Development and Feeding of Fall Armyworm on *Miscanthus × giganteus* and Switchgrass

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ABSTRACT   Observations of fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae), larvae infesting plots of *Miscanthus × giganteus* Greef and Deuter ex Hodkinson and Renvoize prompted laboratory-based tests of survival, development, and feeding preferences on leaf tissue from *M. × giganteus* and switchgrass, *Panicum virgatum* L. Survival from hatch to pupation was >70 and 50% for fall armyworms reared on switchgrass and *M. × giganteus*, respectively, although survival of the *S. frugiperda* rice strain was significantly greater than the corn strain on both crops. Developmental times from hatch to pupation or adult emergence showed effects of crop and *S. frugiperda* host strain, but analysis of an interaction revealed developmental times for the rice strain were similar on both crops, whereas corn strain larvae showed delayed development on *M. × giganteus* relative to switchgrass. Analysis of larval (10 d) and pupal masses showed a similar pattern, with effects of crop and an interaction (at 10 d), but only the mass of corn strain larvae feeding on *M. × giganteus* was reduced relative to the other crop and strain combinations. In choice tests, neonates of both corn and rice strains showed a strong preference for feeding on young tissues rather than mature leaves of *M. × giganteus* or switchgrass, but they also clearly favored corn, *Zea mays* L., leaves over either of the perennial grasses. Results indicate both plants are potential hosts for *S. frugiperda*, but additional information is needed to understand under which scenarios and to what degree fall armyworms may damage perennial grasses grown for biofuel production.

KEY WORDS   pest, biomass, ethanol, bioenergy, Energy Independence and Security Act

The development of perennial rhizomatous grasses as crops to be grown for biofuel production is aided by a belief that these third-generation feedstocks will require significantly less off-farm inputs (e.g., water, fertilizer, pesticides) than producing biomass from corn, *Zea mays* L. (Hohenstein and Wright 1994, Hill et al. 2006). In particular, grasses such as *Miscanthus × giganteus* Greef and Deuter ex Hodkinson and Renvoize (a sterile hybrid), *Miscanthus sinensis* Andersson (a putative *M. × giganteus* parent), and switchgrass, *Panicum virgatum* L., are often suggested to be low-input crops because they should require little to no management for insect pests (Parrish and Fike 2005, Semere and Slater 2007, Wang 2007, Clifton-Brown et al. 2008). However, observations of feeding by several

orders of herbivorous insects on *Miscanthus* spp. (Gottwald and Adam 1998) suggest that rather than being pest-free, the identity of insect pests and their effects on harvestable biomass are simply not yet known (Mitchell et al. 2008).

During a survey of herbivorous insects on perennial grasses in Illinois, larvae of fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae), were found feeding in the whorls of *M. × giganteus*. During the same period, no fall armyworms were found in switchgrass, though armyworms (species not identified) have been noted as possible switchgrass pests (Barnhart et al. 2007). Given the broad host range of fall armyworm and its preference for grasses (Pashley 1988), *S. frugiperda* seems likely to feed on many of the grasses being explored as possible biofuel feedstocks. However, fall armyworms may not be easily detected because larvae are often hidden, feeding within concealed areas of host plants (Quisenberry 1999).

Projected areas of cultivation for *M. × giganteus* and switchgrass include most of the eastern United States (USDOE 2006), suggesting *S. frugiperda* could regularly encounter and feed on these biofuel grasses. However, the potential to impact biofuel feedstocks is

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likely to increase moving from north to south, as fall armyworms only successfully overwinter in southern Florida and Texas; adults must migrate from overwintering areas, meaning only a single generation may occur in the northernmost states. Predicting the degree to which *M. × giganteus* or switchgrass may be affected by *S. frugiperda* is complicated by the existence of two host strains associated with large grasses such as corn and sorghum (*Sorghum* spp.) (corn strain) and smaller grasses such as rice, *Oryza sativa* L., and forage grasses (*Cynodon* spp.) (rice strain) (Pashley 1986). Because the strains are morphologically identical, molecular markers are the most accurate indicators of strain identity (McMichael and Prowell 1999, Prowell et al. 2004). Mitochondrial haplotypes are among the most convenient of these as they can be assayed by polymerase chain reaction amplification of individual samples (Levy et al. 2002, Meagher and Gallo-Meagher 2003, Nagoshi et al. 2006). Consequently, effects of fall armyworm may depend on the mixture of crops grown regionally, as the corn and rice strains differ in their preference for and development on various host plants (Whitford et al. 1988; Veenstra et al. 1995; Meagher et al. 2004, 2007; Stuhl et al. 2008).

