-way analysis of variance test and pairwise multiple comparison tests (Holm-Sidak method) were performed using SigmaPlot (Systat Software, San Jose, CA).

Results

Feeding performance among Shawnee, Kanlow and Big bluestem

There was no weight loss of any grass observed in control treatments. The mean water uptake for Shawnee was 75 mg, Kanlow 60 mg and big bluestem 12 mg. All three grasses ranged from approximately 1% to 7% in water uptake. We found statistically significant ($P < 0.05$) mass gain in control treatments. Tukey HSD test showed no significant difference in water uptake between switchgrass cultivars, Shawnee and Kanlow, but both were greater than big bluestem. Thus, we subtracted the mean uptake of water for each grass at the end of experiment when we weighed the grasses after three days of feeding.

We found statistically significant interactions of grasshopper and grass ($P < 0.001$) (Table 1). The mean amount consumed per day by *M. differentialis* was greater for Shawnee at 234.05 mg/day, while for Kanlow *M. differentialis* consumed about 139.52 mg/day. Among all grasshopper species, *E. simplex* consumed the least Shawnee (12.73 mg/day) but consumed the most big bluestem. Other grasshopper species in this study fall in between these two species in consumption (Fig. 1). We found statistically significant differences in pairwise comparison of *M. differentialis* with *M. femurrubrum*, *P. delicatula*, *E. simplex* and *A. xanthoptera* ($P < 0.01$). All other pairwise comparisons were not significant. When we grouped grasshopper species to their respective subfamilies and analyzed the data, significant interaction between sub-

Table 1. Summary of analysis of variance for feeding performances based on grasshopper species and grass. Significant interaction effect between grass and grasshopper species was found.

Source of Variation	Df	SS	MS	F	P
Grasshopper	4	201841.496	50460.374	57.845	<0.001
Grass	2	43253.845	21626.922	24.478	<0.001
Grasshopper × Grass	4	151137.329	18892.166	21.657	<0.001
Residuals	156	136084.849	872.339		

Table 2. Summary of analysis of variance for feeding performances based on grasshopper subfamilies (Melanoplinae, Gomphocerinae, Oedipodinae) and grass.

Source of Variation	Df	SS	MS	F	P
Subfamily	2	29570.67	14785.33	6.22	0.002
Grass	2	15056.50	7528.25	3.17	0.045
Subfamily × Grass	4	74445.65	18611.41	7.83	< 0.001
Residuals	162	385047.35	2376.84		

Table 3. Mean amount of consumption (mg/day/grasshopper) ± SE by grasshoppers belonging to subfamilies Gomphocerinae, Melanoplinae and Oedipodinae on switchgrass cultivars (Shawnee and Kanlow) and big bluestem.

	Big Bluestem	Kanlow	Shawnee
Gomphocerinae	46.95 ± 10.90a	28.00 ± 10.90a	15.58 ± 10.90b
Melanoplinae	18.28 ± 8.75a	55.05 ± 8.75a	97.54 ± 8.75a
Oedipodinae	15.22 ± 19.90a	27.77 ± 19.90a	52.72 ± 19.90a

Explanations: Means (± SE) in the same column bearing different letters are significantly different ($P = 0.05$).

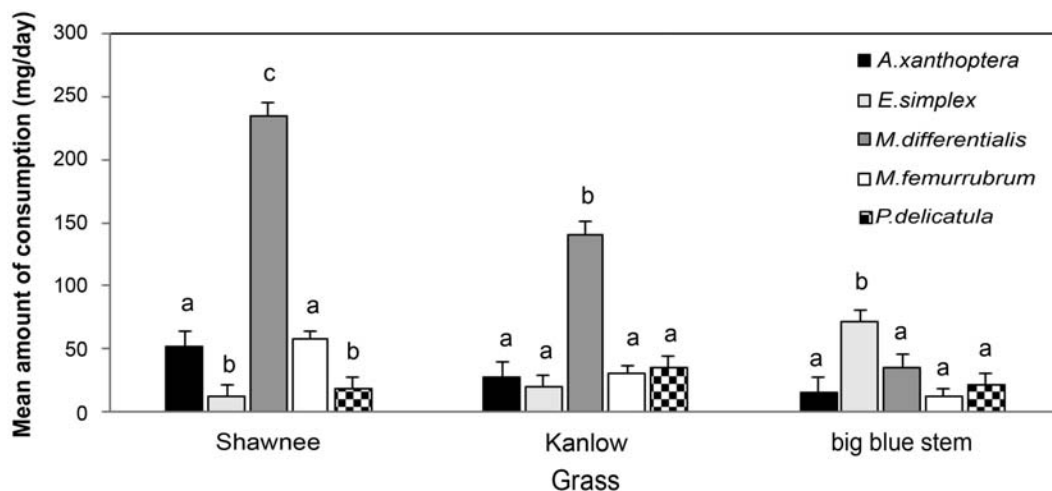


Fig. 1. Mean consumption (mg/day/grasshopper) ± SE by grasshoppers, *A. xanthoptera*, *E. simplex*, *M. differentialis*, *M. femurrubrum* and *P. delicatula* on grasses Shawnee, Kanlow and big bluestem. Different letters on group of bars show significant difference ($P = 0.05$).

family and grass was found (Table 2). The subfamily Melanoplinae consumed the maximum observed amounts of Shawnee (97.55 mg/day) and Kanlow (55.05 mg/day) while Gomphocerinae consumed about 46.95 mg/day of big bluestem. Oedipodinae consumed more Shawnee (52.72 mg) and the least amount of big bluestem (Table 3).

