

Suspected Selective Herbivory of Bioenergy Grasses by Meadow Voles (*Microtus pennsylvanicus*)

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Highly productive native and non-native perennial grasses are being grown for bioenergy purposes in North America, and ecological risks of their large-scale production are being assessed to inform breeding and management practices. Giant *Miscanthus* (*Miscanthus* × *giganteus*) and Switchgrass (*Panicum virgatum*) were introduced into an old-field habitat in Guelph, Ontario, in 2012. Seedlings of these species suffered severe selective herbivory, being severed at the plant base by an unknown herbivore. We therefore performed a live-trapping survey and mark-recapture analysis of the small mammal community in 2012 to identify the probable herbivore and estimate its population density. Meadow Voles (*Microtus pennsylvanicus*) were the most abundant herbivore in the area, with an estimated population of 265 individuals/ha, a relatively high density. This and other evidence indicate that Meadow Voles were likely responsible for herbivory of >80% of the transplants. Such herbivory could have a substantial effect on the establishment and survival of these grasses, suggesting that future crop breeding programs and ecological risk assessments should take this into consideration.

Key Words: bioenergy, herbivory, invasion, Meadow Vole, *Microtus pennsylvanicus*, *Miscanthus* × *giganteus*, *Miscanthus* × *giganteus* 'Illinois', *Miscanthus* × *giganteus* 'Nagara', *Miscanthus* × *giganteus* 'Amuri', *Panicum virgatum*, Switchgrass, *Panicum virgatum* 'cave-in-rock', old field, Ontario.

A number of highly productive perennial grasses are currently under development in North America for large-scale agricultural production for bioenergy purposes (Lewandowski et al. 2003; Vermerris 2008). Some of these species are native to North America, whereas others are introduced. For example, cultivars of native tallgrass prairie species such as Switchgrass (*Panicum virgatum*) that were previously developed as forage crops are now being evaluated for biomass production (McLaughlin and Kszos 2005; Dohleman et al. 2012). Similarly, there are several breeding programs and biomass production trials for Asian *Miscanthus* species for improvement as bioenergy crops (Clifton-Brown et al. 2001; Pyter et al. 2009; Dohleman et al. 2012). In addition, various assessments are underway throughout the potential North American cultivation area of these crops to determine ecological risks associated with their large-scale production (e.g., Barney and DiTomaso 2010; Anderson et al. 2011).

In one such study to evaluate the potential effects of these species on local biodiversity (in the event that they escape production fields), one Switchgrass cultivar and three *Miscanthus* × *giganteus* cultivars were transplanted into an old-field habitat at the University of Guelph Turfgrass Institute in Guelph, Ontario, in spring 2012. Two days after the *Miscanthus* cultivars were planted, selective herbivory of some of the transplants was noted. The stems of these plants had been severed at an angle close to the base, and the top of the plant was usually left beside the stem. Two weeks after the Switchgrass was planted, 80.6% (187 of 232) (HAH, unpublished data) of those transplants had suffered complete herbivory: the plants were severed near

the base of the stem and the top of the plant was usually removed. Most of the surrounding plants of the local vegetation remained intact. This selective herbivory continued throughout the summer and autumn.

By autumn 2012, 80.0% (557 of 696) of the *Miscanthus* transplants and 92.7% (215 of 232) (HAH, unpublished data) of the Switchgrass transplants had experienced mortality that was attributed to the observed herbivory. In addition, a notable proportion of transplant locations showed signs of digging, with Switchgrass roots removed and *Miscanthus* rhizomes showing evidence of chewing. We also observed abundant rodent feces and grass tunnels or runways. Such unusual and extreme selective herbivory of these species has not been noted before, and it could have implications for the establishment of these crops as well as any possible invasion into novel habitats.

Herbivory by small mammals can dramatically affect plant survival and recruitment and the resulting plant composition and diversity in old fields (e.g., Howe and Brown 1999; MacDougall and Wilson 2007; Parker et al. 2010), particularly when population densities of small mammals are high (Howe et al. 2002). Indeed, Parker et al. (2010) recorded 71% (2699 of 3808 plants) mortality of Common Evening Primrose (*Oenothera biennis*) transplants caused by Meadow Vole (*Microtus pennsylvanicus*) herbivory in an experimental old-field habitat; signs of stem girdling and root consumption were considered to be indicators of Meadow Vole herbivory (Parker et al. 2010).