M. × giganteus and switchgrass are grown across the United States for research and other purposes, but with far fewer hectares than would be needed to meet goals for biofuel production (Bouton 2007). However, legislative requirements for advanced biofuels, including ethanol from sources other than corn grain (Energy Independence and Security Act of 2007, 42 U.S.C. § 17001), suggest production of these perennial grasses could increase rapidly. To facilitate successful commercialization of perennial grasses as biofuel feedstocks, identification of potential pest species and crop-specific information on pest life histories are necessary tools for economically and environmentally sustainable crop production. Accordingly, to help evaluate fall armyworm as a potential pest of *M. × giganteus* and switchgrass, laboratory trials with *S. frugiperda* were conducted to quantify survival, development, and feeding preferences for the two host strains.

Materials and Methods

Insect and Plant Material. *S. frugiperda* rice and corn strains each were represented by a single colony for laboratory trials. The rice strain colony 'Ona' was established in 2002 from collections at the University of Florida's Range Cattle Research and Education Center in Ona, FL. The corn strain 'DRU' was established in 2008 from the University of Florida's Dairy Research Unit in Hague, FL. Both colonies were initiated using the methods of Stuhl et al. (2008) and reared on a pinto bean-based artificial diet (Guy et al. 1985). The Ona colony was in generation 53 and the DRU colony was in generation 6 at the beginning of the experiments. Each strain was tested at the time of establishment and periodically thereafter for the appropriate mitochondrial markers associated with host preference (Levy et al. 2002, Nagoshi et al. 2006).

M. × giganteus plants were grown from field-collected rhizome pieces (10–12 cm) which were planted into soil-less potting medium (Sunshine Mix #1, Sun Gro Horticulture, Vancouver, BC, Canada) in 14-cm-diameter plastic pots. After 100 d in a greenhouse (24°C and a photoperiod of 12:12 [L:D] h), pots were transferred to an environmental chamber (24°C and a photoperiod of 14:10 [L:D] h) with light intensity (600 μmol/m²/s photosynthetically active radiation) adequate to induce growth of new tillers. After 28 d, *M. × giganteus* pots were returned to the greenhouse; growth on the new tillers was used for feeding tests 50 d after plants were moved into the environmental chamber. Switchgrass plants ('Kanlow') came from small (9-cm) pots with one prior summer growing outdoors. During the fall, tillers in each small pot were cut to a height of 3 cm and switchgrass was transplanted into the greenhouse using the same pots and medium as with the *M. × giganteus* rhizome pieces. All pots of switchgrass grew for 70–90 d after cutting, but there was a significant range of tiller sizes at the start of feeding trials; this reflects field data that show an increase in switchgrass tiller density during the first few months of crop development (Heaton et al. 2008). Corn ('Mini Blue') plants were also grown in soil-less medium for 50 d to allow comparisons of *S. frugiperda* larval preference among the perennial rhizomatous grasses and a known host plant. Throughout the experiments, all plants were fertilized weekly with a 15–5–15 ratio of nitrogen, phosphorous, and potassium.

Survival and Development. To assess the effects of feeding on *M. × giganteus* or switchgrass, rice and corn strain fall armyworms were reared concurrently in an environmental chamber (24°C and a photoperiod of 14:10 [L:D] h) with leaf tissue provided *ad libitum.* Individual larvae (n = 40 per strain on each crop) were placed into small (60- by 15-mm) petri dishes containing leaf tissue and a 55-mm disc of filter paper wetted with 0.3 ml water. Pieces of *M. × giganteus* tissue in the small petri dishes were collected from leaves in the whorl; although using newer leaf tissue probably increases survival, it is consistent with the field observation of *S. frugiperda* feeding within the whorl of *M. × giganteus.* Pieces of switchgrass were collected from the lower leaves of less-mature tillers (three to four leaf), which seemed more acceptable to fall armyworm neonates than leaves from mature tillers. The edge of each dish was sealed with a stretched piece of Parafilm M (Pechiney Plastic Packaging, Chicago, IL) to prevent desiccation. After 4 and 7 d, additional tissue was provided even when some of the original tissue remained.

