

Effect of Switchgrass Ecotype and Cultivar on Establishment, Feeding, and Development of Fall Armyworm (Lepidoptera: Noctuidae)

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Abstract

As interest in production of second-generation biofuels increases, dedicated biomass crops are likely to be called upon to help meet feedstock demands. Switchgrass (*Panicum virgatum* L.) is a North American native perennial grass that as a candidate biomass crop, combines high biomass yields with other desirable ecosystem services. At present, switchgrass is produced on limited acres in the United States and experiences relatively minor insect pest problems. However, as switchgrass undergoes breeding to increase biomass yield and quality, and is grown on more acres, insect pest pressure will probably increase. To investigate how currently available switchgrass ecotypes and cultivars may influence herbivory by generalist insect herbivores, we performed feeding trials using neonate and late-instar fall armyworm [*Spodoptera frugiperda* JE Smith (Lepidoptera: Noctuidae)]. No-choice feeding experiments were used to explore how switchgrass varieties influence larval establishment, consumption levels, and life-history traits in contrast to a preferred host, corn (*Zea mays* L.). Neonate *S. frugiperda* consumed greater amounts of corn than switchgrass and increased amounts of upland versus lowland ecotypes. Late-instar larvae, which do the majority of the larval feeding, exhibited lower consumption of lowland ecotypes, which led to increased development time and reduced pupal weights. The exception to these trends was the upland cultivar ‘Trailblazer’, which unexpectedly performed similarly to lowland cultivars. These results suggest that both switchgrass ecotype and cultivar can influence feeding damage by a common generalist herbivore. These findings can be used to help inform current switchgrass planting decisions as well as future breeding efforts.

Key words: bioenergy cropping systems, switchgrass herbivory, plant breeding

Switchgrass (*Panicum virgatum* L.) is a perennial C₄ grass native to much of the central and eastern United States (Casler 2012). An ecologically important prairie plant, switchgrass has also been bred for forage production and, more recently, as a model bioenergy feedstock (Wright et al. 1993). Switchgrass has several advantages as a biomass crop including its large native range (Parrish and Fike 2005), effective use of nutrients (McLaughlin and Walsh 1998), and high biomass yields, even on marginal lands (Fike et al. 2006, Schmer et al. 2008). Another benefit is that switchgrass is generally resistant to insect herbivory, although when planted as monocultures grasses may become more susceptible to pest outbreaks (Tschamtko and Greiler 1995). Indeed, as more switchgrass has been planted as part of breeding efforts in the United States, several insect pests of

switchgrass have been identified (Prasifka et al. 2010; Calles Torrez et al. 2013, 2014). Moreover, as high-yielding cultivars of switchgrass are developed, selection for increased growth rate may lead to reduced plant defenses (Herms and Mattson 1992). Insects that feed on switchgrass and may emerge as pests include thrips (Thysanura; Gottwald and Adam 1998), grasshoppers (Orthoptera; Casler et al. 2004), aphids (Aphididae; Bradshaw et al. 2010, Schrottenboer et al. 2011, Burd et al. 2012), leafhoppers (Cicadellidae; Holguin et al. 2010), and lepidopteran (Lepidoptera) larvae (Prasifka et al. 2009, 2011b; Calles Torrez et al. 2013).

An important factor in switchgrass breeding is consideration of parental ecotype, a term used to differentiate between forms in a species adapted to different environmental conditions (Gregor 1944,

Turrill 1946). At present, two major ecotypes of switchgrass (upland and lowland) are commonly acknowledged in North America (Porter 1966, Newell 1968, Brunken and Estes 1975, Parrish and Fike 2009) though this understanding is evolving (Lowry et al. 2014). Switchgrass ecotypes vary in appearance, with upland ecotypes having thinner, more numerous shoots and thin green leaves, whereas lowland varieties typically have a blue-hue throughout, rough leaves, and fewer but thicker tillers (Porter 1966, Cortese et al. 2010, Zhang et al. 2011). Upland ecotypes are typically octoploid and lowlands typically tetraploid, although there are exceptions, including the tetraploid upland cultivar ‘Summer’, included in this study (Brunken and Estes 1975, Martinez-Reyna et al. 2001, Zhang et al. 2011). Many recognized lowland ecotypes have southern origins, whereas many upland types originate from more northerly latitudes. Thus, lowland ecotypes often have longer growing seasons and produce higher yields but may have poor winter survival in northern regions (Lemus et al. 2002, Alexopoulou et al. 2008, Wullschlegler et al. 2010); in contrast, upland ecotypes are generally better adapted to higher latitudes and drier sites (Casler et al. 2004). How insect herbivory of switchgrass may be influenced by ecotype is poorly known, as previous work has focused on one ecotype at a time (Dowd and Johnson 2009; Prasifka et al. 2009, 2011a).

The fall armyworm [*Spodoptera frugiperda*] JE Smith (Lepidoptera: Noctuidae) is a generalist noctuid whose larvae feed on more than 60 plant species, with a noted preference for grasses (Poaceae; Luginbill 1928). In the United States, the fall armyworm overwinters at southern latitudes and adults move northward over the growing season aided by air currents and storms (Alton 1979, Flanders et al. 2011). In the northern United States, fall armyworm is an occasional pest of sweet corn (Flanders et al. 2011, Bohnenblust and Tooker 2012). As a widespread generalist pest, fall armyworm has been used as model species to investigate host plant and cultivar impacts on insect feeding and development. Previously, fall armyworm larval development and mortality has been evaluated for differential responses to feeding on cultivars of peanuts (Leuck and Skinner 1971), corn (Pair et al. 1986a), several types of turf grasses (Leuck and Skinner 1970, Braman et al. 2000, Hong et al. 2015), and wild grasses (Pencoe and Martin 1981). The effects of switchgrass ecotypes and cultivars on fall armyworm performance are less

well known. Prasifka et al. (2009) showed that fall armyworm survived through pupation on switchgrass at rates similar to that of Bermuda grass, a host on which fall armyworm is a known economic pest (Leuck et al. 1968, Prasifka et al. 2009). Dowd and Johnson (2009) showed that across six upland cultivars, neonate fall armyworm mortality during initial establishment was minimal; however, subsequent leaf consumption varied significantly by cultivar.