As a result of observing such unexpected herbivory of the biofuels grasses in Guelph, we performed two additional studies. In mid-summer 2012, we transplant-

ed seedlings of *M. × giganteus* cultivars and seedlings of a *P. virgatum* cultivar inside and outside small mammal enclosures to follow their survival. In late autumn to early winter, we performed a live-trapping survey and mark-recapture analysis of the small mammal community within the transplant experiment to determine the species composition, abundance, and density of small mammals. Our aim was to identify the potential herbivore of the experimentally introduced grasses using this indirect evidence.

Methods

Study site

The study area was located at the University of Guelph Turfgrass Institute in Guelph, Ontario (43°32'56"N, 80°12'39"W), in a decommissioned apple orchard that has been maintained in an old-field succession by occasional mowing since approximately 1992 (Yurkonis et al. 2012). The old field was composed primarily of non-native grasses such as Kentucky Bluegrass (*Poa pratensis*), Smooth Brome (*Bromus inermis*), Quackgrass (*Elymus repens*), and Reed Canary Grass (*Phalaris arundinacea*). It included forbs such as vetches (*Vicia* spp.), thistles (*Cirsium* spp.), goldenrods (*Solidago* spp.), and asters (*Aster* or *Symphyotrichum* spp.).

The study area consisted of eight blocks. Each block comprised 16 experimental plots (5 × 5 m each) for a total of 128 plots, with a 1-m laneway between plots that was mowed two to three times during the summer. The experiment covered a total of 0.46 ha, including a 1-m buffer around each block. Each of the 16 plots within a block received transplants of one of four bioenergy grasses at one of four densities in a randomized design. The grasses were *M. × giganteus* cv. 'Illinois', 'Nagara', and 'Amuri' and Switchgrass (*P. virgatum* cv. 'cave-in-rock'). They were planted at densities of 0 (control), 4, 9, and 16, evenly spaced within a 4 × 4 m area central to each plot. This provided a 1-m buffer between transplants and the laneway. Ninety-six plots received transplants and 32 plots served as controls.

Miscanthus transplants were started from rhizomes (New Energy Farms, Leamington, Ontario) in the greenhouse and hardened off outdoors for one week prior to transplanting. Switchgrass transplants were started from seed (Ernst Conservation Seeds, Meadville, Pennsylvania) in the greenhouse and hardened off outdoors for two weeks prior to transplanting. *Miscanthus* was transplanted into the old field in mid-May 2012, and Switchgrass was transplanted in early June 2012. Care was taken to minimize disturbance of the local vegetation. Transplant survival and confirmed or putative cause of death were determined several times throughout the growing season, with a final census in autumn 2012.

Small mammal enclosures

Subsequent to the unexpected herbivory of transplanted biofuels grasses, we performed a small mam-

mal enclosure study in the same old-field habitat to examine the survival of transplants that had and had not been exposed to small mammals. Thirty-seven small mammal enclosures were installed in a completely randomized design in mid-summer 2012, and an equal number of controls (i.e., no enclosure) were established. Enclosures comprised solid PVC pipe (15 cm in diameter) inserted 10 cm into the ground, with 5 cm above-ground, and hardware cloth (1.3 cm mesh) fitted around the pipe aboveground to 30 cm in height. Enclosure tops were left open to allow for plant growth.

A single seedling was transplanted into each enclosure or control on 12 June 2012 for *Miscanthus* and on 16 July for Switchgrass. Because of the availability of transplants, 9 enclosures and 9 controls received the 'Illinois' cultivar, 7 enclosures and 7 controls received 'Nagara', and 6 enclosures and 6 controls received 'Amuri'; 15 enclosures and 15 controls received Switchgrass. Seedlings were watered after transplanting to reduce the risk of mortality due to drought. Transplant survival was assessed periodically until late autumn.

Small mammal survey

We used live-trapping and a mark-recapture analysis to census the small mammal community at the study location and determine the probable herbivore of the experimentally introduced grasses. Small mammals were live-trapped between 8 November and 13 December 2012 once trapping protocols and procedures were approved by the University of Guelph Animal Care Committee (protocol eAUP 1638) and trained personnel were available. One collapsible Sherman live-trap was placed within each of the 128 experimental plots so that traps were set at 6-m intervals. The eight blocks of the study area were divided into two sets, such that blocks 1 through 4 were trapped for three consecutive nights and blocks 5 through 8 were trapped for the following three consecutive nights.