After 10 d, the mass of each larva was measured and individuals were transferred into large (100- by 20-mm) petri dishes containing leaf tissue and a 90-mm disc of filter paper wetted with 0.3 ml of water. After the transfer at 10 d, pieces of *M. × giganteus* or switchgrass leaf tissue were no longer selected from plant tops, but arbitrarily chosen from all remaining leaves. From this point, tissue was added as needed (usually every 1–2 d). Throughout the trials, survival was as-

sessed whenever leaf tissue was added. Pupal rather than adult mass was measured to permit comparison to related work on host-plant effects (Meagher et al. 2004, 2007). However, because preliminary work with field-collected *S. frugiperda* and *M.* × *giganteus* indicated the potential for considerable pupal mortality (J.D.B., unpublished data), pupae were held in the large petri dishes (where many constructed pupal cells from filter paper or plant tissue) until adult emergence.

Leaf Area Consumption. Data on the area of plant tissue consumed can be useful for simulating insect defoliation (Ostlie and Pedigo 1985), and amounts of leaf feeding may also be indicators of relative nutritional quality (Wheeler and Slansky 1991). Consequently, leaf area consumed was measured for a subset ($n = 20$) of each of the four strain and crop combinations starting at 10 d after hatch. Previous rearing of *S. frugiperda* on switchgrass suggested that larvae would not be capable of chewing through leaves until at least 8 d after hatch, and it was expected that most leaf tissue would be consumed during the last and penultimate stadia (Luginbill 1928). The area of tissue consumed was assessed by scanning ($\approx$118 pixels/cm at 1 bit/pixel) images of leaf tissue before and after feeding by using a digital scanner. Leaf area consumed was assessed as the difference of tissue added and tissue removed using a black-pixel comparison technique similar to Bradshaw et al. (2007).

Larval Choice. Preliminary feeding tests of *S. frugiperda* on *M.* × *giganteus* or switchgrass indicated that survival of neonates may be more influenced by the maturity of the leaf tissue provided than by the grass species. Concurrent with the beginning of tests on survival and development, separate choice tests were used to assess possible larval preferences for younger leaf tissue or for a common cultivated host plant. For both tests, rectangular leaf pieces (10 by 50 mm) were placed in 100-mm-diameter petri dishes (containing a 90-mm disc of filter paper wetted with 0.3 ml water). After 20 neonates of either the corn or rice strain were placed into the center of a dish, the edge was sealed with a stretched piece of Parafilm M. After 24 h in an environmental chamber (24°C and a photoperiod of 14:10 [L:D] h), each dish was opened and the number of larvae on each leaf piece was counted. For the first test (crop by tissue type), four leaf pieces were added: leaf tissue from 1) mature *M.* × *giganteus* and 2) mature switchgrass, 3) *M.* × *giganteus* whorl tissue, and 4) switchgrass tissue from the lower leaves of late-emerging tillers. In the second test (perennials with corn), three leaf pieces were used: mature leaf tissue from 1) *M.* × *giganteus*, 2) switchgrass, and 3) corn (Mini Blue). For each type of choice test, 12 separate dishes of each strain ($n = 240$ larvae) were used.

Statistical Analyses. All analyses were conducted using SAS (SAS Institute 1999) statistical software with the specific procedures or options used indicated in capital letters. Data on survival were grouped for the periods between hatch and 10 d, 10 d and pupation, and from pupation to adult emergence. However, only pupal mortality and overall survival (from hatch to
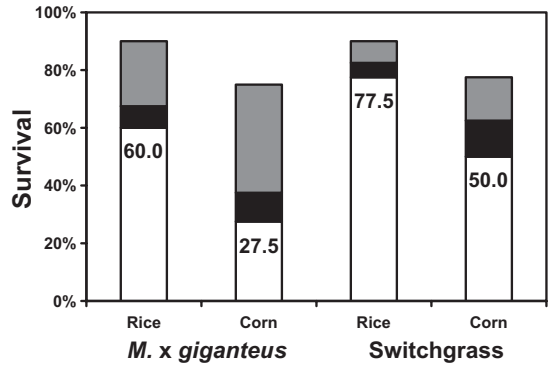