There was a statistically significant difference ($P = 0.03$) for feeding on wilted versus healthy grass by *M. differentialis* (Table 4). Although the interaction of grasshopper and plant condition was non-significant

($P = 0.109$), *M. differentialis* and *M. femurrubrum* differed significantly in their feeding, while plant condition showed statistically marginal differences (Table 4). *Melanoplus differentialis* fed more both on turgid than wilted switchgrass while no difference was observed for *M. femurrubrum* (Fig. 2).

Discussion

In our laboratory study conducted in August when switchgrass is mature and plant nutritional quality is

Table 4. Summary of analysis of variance for feeding preferences based on grasshopper species and condition (turgid and wilted) of Switchgrass cultivar, Shawnee. Grasshopper species significantly differ for feeding.

Source of Variation	Df	SS	MS	F	P
Grasshopper	1	17892.03	17892.03	4.95	0.03
Plant Condition	1	14878.17	14878.17	4.12	0.05
Grasshopper × Plant Condition	1	9917.07	9917.07	2.74	0.11
Residuals	28	101167.96	3613.14		

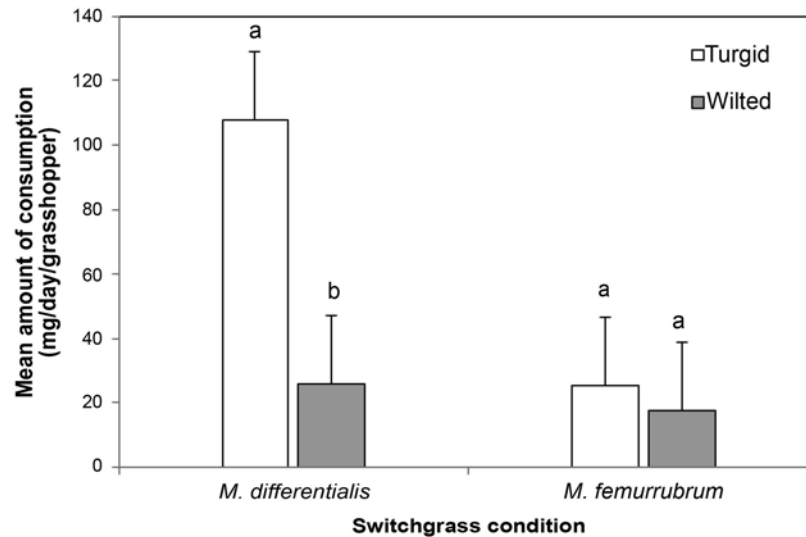


Fig. 2. Mean amount of consumption (mg/day/grasshopper) \pm SE of grasshoppers, *M. differentialis* and *M. femurrubrum* on turgid and wilted grass condition of Shawnee. Different letters on each bar pair indicate significant difference ($P = 0.05$).

declining, the tested grasshoppers belonging to three subfamilies ate all three types of grass (Fig. 1). Despite being housed in similar conditions with no choice of plant to consume, significant differences were observed among species and subfamilies tested (Tables 1, 3) with the Melanoplinae and Oedipodinae consuming more switchgrass and the Gomphocerinae consuming more big bluestem (Table 3). Of the species tested, *Melanoplus differentialis* ate relatively large amounts of the Shawnee cultivar (230 mg/day), and is most likely among the species tested to cause economic loss to switchgrass. *Melanoplus femurrubrum* and *A. xanthoptera* also consumed slightly more of the Shawnee cultivar than big bluestem or the Kanlow cultivar, while *E. simplex* was the only species that consumed more big bluestem than switchgrass (Fig. 1).

Nutritional quality of the host plants may have a role in the amount of feeding as the nutritional value of the host plant and grasshopper growth and reproduction have been found to be directly proportional (Mulkern 1967). In general, insect herbivores prefer C_3 plants over C_4 plants for their feeding (Caswell et al. 1973). Previously, Whipple et al. (2009) found the preference of some Nebraska grasshopper species for non-native cool season grasses over native C_4 grasses. Generally, warm season plants have proteins and carbohydrates which are embedded in thick cell walls while C_3 cells are more easily digested (Caswell & Reed 1976). Thus it can be hypothesized that chewing insects would pre-

fer more nutritive C_3 plants. In cage experiments, *Ageneotettix deorum* (Scudder, 1876) that were offered a choice of C_3 and C_4 grasses from the Nebraska Sandhills preferred C_3 grasses. However, a contradictory result was found when a natural population of *A. deorum* was tested (Heidorn & Joern 1984). This may be the result of having more C_4 grass available for feeding in the later study or could be the result of declining plant condition for the C_3 grasses.