Trapping methods followed field protocols developed by Falls et al. (2007). Traps were baited with cotton bedding, black sunflower seeds (*Helianthus* spp.), and one mealworm (*Tenebrio molitor*). Traps were set at dusk and checked at dawn the following morning. Shrews were identified to genus and immediately released to minimize mortality due to trapping and handling stress. All other animals were identified to species, sexed, and given a numbered monel metal ear tag (National Band and Tag, Newport, Kentucky) upon first capture.

Statistical analysis

For the enclosure experiment, we tested whether the probability of mortality due to herbivory differed between enclosures and controls (no enclosures) for transplants of each cultivar using χ^2 analysis with Yates correction.

For the small mammal survey, we standardized our estimates of small mammal abundance as the number of individuals captured per 100 trap-nights. Our block

study design also provided the spatial coverage desirable for a Schnabel mark-recapture analysis to allow the estimation of population density (Ryan 2011). This analysis assumes that individuals have the same probability of being captured in the first and subsequent samples, that the population is closed, that no marks fall off animals between captures, and that marks are correctly identified by the researcher.

We tested for differences in the number of small mammal captures among species/cultivars (plot types) and planting densities using generalized linear models with a Poisson probability distribution and log link function. We also tested for differences in captures between control plots that received no transplants and the combination of all plots that received transplants (vegetation type) using the same statistical procedure. The first model included block, plot, density, and plot \times density as fixed factors. The second model included block and vegetation type as fixed factors. These analyses were performed using SPSS Statistics 20 software (IBM).

Results

In the enclosure experiment, the number of transplants that died due to herbivory differed between late summer and late autumn (Table 1). By late summer,

only one Switchgrass transplant and no *Miscanthus* transplants had experienced mortality due to herbivory when small mammals were excluded, whereas all Switchgrass transplants and the majority of *Miscanthus* transplants (5 of 6, 8 of 9, and 5 of 7 transplants per cultivar) experienced mortality when small mammals were present ($P < 0.05$, Table 1).

However, by mid-October, stems within the enclosures began to be severed close to the base in a manner similar to those planted in the larger field experiment, indicating that herbivory occurred into the autumn. No holes were apparent in the soil, so the cages were not entered from below, and the cages were too narrow and tall for any animals larger than a small squirrel to enter from the top. In addition, several rhizomes had been partially excavated and showed evidence of having been chewed, similar to those in the larger field experiment. We thus surmise that small rodents learned to climb the cages to enter the enclosures.

Three species were caught during the live-trapping session: the Meadow Vole, the Northern Short-tailed Shrew (*Blarina brevicauda*), and a deer mouse (*Peromyscus* sp.). Meadow Voles far outnumbered any other species captured in the study area, with 4 times the total number of captures/recaptures of other species (Table 2).

TABLE 1. Total numbers of transplants that suffered mortality due to herbivory inside and outside small mammal enclosures at two census times in an old-field bioenergy grass transplant experiment at the University of Guelph Turfgrass Institute in Guelph, Ontario, in 2012. n is the total number of transplants in each treatment level. χ^2 critical value at $df = 1$, $\alpha = 0.05$ is 3.841. χ^2 values for *Miscanthus* \times *giganteus* cultivars 'Illinois' and 'Nagara' could not be determined at the final census date (16 October) due to complete mortality of these cultivars after herbivores learned to climb into the enclosure cages.

Census date	Treatment	Total number of plants consumed			
		Switchgrass 'cave in rock' ($n = 15$)	<i>Miscanthus</i> \times <i>giganteus</i> cultivars		
			'Amuri' ($n = 6$)	'Illinois' ($n = 9$)	'Nagara' ($n = 7$)
8 August	Exclosure	1	0	0	0
	No exclosure	15	5	8	5
	χ^2	22.63*	5.486*	11.03*	4.978*
16 October	Exclosure	1	2	9	7
	No exclosure	15	6	9	7
	χ^2	22.63*	3.375	–	–

* $P < 0.05$

TABLE 2. Summary of the number of individuals, total number of captures, standardized estimate of abundance, and estimate of population density (standard deviation in parenthesis) for species of small mammals caught in an old-field bioenergy grass transplant experiment at the University of Guelph Turfgrass Institute, Guelph, Ontario, in 2012. Population density of the Northern Short-tailed Shrew could not be estimated because Northern Short-tailed Shrews were not tagged (see Methods). Population density of the deer mouse could not be estimated because only one individual was captured during live-trapping.