Here, we use fall armyworm as a model to investigate how differences among switchgrass cultivars may influence the survival, feeding patterns, and development of a generalist insect herbivore. We compared rates of neonate establishment and herbivory on corn (*Zea mays* L.), a known host plant for fall armyworm, versus 16 switchgrass cultivars representing a range of ecotypes and breeding histories. We further compared developmental rates and survival of late-instar fall armyworm on a subset of eight switchgrass cultivars. Based on ecotype differences in leaf traits, we hypothesized that southern lowland switchgrass, which have tougher, more structurally defended leaves, would be less favorable hosts for fall armyworm than northern upland cultivars/populations. Specifically, we predicted that on southern lowland switchgrass fall armyworm would consume less leaf area, develop more slowly, and experience greater mortality.

Materials and Methods

Plants

Switchgrass cultivars for all tests were established from seed and transplanted into the field in spring of 2014 (Table 1). Seeds were cold stratified in distilled water at 4°C and germinated in plug trays (X-72PS, Landmark Plastic Corp, Akron, OH) under high light conditions (16:8 [L:D] day length) in a plant growth chamber at 26°C for 2 wk. Trays were then moved to a greenhouse until seedlings were approximately 0.3 m tall and then acclimated to outdoor conditions in an outdoor courtyard for 1 wk. In mid-June 2014, plants were transplanted to a field (alfisol soil, Marlette sandy loam) at the Michigan State Entomology Farm (East Lansing, MI). The experiment was established as a randomized complete block design with each cultivar represented by two plants grown within 1 m² plots in each of four blocks. Plots were separated by 2 m in all directions by

Table 1. Sources and characteristics of switchgrass cultivars used to assess feeding by fall armyworm *Spodoptera frugiperda*

Variety	Code	Release year	Ecotype	Ploidy ¹	State of origin ²	Seed source
Alamo	ALAM	1978	Lowland	4x	Texas	Ernst Seed
Blackwell	BLCK	1973	Upland	8x	Oklahoma	Ernst Seed
BoMaster	BOMA	2006	Lowland	4x		Ernst Seed
Cave-in-Rock	CIRA	1973	Upland	8x	Illinois	Star Seed
EG 1101	E111	2010	Lowland	4x		Ceres, Inc.
EG 1102	E112	2012	Lowland	4x		Ceres, Inc.
High Tide	HIGH	2012	Upland	NA	Maryland	Cape May Plant Materials Center
Kanlow	KANL	1963	Lowland	4x	Oklahoma	Ernst Seed
Kanlow N1 Syn 2	KLN1	Unreleased	Lowland	4x		Ken Vogel, USDA
MI genotype	MWF		Upland	NA	Michigan	Michigan Wildflower Farm
NE Summer Late Maturity	NBSL	Unreleased	Upland	4x		Ken Vogel, USDA
Performer	PERF	2006	Lowland	4x		Ceres, Inc.
Shawnee	SHAW	1996	Upland	8x		Ernst Seed
Shelter	SHEL	1986	Upland	8x	West Virginia	Ernst Seed
Summer	SUMM	1963	Upland	4x	Nebraska	Ernst Seed
Trailblazer	TRLB	1984	Upland	8x	Nebraska and Kansas	Sharp Brothers Seed

Cultivars highlighted in gray were included in both the fall armyworm neonate and late-instar larvae experiments.

¹Ploidy levels are unknown for wild-type switchgrass varieties.

²State of origin refers to area where germplasm was originally collected.

a buffer of mown turf grass. Within all plots, weeds were controlled by a combination of hand weeding and hand-wand applied herbicide (glyphosate). Plots were fertilized each spring at a rate of 50 kg/ha of nitrogen. For comparison in feeding trials, we grew sweet corn, variety 'Golden Bantam' (Burpee Seeds, Warminster, PA) in 11.4 cm² plastic pots (DSQVP45PFD, Dillen Products, Middlefield, OH) in potting soil in the greenhouse in May 2015. Seedlings were then transplanted into larger pots (Classic 800s Pots, Nursery Supplies Inc., Chambersburg, PA) and moved into an outdoor courtyard where they were watered daily until used in feeding trials.

Insects

Fall armyworm eggs were obtained from French Agricultural Research Inc. (Lamberton, MN) and reared on fall armyworm diet (Southland Products Incorporated, Lake Village, AR). There are two known strains of fall armyworm: corn and rice (Pashley 1988). We used the corn strain because corn is a warm-season C₄ grass more similar to switchgrass than is C₃ rice. All rearing and experiments took place in an insectary with 14:10 (L:D) day length and average temperature of 25°C.

Neonate Establishment and Feeding Trial

The establishment of fall armyworm neonates on switchgrass and corn was tested in a 48-h laboratory no-choice trial, based on the methods of Dowd and Johnson (2009). Sixteen switchgrass cultivars were used in this trial (Table 1), plus corn as a control. The uppermost fully expanded leaf from a healthy switchgrass tiller growing at our field site was clipped in the field and transported to the laboratory in a cooler. In the laboratory, 2-cm-long segments were cut from the center of the leaves and placed in 9-cm-diameter Petri dishes with filter paper moistened with 30 ml of DI water. Similar leaf sections were collected from corn. Ten neonates were randomly selected from a group of concurrently hatching egg masses and transferred into Petri dishes using an artist's paintbrush. The sides of the Petri dishes were then individually wrapped with parafilm and secured with a rubber band to prevent leaf desiccation and minimize neonate escape. There were 15 replicates (dishes) per treatment (cultivar or control), blocked by the time at which neonates were introduced. At 24 and 48 h, dishes were assessed for neonate mortality, with neonates categorized as alive/feeding (on leaf and responsive to stimulus with paintbrush tip), moribund (alive but moving erratically or slow to respond to stimulus), wandering (on filter paper or Petri dish lid and responsive to stimulus), dead (discolored and unresponsive to stimulus), or missing (escaped or cannibalized). At 48 h, all leaves were removed, and leaf area consumed was determined using ImageJ software as described later.