Fig. 1. Survival to various stages of development for rice and corn strain *S. frugiperda* reared on *M.* × *giganteus* or switchgrass leaf tissue ($n = 40$, each strain by crop combination). The top of divisions in each column indicate survival from hatch to 10 d (gray), to pupation (black), and to adult emergence (white); survival to adulthood is shown numerically.

adult emergence) were analyzed, with strain comparisons made within each crop (switchgrass or *M.* × *giganteus*) using a chi-squared test (PROC FREQ). To test for effects of crop, fall armyworm strain, and their possible interaction on developmental time (days to pupation, adult emergence), mass (at 10 d, pupation), and leaf feeding (square centimeters area consumed), separate two-way analyses of variance (PROC MIXED) were used. When a significant main effect was detected, all pairwise comparisons were made using least-squares estimated means (LSMEANS); if significant tissue type × strain interactions were detected, the effects of strain were examined within leaf tissue type (SLICE). To test for differences in the proportion of larvae that selected each tissue type in the choice tests, a chi-squared test (PROC FREQ) was used for each strain in the two choice tests. In this analysis, a petri dish was considered a subsample from a population (strain).

Results

Survival to pupation was >70 and 50% for fall armyworms reared on switchgrass and *M.* × *giganteus*, respectively, indicating that both plants are potential hosts for *S. frugiperda.* No differences between strains were found for the likelihood that pupae survive to adult emergence for *S. frugiperda* reared on switchgrass or *M.* × *giganteus.* For survival from hatch to adult emergence, more rice strain individuals successfully developed on both *M.* × *giganteus* ($\chi^2 = 11.31$, df = 1, $P < 0.001$) and switchgrass ($\chi^2 = 6.54$, df = 1, $P = 0.010$) (Fig. 1).

Larval developmental time (days from neonate to pupa) was influenced by strain ($F = 16.82$; df = 1, 95; $P < 0.001$) and crop ($F = 5.66$; df = 1, 95; $P = 0.019$), with *S. frugiperda* from the corn strain or reared on *M.* × *giganteus* developing more slowly relative to the other strain or crop. However, a significant interaction ($F = 4.04$; df = 1, 95; $P = 0.047$) also was detected;

Table 1.   Developmental times (least-squares–estimated means ± SE) for fall armyworm reared on *M.* × *giganteus* or switchgrass

Leaf tissue	Strain	Developmental time (d)[a]	
		Larval	Total[b]
Switchgrass	Rice	23.3 ± 0.4b	33.7 ± 0.3c
	Corn	24.3 ± 0.4b	35.0 ± 0.4b
Miscanthus	Rice	23.5 ± 0.4b	33.1 ± 0.4c
	Corn	26.3 ± 0.6a	36.5 ± 0.6a

[a] Means within a column sharing the same lowercase letter are not significantly different.
[b] The time from neonate to adult emergence.

examining the effects of strain within each crop showed that development of the corn strain was delayed only for larvae reared on *M.* × *giganteus* ($F = 15.59$; df = 1, 95; $P < 0.001$). Total developmental time (days from neonate to adult emergence) was influenced by strain ($F = 28.39$; df = 1, 82; $P < 0.001$), but again an interaction of strain × crop was found ($F = 5.42$; df = 1, 82; $P = 0.022$). In this case, the tests of strain effects within each crop indicated that development of the corn strain was delayed on switchgrass ($F = 5.88$; df = 1, 82; $P = 0.018$), and *M.* × *giganteus* ($F = 23.75$; df = 1, 82; $P < 0.001$); the interaction reflects a greater relative delay for corn strain reared on *M.* × *giganteus.* Pairwise comparisons and least-squares estimated means for developmental times are shown in Table 1.

After 10 d of feeding, larval mass was not influenced by strain, but there was a significant effect of crop ($F = 5.50$; df = 1, 129; $P = 0.021$) with a strain × crop interaction ($F = 9.24$; df = 1, 129; $P = 0.003$). However, when the effects of strain were examined within each crop, the average mass for corn-strain larvae was significantly less than that of rice-strain larvae on *M.* × *giganteus* ($F = 6.08$; df = 1, 82; $P = 0.015$) (Table 2). Pupal mass was affected only by crop ($F = 6.91$; df = 1, 95; $P = 0.010$); pupae of *S. frugiperda* reared on switchgrass were generally heavier than those reared on *M.* × *giganteus.* Mean leaf areas consumed by the four combinations of crop and strain ranged from 90 to 111 cm^2, but no significant effects were detected. Pairwise comparisons for 10 d and pupal mass and least-squares estimated means for 10 d mass, pupal mass and leaf area consumption are shown in Table 2.