Species	Total number of captures	Total number of individuals captured	Standardized estimate of abundance (per 100 trap-nights)	Population density (individuals/ha)
Meadow Vole	76	49	7.9	265 (14)
Northern Short-tailed Shrew ¹	19	–	1.9	–
Deer mouse	1	1	0.1	–

¹To minimize mortality due to handling stress, Northern Short-tailed Shrews were not marked; therefore, only the total number of captures is known.

Trapping success varied across the study period, ranging from 0 to 12 captures of Meadow Voles during a single trapping session. Using a Schnabel mark-recapture analysis, we estimated Meadow Vole population density as 275 individuals/ha (95% confidence intervals (CI) 273; 285 individuals/ha) for blocks 1 through 4 and 255 individuals/ha (95% CI 240; 264 individuals/ha) for blocks 5 through 8. Averaging these two estimates gives a mean Meadow Vole population density estimate of 265 (SD 14) individuals/ha for the study area during November and December 2012.

Northern Short-tailed Shrew and deer mouse population densities could not be estimated because Northern Short-tailed Shrews were not marked (following animal care protocols), and only one deer mouse was captured during the entire trapping session.

There was no significant difference in the number of Meadow Vole captures among plot types or planting densities (Table 3). There was also no significant difference in the number of Meadow Vole captures among control and transplanted plots (vegetation type, Table 3). The block effect was not significant in either analysis.

Discussion

By the time of trapping, the majority of transplants had been removed aboveground by herbivory. However, 24% of the 96 plots in the initial experiment that received transplants where the trapping was subsequently performed had 1–5 live transplants at the time of the last census in mid-October (HAH, unpublished data). In addition, *Miscanthus* rhizomes were present belowground and also presented a feeding opportunity for small mammals at the time of live-trapping.

At the time of trapping, the Meadow Vole was by far the most abundant species in the study area. It is primarily a herbivore, consuming mainly green shoots, with seeds and roots becoming important in winter (Lindroth and Batzli 1984). The species is known to dig up rhizomes and cut off both native and agricultural plants at the base to consume the nutrient-rich seeds (Reich 1981). In contrast, we captured few deer mice (one), which consume mainly insects, seeds, and fruits, with green plant matter forming only a small portion of the diet (Hamilton 1941). We also captured a small number of Northern Short-tailed Shrews; however, this species consumes mainly invertebrate and vertebrate prey, with plant matter such as seeds and berries composing only a small portion of the diet (Hamilton 1930, 1941; Whitaker and Ferraro 1963).

The patterns of herbivory observed in the study area were similar to those noted previously for Meadow Voles (i.e., stem girdling and root excavation and consumption) (Howe et al. 2002; Parker et al. 2010). We also observed abundant grass tunnels, which are indicative of the presence of Meadow Voles (Caras 1967; Reich 1981). Although we do not have direct evidence

TABLE 3. Results of two generalized linear models for frequency of Meadow Vole (*Microtus pennsylvanicus*) captures in an old-field bioenergy grass transplant experiment at the University of Guelph Turfgrass Institute in Guelph, Ontario, in 2012. Top: Among plots (four cultivars: *Miscanthus* × *giganteus* cv. ‘Illinois’, ‘Nagara’, and ‘Amuri’, and *Panicum virgatum* cv. ‘cave-in-rock’) and planting densities (four densities: 0 (control), 4, 9, and 16). Bottom: Among vegetation types, i.e., control (no transplants) and transplants of the four cultivars combined (as above).

Source	Likelihood ratio χ^2	df	P value
Block	5.876	7	0.55
Plot	1.291	3	0.73
Density	0.845	3	0.84
Plot × density	10.20	9	0.34
Block	4.082	7	0.77
Vegetation type	0.505	4	0.97

such as infra-red video of consumption of transplants or rhizomes or herbivore stomach content analysis, our observations and live-trapping data support the conclusion that Meadow Voles were the most likely herbivore of the *Miscanthus* and Switchgrass seedlings that were transplanted into the old-field habitat.

Meadow Vole population densities can vary dramatically among geographic locations, seasons, and habitats (Banfield 1974; Boonstra et al. 1998). In old-field habitat, Meadow Vole population densities average between 37 and 111 individuals/ha, but in peak years, they can reach in excess of 369 individuals/ha (Banfield 1974). Meadow Voles are active throughout most of the year, and population densities generally are at a minimum in late winter to early spring and then peak in late summer to early autumn (e.g., Johnson and Johnson 1982; Krebs and Wingate 1985).