Late-Instar Feeding Trial

Fall armyworm larvae do most of their feeding in the final two instars (Alton 1979, Flanders et al. 2011), and a nonpreferred diet can slow development (Leuck and Skinner 1970, 1971). To test how switchgrass cultivars influence life-history characters and leaf area consumption in fall armyworm, a feeding trial with late-instar larva was performed based on the methods of Prasifka et al. (2011a) and Nabity et al. (2011). Eight switchgrass cultivars (Table 1, highlighted) were tested against a standard fall armyworm diet and corn as controls, with 15 blocks each containing one replication of each treatment. Leaves were harvested from healthy plants as described earlier and cut into 5-cm-long segments with four to five segments added to each dish. A comparable amount of corn leaf or fall armyworm diet was added to control dishes. Larvae for this trial were

previously grown from neonates in 60-ml plastic cups containing 1 cm of diet. After 9 d on diet, larvae were moved into empty 60-ml cups and starved for 24 h, removed, and individually weighed. Based on assessment of head capsule widths, these 10-d-old larvae ranged from late third to early fifth instar. To account for differences in subsequent larval development, each larva was individually weighed and replicates were blocked by starting weight with larvae placed in individual dishes as described earlier. Individual leaves were replaced daily as needed and all leaves were changed every 2–3 d. As larvae entered the nonfeeding prepupal stage (Luginbill 1928), leaf replacement halted. When a larva molted to a pupa, it was individually weighed, placed in a 60-ml cup with a small amount of diet to provide moisture, and checked daily for survival and adult emergence. Voucher specimens of arthropods used in this study have been deposited in the Michigan State University's A.J. Cook Arthropod Research Collection.

Determining Leaf Area Consumed

Leaf consumption was measured using scanned images analyzed with ImageJ, modified from the protocol described in O'Neal et al. (2002). Leaves were scanned in 24-bit color at 300 dpi, with a ruler included to set the scale of the image (~114 pixels/cm) using a scanner (Epson Perfection V39, Long Beach, CA). Images were edited with the ImageJ paintbrush tool to create clear borders between consumed and unconsumed leaf area. The threshold tool was then used and adjusted until the unconsumed leaf area was differentiated from the white background, and then the magic wand tool was used to highlight these areas. The measurement function was then used to quantify the leaf area consumed (square centimeter). In the neonate trial, herbivory was minimal, so the leaf borders and amount consumed could easily be measured from a single image at the end of the trial. In the trial with late instars, much of each leaf was consumed, so two images per leaf were needed to quantify consumption. We thus scanned and quantified the total area of each leaf before (L_o) and after consumption (L_c) and then quantified leaf area consumed as $L_o - L_c$.

Plant Traits

Specific leaf area (SLA, leaf area per unit dry mass) is a measure of leaf thinness that is a fundamental metric in plant ecology studies because it is a strong predictor of a suite of plant growth characteristics (Field and Mooney 1986; Reich et al. 1997, 1999). To quantify the leaf characteristics of the cultivars used in this experiment, we measured the mid-summer SLA of the field-grown plants from which material was taken for the fall armyworm laboratory experiments. Leaf samples for SLA measures were collected on 28 July 2016, during the same seasonal period in which tissue was collected for fall armyworm consumption, but 1 yr later, as there were not enough leaves per plant to do both activities simultaneously without compromising plant health and tissue availability for the feeding experiment. The year offset in collection time may have influenced absolute SLA values and introduced additional variance, but it probably did not obscure relative cultivar differences because SLA in switchgrass has a strong genetic basis (Milano et al. 2016). For the measures, we collected two fully expanded leaves from each of the two individual plants per replicate plot. On each plant, we selected the third leaf from the top on each of two different stems (tillers). Tillers were chosen randomly from among those that were tall and mature, most of which were generally flowering. In the few instances where there was only one individual plant in a replicated plot, we collected four leaves from that individual. Leaves were kept in sealed plastic bags

on ice and transported quickly to the lab, where leaf area (square centimeter) was quantified with a benchtop leaf area meter (LI-3000, LI-COR, Lincoln, NE). Leaves were then dried in a 25°C temperature oven with fan for 3 d to constant mass and weighed. SLA was calculated as (fresh leaf area, square centimeter)/(leaf dry mass, gram). Mean area (square centimeter) of leaves consumed in 48 h per cultivar by fall army worm was assessed as a function of mean specific leaf per cultivar using standard least squares in JMP Pro 13.1 (SAS, Inc., Cary, NC).

Statistical Analysis

All response variables were modeled using linear or generalized linear mixed models (R 3.0.3, R Development Core Team 2014), followed by chi-square analyses of deviance to determine differences between treatments. Days to pupation was modeled using Poisson regression, a binomial regression was used when modeling late-instar and neonate mortality, and all other measures met normality assumptions. Model fit was compared using Akaike information criterion (AIC) from the following factors: initial larval weight, ecotype or cultivar, and block (Burnham and Anderson 2004). For the older larvae, initial weight was used as a model factor to account for variation in subsequent larval growth. In both experiments, including the blocking variable in the model structure did not substantially improve model fit according to AIC, so it was not used in analysis. Across all measures, analyses were performed on ecotype and cultivar, as both were of interest and captured variation in different ways. The ecotype model included upland and lowland ecotypes, as well as the corn and/or diet control category. Models were then subjected to analysis of deviance with χ^2 as the test statistic and $\alpha = 0.05$. When significant deviances were detected, models were rerun to exclude the factor of interest, which were then used to create residual data sets that controlled for variation due to other factors (e.g., initial weight). Using these residual data, factors of interest (e.g., cultivar, ecotype) were compared using paired *t*-tests that had been Holms adjusted for multiple comparisons (Aickin and Gensler 1996).