The Shawnee cultivar is characterized as providing excellent forage quality and being drought resistant. The early growth stages in switchgrass are more nutritive, but its nutritive values drop rapidly after the seed head emergence in late July or early August (Moser & Vogel 1995). In Nebraska, switchgrass has higher crude protein than big bluestem. In one study, switchgrass crude protein contents were high in early June (17.5%) and decreased to 11.4% in late June and 8.4% by mid-July (Newell 1968). In Nebraska, big bluestem had crude protein around 14.4% in early June and 10.6% in late June (Newell & Moline 1978) with further decreases later in the season. Our feeding trials were conducted in a greenhouse with adult grasshoppers. It is likely that switchgrass cultivars had higher protein than big bluestem although these characters were not measured in this study.

Secondary toxic plant chemicals often act as a barrier or serve as deterrent against grasshopper herbivory (Bernays et al. 1977), however, grasses have limited

chemical defenses (Bernays 2001) and it is unlikely that switchgrass varieties vary substantially in chemistry, and thus, the high feeding rates on Shawn by *M. differentialis* are not likely explained by chemistry. Switchgrass matures later in the growing season than big bluestem, thus switchgrass typically has higher quality (Newell 1968) when harvested on the same date. The observed higher feeding rates of Melanoplineae and Oedipodinae may be a result of higher nutritional food quality of switchgrass as compared to big bluestem. However the higher consumption rate of big bluestem by *E. simplex* suggests that nutrition alone does not explain our results.

Although it is primarily a forb feeder *M. differentialis* can also feed on grasses and field observations have revealed grasshoppers feeding on plants that exhibit water stress. This species has been previously shown to feed on wilted or damaged sunflower (Lewis 1984) and other plant species (Lewis 1979). Kaufmann (1968) reported feeding of *M. differentialis* on desiccated plants even in the presence of fresh plants. Others reported preference for dead (Gangwere 1961), wilted (Kaufmann 1968), or succulent tissue. In our study, *M. differentialis* ate more turgid switchgrass (approximately 100 mg/day) than wilted switchgrass (25 mg/day). In contrast, *M. femurrubrum* did not differentiate between turgid and wilted switchgrass (Fig. 2). These results should be further investigated because they may vary seasonally or depend on environmental conditions such as humidity and rainfall.

Short-horned grasshoppers (Orthoptera: Acrididae) are the most important insect pests of rangelands in the United States (Rodell 1977; Olfert & Weiss 2002; Pfadt 2002; Vermeire et al. 2004). Grasshoppers are estimated to consume between 21% and 23% of available range forage in the western United States annually (Hewitt & Onsager 1983), with an estimated \$400 million economic impact (Hewitt & Onsager 1983). These estimates do not include additional damage from clipping of vegetation (Mitchell & Pfadt 1974).

Approximately twelve grasshopper species are economically important for crops and rangeland in the western U.S. (Brust et al. 2008). Most grasshopper species are generalist feeders, although some specialist exist (Mulkern 1967). The members of the subfamily Melanoplineae have broader diet breadth relative to Oedipodinae, which are mostly grass feeders and the Melanoplineae can cause economic losses to pasture and field crops. In Nebraska, *M. differentialis* and *M. femurrubrum*, have the ability to damage a variety of crops including soybean, maize and alfalfa (Pfadt 1994). It is likely that Melanoplineae species also have the potential to cause economic losses to switchgrass.

Besides orthopteran insects, Lepidoptera including stem borers pose threats to grasses and in general for graminaceous plants (White et al. 2005). Grass loopers (*Mocis* spp.) and fall armyworm [*Spodoptera frugiperda* (J. E. Smith, 1797)] are major pests in different grass species, and may contribute to economic losses. Previous research has identified and reported insects feed-

ing on switchgrass including thrips (Gottwald & Adam 1998), the yellow sugar cane aphid and grasshoppers, but not as preferred hosts (Parrish & Fike 2005). Holguin (2010) also studied switchgrass for insect dynamics and their effect on switchgrass yield.

Seasonal variation and other factors may alter the chemical composition and nutritional value of plants and can result in switching of herbivores from one plant species to another. Differences in grass maturity and succulence could result in preference for local grasshopper feeding (Chu & Knutson 1970). Chu and Knutson (1970) tested the preference of a number of grasshoppers to different grasses and found that adult *P. nebrascensis* preferred mature switchgrass over big bluestem while *M. differentialis* also preferred switchgrass over others.

Plant productivity can be greatly influenced by insect herbivory, especially when grasshopper densities are high. However, the net effect of herbivory has been shown to be positive in some situations (Dyer et al. 1982) and negative in others (Belsky 1986). Presently, the influence of insect herbivores on dominant grasses is not clearly understood. Parrish and Fike (2005) reported few insects in switchgrass and Vogel (2004) found the potential for negative effects of grasshoppers on switchgrass biomass production. This study provides evidence that grasshoppers, especially *Melanoplus*, may cause economic losses. However, additional field research will be required to determine the likelihood of economic damage caused by grasshoppers feeding on switchgrass.

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