Table 2.   Larval mass, pupal mass and leaf feeding (least-squares–estimated means ± SE) for fall armyworm reared on *M.* × *giganteus* or switchgrass

Leaf tissue	Strain	Mass (mg)[a]		Leaf feeding (cm^2)[b]
		Larval (10 d)	Pupal	
Switchgrass	Rice	29.7 ± 2.9ab	152.8 ± 5.1a	111.2 ± 5.2
	Corn	37.4 ± 3.1a	145.4 ± 5.9a	104.3 ± 5.7
Miscanthus	Rice	31.8 ± 2.9a	140.2 ± 5.8ab	108.8 ± 6.6
	Corn	21.3 ± 3.1b	125.5 ± 7.6b	90.0 ± 8.3

[a] Means within a column sharing the same uppercase letter are not significantly different.
[b] No letters are present, because the analysis of variance indicated no significant main effects.

Table 3.   Choices of fall armyworm neonates (percentage) among tissues after 24 h with combinations of *M.* × *giganteus*, switchgrass and maize

Test[a]	Strain	Switchgrass		*M.* × *giganteus*		Corn
		Young	Old	Young	Old	Old
Crop by tissue type	Rice	48	8	40	4	*
	Corn	41	4	49	6	*
Perennials with corn	Rice	*	4	*	0	96
	Corn	*	5	*	4	91

[a] Asterisks (*) indicate options not included in a specific choice test. Percentages rounded to nearest whole number.

In larval choice tests, 92% (crop by tissue type) or 96% (perennials with corn) of neonates were found on one of the leaf tissues after 24 h. Based on the observation of visible leaf material in their guts, some larvae crawling off of leaf tissue also had been feeding within the previous several hours. The test of crop by tissue type indicated a preference for whorl tissue (*M.* × *giganteus*) or leaves from young tillers (switchgrass) compared with mature leaves of either crop for both the rice ($\chi^2 = 140.95$, df = 3, $P < 0.001$) and corn ($\chi^2 = 142.18$, df = 3, $P < 0.001$) strains (Table 3). When mature leaf tissue from the perennial rhizomatous grasses was compared with corn, a strong preference for corn was observed for both the rice ($\chi^2 = 394.42$, df = 2, $P < 0.001$) and corn ($\chi^2 = 353.75$, df = 2, $P < 0.001$) strains (Table 3).

Discussion

Laboratory-based feeding trials demonstrated that fall armyworms are capable of developing on *M.* × *giganteus* and switchgrass, two perennial, rhizomatous grasses intended as new crops used for biofuel production. In testing survival and development, there were differences in the suitability of the two grasses, particularly for the corn strain of *S. frugiperda*, which generally showed lower survival, lower mass, and slower development on *M.* × *giganteus* (Fig. 1; Tables 1 and 2). During larval development, fall armyworms consumed leaf areas that were approximately equal for all combinations of strain and crop (Table 2). Neonates of corn and rice strains both showed a strong preference for feeding on young tissues rather than mature leaves of the perennial grasses. However, newly hatched larvae also clearly favored corn leaves over *M.* × *giganteus* and switchgrass (Table 3).

Specific results of feeding trials are best understood in the context of previous studies of *S. frugiperda* development on primary and alternate hosts. In particular, Meagher et al. (2004, 2007) provide ideal data for comparison, as their methods for assessing survival and development were used as a template for the laboratory tests with switchgrass and *M.* × *giganteus.* Comparing 10 d mass, pupal mass and time to pupation, fall armyworm development seems slowed relative to corn but similar to some alternate hosts for *S.*

frugiperda (Tables 1 and 2 compared with Meagher et al. (2004). However, when data on survival to pupation are considered (Fig. 1), the rice strain on switchgrass (82%) and *M.* × *giganteus* (68%) and the corn strain on switchgrass (62%) compare favorably to alternate hosts, including Bermuda grass, *Cynodon dactylon* (L.) Persoon; stargrass, *Cynodon nlemfuensis* Vanderyst variety *nlemfuensis;* cowpea, *Vigna unguiculata* (L.) Walpers ssp. *Unguiculata;* and sunn hemp, *Crotalaria juncea* L.) (Meagher et al. 2004, 2007).