Results

Neonates

Mortality of neonate fall armyworm larvae was minimal, with an average of approximately one neonate dead per dish by 48 h (Table 2). Overall neonate mortality was significantly higher at 48 h than at 24 h ($P < 0.001$) but did not differ significantly among food types (lowland, upland switchgrass, and corn; $\chi^2 = 104.03$, $df = 2$,

Table 2. Mean (\pm SEM) fall armyworm neonate mortality at 24 and 48 h fed on control (sweet corn) and switchgrass ecotypes (lowland and upland)

Hour	Ecotype	N	Mean mortality (\pm SEM) ¹
24	Control	15	7.2% \pm 3.1a
	Lowland	104	4.9% \pm 0.7a
	Upland	135	4.5% \pm 0.9a
48	Control	15	9.7% \pm 3.7b
	Lowland	104	13.3% \pm 1.4b
	Upland	134	10.9% \pm 1.4b

Means sharing a letter are not significantly different ($\alpha = 0.05$). There were no differences by cultivar or ecotype, though differences were present by time ($\alpha = 0.05$).

¹A χ^2 analysis of deviance was performed, followed by a Holms adjusted *T*-test for treatment comparisons.

$P = 0.85$) or among switchgrass cultivars ($\chi^2 = 98.74$, $df = 16$, $P = 0.991$). Cannibalism was occasionally observed but could not be specifically quantified as neonates also occasionally escaped, and the presence of head capsules could not be reliably attributed to cannibalism or molting. In some less-preferred cultivars, extensive neonate wandering was evidenced by copious trails in the condensation on the Petri lid.

Overall, neonates consumed little switchgrass, with total consumption ranging from 0.006 cm² (in the Nebraska Summer Late Maturation germplasm) to 1.29 cm² (in ‘Performer’) compared with a maximum consumption of 3.13 cm² in corn. Food type significantly affected consumption ($\chi^2 = 10.906$, $df = 2$, $P < 0.001$). Neonates consumed more leaf area of corn than of either northern upland ($P < 0.001$) or southern lowland switchgrass ($P < 0.001$). Among the switchgrass, neonates ate more leaf area of the upland ecotypes than the lowland ones ($P < 0.001$; Fig. 1). Neonates consumed significantly different amounts from different switchgrass cultivars ($\chi^2 = 9.360$, $df = 16$, $P < 0.001$), with all switchgrass cultivars fed on less than corn ($P < 0.05$). Specifically, the lowland cultivars ‘BoMaster’, ‘EG 1102’, ‘Kanlow’, ‘Kanlow N1 Syn 2’, ‘Alamo’, ‘EG 1101’, and upland cultivars ‘Trailblazer’, ‘Michigan genotype’, and ‘NE Summer Late Maturity’ were fed on less than ‘Cave-in-Rock’ ($P < 0.05$; Fig. 1).

Late-Instar Larvae

Mean mortality of late-instar fall armyworm larvae ranged from 0.06% on Cave-in-Rock and Summer to 0.26% in Kanlow and was similar in the control and experimental treatments, although variability was greatest among upland cultivars (Table 3). Mortality was not significantly influenced by switchgrass ecotype ($\chi^2 = 142.78$, $df = 2$, $P = 0.36$) or cultivar ($\chi^2 = 139.15$, $df = 9$, $P = 0.77$) or by larval starting weight (ecotype model: $\chi^2 = 140.72$, $df = 1$, $P = 0.15$; cultivar model: $\chi^2 = 137.07$, $df = 1$, $P = 0.15$). Late-instar larvae that fed on switchgrass tended to develop more slowly than those that ate corn or artificial diet (Table 4). The minimum observed days to pupation for an individual in this experiment ranged from 19 d (‘Shawnee’) to 38 d (Trailblazer), with larvae fed Trailblazer taking the longest to reach pupation on average (Table 4). Analysis of deviance in the ecotype model revealed marginal differences by ecotype ($\chi^2 = 40.73$, $df = 2$, $P = 0.054$) with larvae developing faster on corn and artificial diet than those on switchgrass. There were significant differences among starting weights ($\chi^2 = 26.50$, $df = 1$, $P = 0.002$) with initially heavier individuals reaching pupation faster. In the cultivar model, differences were not present by cultivar ($\chi^2 = 36.10$, $df = 9$, $P = 0.315$), but starting weight significantly affected time to pupation ($\chi^2 = 20.917$, $df = 1$, $P < 0.001$).

Fall armyworm larvae fed diets of switchgrass or corn consumed different amounts of leaf area per day ranging from 2.2 cm²/d (corn) to 9.4 cm²/d (Cave-in-Rock). Ecotype significantly influenced daily consumption ($\chi^2 = 201.47$, $df = 2$, $P < 0.001$) but starting weight did not ($\chi^2 = 198.85$, $df = 1$, $P = 0.23$). Post hoc tests revealed differences between lowland ecotypes and both corn ($P = 0.002$) and upland ecotypes ($P < 0.001$), whereas similar amounts of corn and upland ecotypes were eaten ($P = 0.10$; Fig. 2A). When examining variation in daily consumption by cultivar, analysis of deviance found significant differences ($\chi^2 = 166.52$, $df = 8$, $P < 0.001$); with no variation by starting weight found in this analysis ($\chi^2 = 163.32$, $df = 1$, $P = 0.159$). BoMaster, Trailblazer, Kanlow, and Performer experienced lower daily consumption than corn, Shawnee, and Cave-in-Rock ($\alpha = 0.05$; Fig. 2B).