In comparison with previous studies in old-field habitat (Banfield 1974), our estimate of 265 individuals/ha is a relatively high population density for the season in which these data were collected. This suggests that the population density of Meadow Voles in the previous summer (i.e., summer 2012) might have been exceptionally high or rapidly increasing, resulting in the rates of herbivory documented in this experimental grassland (HAH, unpublished). Additional live-trapping and experimental transplanting in years of differing Meadow Vole population density would indicate whether there is a lower population density threshold of Meadow Voles that would allow for increased transplant survival.

Population structure, season, and food density may be factors that influence home range size in Meadow Voles (Getz 1961; Jones 1990). However, Meadow Voles showed no difference in spatial distribution or frequency of capture among blocks, plot types, vegetation types, or transplanting densities (Table 3). The lack of association with the presence of the *Miscanthus* cultivars is somewhat surprising, given that rhizomes

were still present belowground and roots are an important winter food source for Meadow Voles (Lindroth and Batzli 1984). Trapping immediately after transplanting, when *Miscanthus* and Switchgrass densities were highest, might have improved the likelihood of detecting a distinct pattern of Meadow Vole distribution. The lack of a block effect indicates that capture numbers were similar across the whole study area. The observed uniform distribution of Meadow Voles during our trapping period may be a result of the decreased territorial behaviours that occur after the breeding season (McShea 1989, 1990).

In our experiment, stems of *M. × giganteus* were severed, but tops did not appear to have been consumed. However, some smaller shoots and the regrowth from cut shoots were consumed, so it is possible that the older plants were unpalatable to the herbivore.

Meadow Voles often show selective preferences for certain plant species in contrast to plant abundances within a habitat (Bergeron and Juillet 1979; Lindroth and Batzli 1984). Selective preferences have been related to plant tissue chemical content, specifically to low total phenolics (Bergeron and Jodoin 1987), but with little consistency in relation to concentrations of other compounds such as water, nitrogen, and alkaloids (Bélanger and Bergeron 1987; Marquis and Batzli 1989). Cafeteria-style feeding trials and plant tissue analyses would be necessary to determine whether Meadow Voles prefer *Miscanthus* and Switchgrass to other old-field species and whether this is related to nutritional content.

We do not know why the herbivore seemed to prefer the transplanted species, but this has also been observed previously. For example, Parker et al. (2010) recorded 71% mortality of transplanted Common Evening Primrose caused by Meadow Voles in an old field near Ithaca, New York. Similarly, Barney et al. (2012) noted minor mortality due to herbivory of *Miscanthus* and Switchgrass transplants in a field experiment in California, but did not attempt to identify the herbivore. In all cases, the plants affected were not naturally present in the habitat.

One hypothesis is that transplants of non-native plants that have been raised in a greenhouse or other protected environment may have lower levels of phenolics and other photo-protective chemicals and better nitrogen availability, and thus may be more palatable than those that have been grown in the field (Close and McArthur 2002). If this is the case, breeding programs that aim to reduce levels of lignins and other phenolics in certain plants to improve their use as biomass or forage (e.g., Sarath et al. 2007) could also make them more palatable to unwanted herbivores. Plant tissue analyses could be used to compare levels of photo-protective compounds in field- and greenhouse-grown plants as a first step in evaluating this hypothesis, followed by palatability tests with selected herbivores.

Selective herbivory by Meadow Voles and other vertebrate herbivores can dramatically reduce both plant diversity and the abundance of specific plant species (Howe and Brown 1999; Howe et al. 2002; MacDougall and Wilson 2007; Parker et al. 2010). Howe et al. (2002) compared experimental plantings of 18 prairie species in plots with and without Meadow Voles, and effects similar to our findings were evident only when the densities of Meadow Voles were >155 individuals/ha. This is a much lower density than our early winter population density estimate of 265 individuals/ha.

Selective herbivory of *M. × giganteus* and Switchgrass seedlings could be a factor affecting their establishment in planted fields and their invasion into novel habitats. Fields planted with these crops tend to have diverse assemblages of weedy species in the initial establishment years, and poor crop establishment could be related to competition from weeds as well as apparent competition mediated by vertebrate herbivory, particularly in years of high herbivore population density. More importantly, however, the escape and spread of these grasses into novel habitats could be mediated by vertebrate herbivory. Experiments will be required to assess the risk of invasion in habitats both with and without vertebrate herbivores such as Meadow Voles, and in years of high and low herbivore population density, to obtain a balanced assessment.

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