Similar methods for testing corn and rice strain *S. frugiperda* on Bermuda grass and corn also were used by Pashley et al. (1995). However, direct comparisons to data on switchgrass and *M.* × *giganteus* may be less useful, as Pashley et al. (1995) found dramatic differences in 10 d mass (>10-fold) and time to pupation (>8 d) relative to Meagher et al. (2004, 2007). The discrepancies suggest there may be some important differences in the fall armyworm populations (established from Louisiana or Florida) or host plants used by Pashley et al. (1995) that are not clear from published information. However, Pashley et al. (1995) noted that measures of larval performance on alternate hosts may not always be correlated with adult fecundity or choice of oviposition site, underscoring the value of data on adult performance and behavior to evaluate the potential impact of fall armyworm on grasses grown as biofuel feedstocks.

If the areas of *M.* × *giganteus* and switchgrass cultivation significantly increase, the ability of fall armyworm to develop on these perennial grasses may be important under a variety of circumstances. First, when local armyworm populations reach outbreak conditions, they may consume perennial grasses grown for biofuel production as suitable alternatives to food and forage crops. Second, in areas where several generations of *S. frugiperda* occur (e.g., the southern United States), survival of the rice strain could be great enough to threaten switchgrass and *M.* × *giganteus.* However, *M.* × *giganteus* provides considerably more leaf tissue than maize (Dohleman and Long 2009), suggesting that for larvae that consume ≈110 cm² of leaf area, extremely high numbers of larvae would be required to significantly reduce biomass. However, multiple switchgrass cuttings for biomass production (recommended for upland cultivars grown in the southeastern United States; Fike et al. 2006) could exacerbate either of the two previously noted scenarios, as regrowth would provide the less mature tissue preferred by neonate fall armyworms. Perhaps most importantly, the successful development of *S. frugiperda* on switchgrass and *M.* × *giganteus* suggests potential problems from similar species. For example, the armyworm, *Pseudaletia unipuncta* Haworth, may consume considerably more tissue than the fall armyworm (Rice et al. 1982), and *P. unipuncta* also is capable of overwintering at least as far north as Tennessee. Therefore, perennial grasses grown for biofuel production could be infested early in the season, when tillers of *M.* × *giganteus* or switchgrass are small enough to be consumed by a single larva.

The projected distribution of dedicated crops for biofuel production is almost entirely based on abiotic conditions like temperature and rainfall. However, early results with perennial grasses suggest that biotic variables, including the abundance of herbivores and plant pathogens (Huggett et al. 1999), may influence the distribution of crops such as switchgrass and *M.* × *giganteus.* Furthermore, because most of the herbivores associated with crops intended for production of advanced biofuels also are shared with food crops, the effects of biomass production on pest management in conventional crops may help determine the areas over which dedicated crops for biofuel production are desirable.

Efforts to identify likely pests of *M.* × *giganteus* and switchgrass in the United States have been initiated only recently, suggesting species other than *S. frugiperda* may prove to be more serious threats to the productivity of these potential new crops. However, some key research needs that could apply to fall armyworm are probably important to assess the potential impact of other herbivores. First, an understanding of how herbivores use biomass crops in the mosaic of cultivated and noncrop hosts is necessary. For example, fall armyworm is much less likely to affect switchgrass if adult moths do not find it attractive as an ovipositional site. Second, it is important to determine the capacity for compensatory growth in these grasses and under what circumstances they may recover from insect feeding (Anten and Ackerly 2001). If switchgrass and *M.* × *giganteus*, which emerge near the last spring freeze, are only attractive before seasonal development of food crops such as corn or rice, reserves within plant rhizomes may permit recovery from an early-season infestation of *S. frugiperda.* Attempts to address these research needs could be characterized as premature for new crops like *M.* × *giganteus* and switchgrass, which are not yet widely grown. However, if the distribution or abundance of insect herbivores increases along with the cultivation of biofuel grasses, proactive research in insect management may seem prudent in hindsight.

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