Overall, late-instar fall armyworm larvae consumed a minimum of 56 cm² (corn) and a maximum of 240 cm² (Shawnee) before reaching

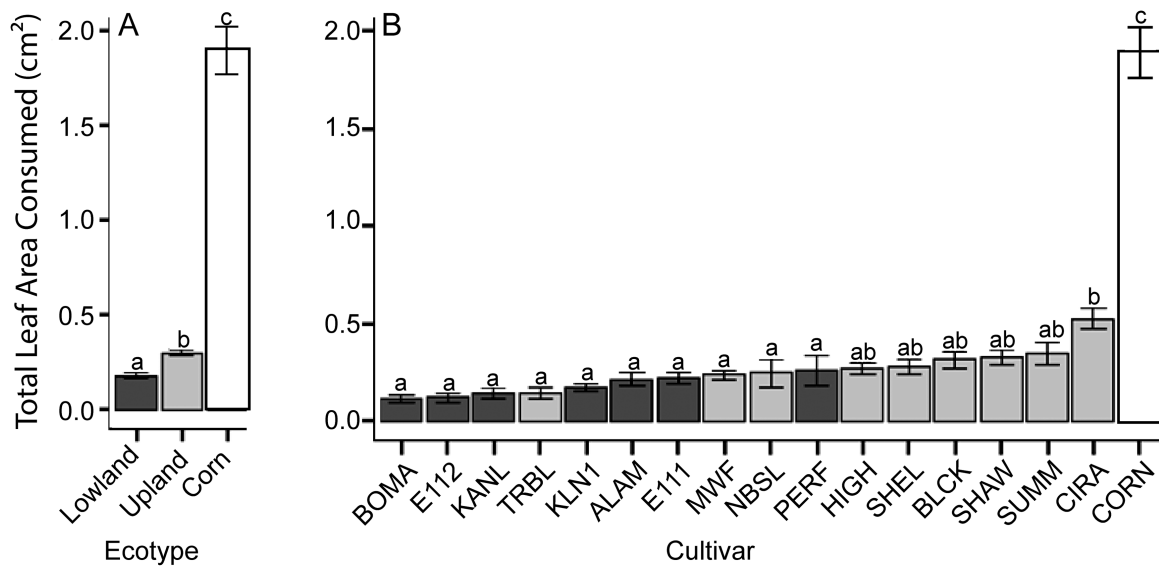


Fig. 1. Mean (\pm SEM) square centimeter of leaf consumed in 48 h by neonate fall armyworm by ecotype (A) and cultivar (B). A χ^2 analysis of deviance was performed followed by pairwise t -tests that had been using Holms adjusted for multiple comparisons. Significant differences between treatments were found between ecotypes, but not cultivars ($\alpha = 0.05$).

Table 3. Mean (\pm SEM) fall armyworm mortality prior to pupation for late instars fed on controls (sweet corn and fall armyworm diet) and switchgrass ecotypes (lowland and upland)

Ecotype	<i>n</i>	Mean mortality per 15 larvae (\pm SEM) ¹
Control	30	19.3% \pm 6.3a
Lowland	60	23.3% \pm 6.5a
Upland	60	13.3% \pm 5.8a

¹A χ^2 analysis of deviance detected no differences in mortality between treatments.

Table 4. Mean days (\pm SEM) to pupation for fall armyworm larvae fed different diets

	Mean days to pupation (\pm SEM) ¹
Ecotype	
Lowland	26.20 \pm 0.33a
Upland	26.27 \pm 0.53a
Control	23.43 \pm 0.43a
Cultivar	
BOMA	25.83 \pm 0.46a
KLN1	26.18 \pm 0.69a
PERF	26.33 \pm 0.76a
KANL	26.45 \pm 0.81a
CIRA	25.29 \pm 0.95a
SHAW	25.46 \pm 1.05a
SUMM	25.79 \pm 0.76a
TRLB	29.09 \pm 1.36a
CORN	22.82 \pm 0.60a
DIET	24.00 \pm 0.60a

¹A χ^2 analysis of deviance detected no differences in mean days to pupation between treatments.

pupation, with mean leaf area consumption across all treatments at 137.3 cm². There were significant differences detected between both ecotype ($\chi^2 = 100,077$, $df = 2$, $P = 0.001$) and starting weight ($\chi^2 = 96,400$, $df = 1$, $P = 0.04$). Post hoc tests revealed differences in total leaf area (square centimeter) consumed between lowland

and upland ecotype ($P = 0.002$), but no differences between either lowland or upland switchgrass and the corn control ($P = 0.17$ and $P = 0.34$, respectively; Fig. 2C). Lowland switchgrass was fed upon at lower levels than upland ecotypes (Fig. 2C). When total leaf consumption was examined by cultivar, there were significant differences among treatments ($\chi^2 = 87,941$, $df = 8$, $P < 0.001$) and starting weight ($\chi^2 = 84,573$, $df = 1$, $P = 0.04$). Post hoc analyses revealed differences between some of lowland and upland cultivars, with BoMaster being fed upon less than Cave-In-Rock and Shawnee (Fig. 2D).

Individual pupal weights ranged from 0.07 g (Performer) to 0.31 g (diet). Pupal weights varied by both ecotype ($\chi^2 = 0.11$, $df = 3$, $P < 0.001$) and cultivar ($\chi^2 = 0.10$, $df = 9$, $P < 0.001$). Both upland ($P < 0.001$) and lowland ecotypes ($P < 0.001$) had lower pupal weights than the control treatments (diet, $P > 0.01$; corn, $P > 0.01$), and fall armyworm fed lowland ecotypes had lower pupal weight than those fed upland ecotypes ($P = 0.047$; Fig. 2E). Analysis of deviance found differences in starting weight ($\chi^2 = 0.10$, $df = 1$, $P < 0.001$). By cultivar, pairwise t -tests suggested that all larvae fed switchgrass cultivars had lower pupal weights than those fed on diet, and Trailblazer, Kanlow N1 Syn 2, Performer, and BoMaster all had pupal weights significantly less than corn ($P < 0.05$; Fig. 2F). Again, analysis of deviance results found starting weight varied by cultivar ($\chi^2 = 0.09$, $df = 1$, $P < 0.001$). Nearly all pupae successfully emerged as viable adults, with the exception of two individuals on Performer and one on Kanlow N1 Syn 2.

Plant Traits

On average, fully expanded leaves of lowland cultivars had SLA values that were 12% lower than that of upland cultivars (mean \pm SEM: 103.8 \pm 2.252 cm²/g vs 115.8 \pm 1.986 cm²/g; $F_{1,14} = 16.1$, $P = 0.0013$), indicating that the lowland foliage weighed more per unit area (Fig. 3A). Among cultivars, mean SLA predicted 60% of the variance in the mean amount of foliar area consumed by fall armyworm in 48 h ($R_2 = 0.603$, $P = 0.0004$; Fig. 3B). In general, lowland cultivars exhibited both the lowest mean SLA and lost the least leaf area to fall armyworm consumption, whereas upland cultivars displayed greater SLA and lost the most leaf area. Among the upland ecotypes, the two wild-type populations had the lowest SLA, similar to that of several lowland cultivars.

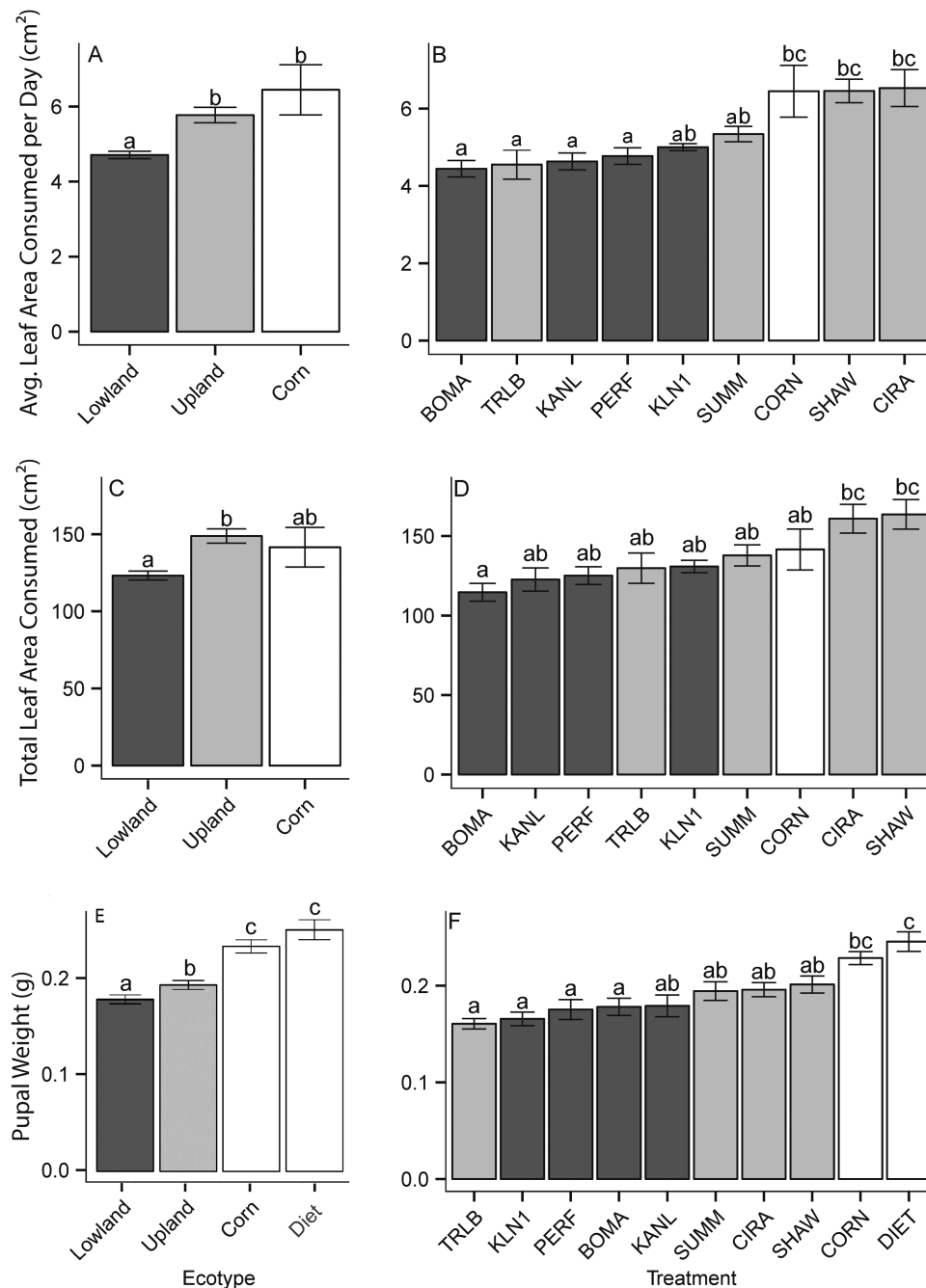


Fig. 2. Response of late-instar fall armyworm to feeding on different switchgrass cultivars and ecotypes. Mean (\pm SEM) square centimeter of leaf consumed per day until pupation by late-instar fall armyworm ecotype (A) and cultivar (B). Mean (\pm SEM) square centimeter of leaf consumed prior to pupation by late-instar fall armyworm larvae by ecotype (C) and cultivar (D). Mean (\pm SEM) fall armyworm pupal weight by ecotype (E) and cultivar (F). A χ^2 analysis of deviance was performed followed by pairwise *t*-tests that had been using Holms adjusted for multiple comparisons on residual data sets. Means sharing a letter are not significantly different ($\alpha = 0.05$).

Discussion

As switchgrass production in the United States increases, understanding how different cultivars vary with respect to feeding and development of generalist herbivores is increasingly important. In this study, we used fall armyworm as a model generalist pest with a preference for grasses to investigate which switchgrass cultivars may be more or less susceptible to insect pests. Overall, as predicted, corn was preferred to switchgrass, and lowland switchgrass experienced reduced feeding. Fall armyworm that fed on lowland switchgrass consumed less foliar area and weighed less at pupae than those that

fed on upland ecotypes. The exception in this study was the upland cultivar Trailblazer, where fall armyworm preference and performance parameters exhibited response patterns more closely resembling lowland varieties.

Neonates

Neonate fall armyworm were able to establish on switchgrass with low rates of mortality, although leaf area consumed was small compared with that of corn. In a prior study using a similar experimental design, Dowd and Johnson (2009) also saw low levels of neonate

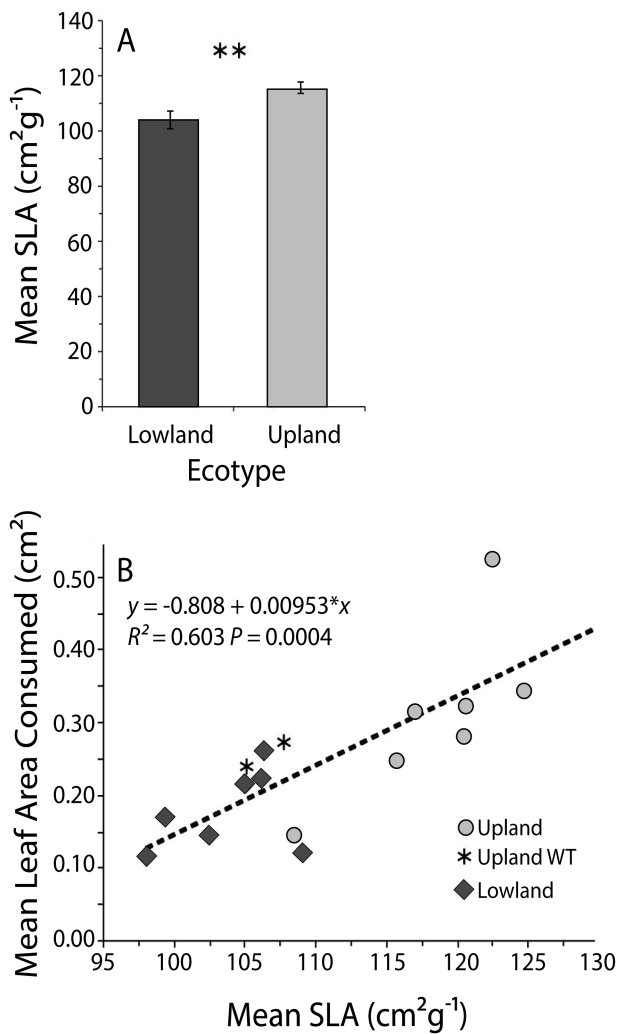


Fig. 3. SLA of switchgrass. (A) Mean SLA of lowland and upland ecotypes (calculated from per cultivar means within each ecotype). Lowland $N = 7$, Upland $N = 9$. (B) Mean total area (square centimeter) of switchgrass leaves consumed by fall armyworm in 48 h, as a function of the mean SLA (square centimeter per gram) of each switchgrass cultivar ($N = 16$). For each cultivar, values of area consumed are the means of 15 replicate feeding trials. Values for SLA are the means of two fully expanded leaves from each of two plants (one replicate) of that cultivar in four field blocks, measured on July 28. Solid circles represent upland ecotypes (asterisks highlight the two upland wild types), and open diamonds represent lowland ecotype.

mortality on six upland cultivars (including ‘Blackwell’, Cave-in-Rock, Trailblazer), though they did note increased mortality on wild-type switchgrass collected from roadways. Our study included two ‘wild-type’ cultivars: ‘High Tide’, a germplasm release drawn from switchgrass population on the eastern seaboard, and a Michigan native switchgrass germplasm purchased from Michigan Wildflower Farms (Portland, MI). At 48 h, mortality on these varieties (1.07 ± 0.34 in High Tide and 1.26 ± 0.41 in Michigan Wildflower Farms) was comparable to all other varieties. Although this study was not exhaustive, our results suggest that, among varieties tested, breeding efforts have not negatively affected plant defenses against neonatal fall armyworm.

A factor affecting mortality that we were unable to control for was cannibalism. Cannibalism occurs in fall armyworm when neonates are present at high densities (Andow et al. 2015) or are limited to a nonpreferred diet (Raffa 1987). We observed fall armyworm neonates in the act of cannibalism only in switchgrass treatments,

with multiple observations in experimental units where the larvae were exposed to the cultivar Trailblazer. Cannibalism was not observed in corn treatments. These observations align with prior work on diet quality in fall armyworm, which often show the highest growth rate on a preferred diet (here corn), and that cannibalism can support a higher growth rate than feeding on a nonpreferred diet (Raffa 1987).

In regards to leaf consumption, neonate larvae preferred corn over switchgrass and fed less on lowland ecotypes when compared with upland ecotypes. Neonates prefer the most tender parts of a leaf (Luginbill 1928), which was controlled for in this study by selecting the middle 2 cm of the uppermost fully expanded leaf, although evident differences in SLA indicate that leaf tenderness probably varies between cultivars. Different trends might be observed if this study were repeated to examine feeding closer to the whorl, as this is a preferred area when fall armyworm feeds on corn (Capinera 1999). When comparing amounts eaten by neonates of older switchgrass plants, Dowd and Johnson (2009) observed a range from approximately 2.98 cm² (Blackwell) to 4.54 cm² (Cave-in-Rock) in 48 h. This is a higher consumption rate than observed in the present study, though their study used first-year, greenhouse-grown plants, not field-grown plants as in our study. Because plants grown in the greenhouse are typically more tender than those grown outside, the growth conditions of switchgrass probably partially contributed to the differences in consumption.

In fall armyworm, the first three instars generally cause less than 2% of total consumption (Alton 1979), so our neonate results reflect the establishment phase rather than direct economic damage. These results, when taken together, suggests that neonate fall armyworm can survive on switchgrass, but their escape from sealed Petri dishes, cannibalism, and general neonate behavior of increased movement and searching on less-preferred diets (Eigenbrode et al. 1991, Zalucki et al. 2002), suggests that fall armyworm are unlikely to stay on switchgrass if a preferred host is available (Zalucki et al. 2002, Nabity et al. 2011). It is unknown if fall armyworm adults will oviposit on switchgrass, especially in a field settings, as nonpreferred plant species fall armyworm feed on in the laboratory may be ignored by ovipositing adults (Meagher et al. 2004). A caveat is that the fall armyworm corn strain we used was continuously reared on diet, and it would be useful to repeat similar studies with recently field-collected strains.

Late-Instar Larvae

Increased development times and lower pupal weights observed for fall armyworm fed on switchgrass are consistent with other studies addressing development on nonpreferred diets (Ali et al. 1990) and to studies comparing development on switchgrass and corn (Nabity et al. 2011). Pupal weight in fall armyworm has been linked to adult fecundity (Leuck and Perkins 1972). This suggests that regardless of cultivar, continuous feeding on switchgrass could have increased negative impacts across subsequent generations, which has been observed in other Lepidoptera fed nonpreferred diets (Rossiter 1991, 1996). In addition, the tendency for slower development on switchgrass could also lead to an increase in predation and parasitism (Moran and Hamilton 1980, Price et al. 1980), which may in turn decrease net consumption rates. For example, the increased movement elicited by nonpreferred diets has been suggested to increase the exposure of fall armyworm to potential parasites (Pair et al. 1986b). Thus, the realized impact of fall armyworm feeding on switchgrass under field conditions remains an open question.

The amount of feeding we observed, measured both as average daily and total consumption, is consistent with other work

on lepidopteran larvae on nonpreferred diets. Fall armyworm fed diluted diet (food source with decreased nutritional value) have been observed to eat more to compensate for the lack of nutrients (Wheeler and Slansky 1991). This could explain the high amounts of feeding in Cave-in-Rock and Shawnee, as these cultivars may be palatable but of decreased nutrient quality, causing the larvae to eat more to compensate. Other studies in Noctuid moths have suggested that increased feeding could lead to a buildup of toxic chemicals, although we observed low, relatively unvaried mortality rates across treatments in this study, suggesting this was not a factor in the present experiment (Slansky and Wheeler 1992).

Plant Traits

Lowland and upland switchgrass ecotypes differ in multiple genetically based traits that may influence insect herbivory, including chemical and mechanical characteristics (e.g., Bhandari et al. 2014, Milano et al. 2016). For example, lowland ecotypes may contain more hemicellulose and sometimes also more cellulose, whereas upland ecotypes may contain more lignin and nitrogen (Lemus et al. 2002, Bhandari et al. 2014, Aurangzaib et al. 2016). Within upland ecotypes, foliar lignin content was negatively associated with leaf digestibility but was not a good predictor of aphid preferences or pathogen susceptibility (Schrotenboer et al. 2011).

For the chewing insects studied here, we considered the influence of SLA on consumption and larval development. SLA is negatively correlated with leaf mechanical properties that deter chewing insects (e.g., resistance to shearing, punching, and tearing; Caldwell et al. 2016). Plants species with low SLA typically grow slower, exhibit more structural defenses, and experience less herbivory than those with greater SLA, which typically have thinner, less-defended leaves (Coley et al. 1985, Reich et al. 1999). Consistent with previous work (Milano et al. 2016), we found that the SLA of lowland ecotypes used in this study was lower than that of upland ecotypes; in other words, the foliage of lowland cultivars on average weighed more per unit area. We found that differences in SLA among cultivars explained 60% of the difference in fall armyworm consumption of foliar area, suggesting that this foliar trait either directly reduces leaf area consumption and/or is associated with additional traits that deter feeding. Fall armyworm might feed more slowly on foliage with low SLA because mechanical properties of the leaves deter chewing and digestion or because the greater biomass available per unit area sates fall armyworm appetite more quickly.

Fall armyworm may be further deterred by other defense mechanisms and chemical differences in foliar composition between ecotypes, which have been previously observed. For example, lowland cultivars have been found to demonstrate greater resistance to fungal and virus infections (Uppalapati et al. 2013, Alexander et al. 2017) and exome capture sequencing has found higher gene copy number for some defense-related biosynthetic pathways in lowland Kanlow (Evans et al. 2015). The genetic diversity present in switchgrass may also influence plant defensive traits. Dowd and Johnson (2009) suggested that increased ploidy may lead to increased defenses, though no evidence supporting this assertion was found in our study. Beyond this, within cultivars themselves there are often high levels of genetic variation (Vogel 2000, Casler et al. 2007, Mutegi et al. 2014). Further breeding efforts may lead to more genetic similarity within cultivars, as is typical with hybrid field crop plants, which may lead to increased herbivory (Wetzel et al. 2016).

In this experiment, fall armyworm was used as a model generalist insect herbivore to explore the potential differences in plant defense present in current switchgrass varieties that resulted from different accession and breeding history. Our results suggest

that switchgrass ecotypes and cultivars do vary in their potential to influence insect establishment, feeding, and development. As switchgrass breeding efforts continue to develop biofuel feedstocks, it is important to consider how breeding for these characteristics may affect insect herbivores, which are likely to increase in number and damage potential as switchgrass production increases. More work is required to understand the defenses mechanisms present in switchgrass and how these may be altered by plant breeding.

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