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Gene flow matters in switchgrass (*Panicum virgatum* L.), a potential widespread biofuel feedstock

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Abstract. There currently exists a large push for the use, improvement, and expansion via landscape modification of dedicated biofuel crops (feedstocks) in the United States and in many parts of the world. Ecological concerns have been voiced because many biofuel feedstocks exhibit characteristics associated with invasiveness, and due to potential negative consequences of agronomic genes in native wild populations. Seed purity concerns for biofuel feedstock cultivars whose seeds would be harvested in agronomic fields also exist from the agribusiness sector. The common thread underlying these concerns, which have regulatory implications, is gene flow; thus detailed knowledge of gene flow in biofuel crop plants is important in the formulation of environmental risk management plans. Here, we synthesize the current state of knowledge of gene flow in an exemplary biofuel crop, switchgrass (*Panicum virgatum* L.), which is native to eastern North America and is currently experiencing conventional and technological advances in biomass yields and ethanol production. Surprisingly little is known regarding aspects of switchgrass pollen flow and seed dispersal, and whether native populations of conspecific or congeneric relatives will readily cross with current agronomic switchgrass cultivars. We pose that filling these important gaps will be required to confront the sustainability challenges of widespread planting of biofuel feedstocks.

Key words: bioenergy; environmental risk; hybridization; introgression; invasiveness; seed purity; sustainability.

The current push for widespread agronomic planting of dedicated biofuel feedstocks in the United States comes from a number of fronts. Arguably the most influential driver at present involves meeting U.S. government-mandated biofuel utilization milestones set forth in bioenergy-associated Acts, especially the Energy Policy Act of 2005, the Energy Independence and Security Act of 2007, and the Food, Conservation, and Energy Act of 2008. In brief, these provisions call for a short-term (over the next few decades) exponential increase in the amount of liquid transportation fuels in the United States originating from renewable energy sources (to 36 billion gallons by 2022 [1 gallon = 3.79 L]), and provide subsidies, especially for cellulosic biofuel feedstocks, to attain these goals. Not only are such policies expected to lessen U.S. dependence on foreign oil and promote rural development, but they are also integral to and consistent with science-based climate change mitigation efforts (Liebig et al. 2008, Schmer et al. 2008, Jaradat 2010, Geogescu et al. 2011). The amount of non-crop land in need of conversion to accommodate renewable fuel benchmarks via feedstocks will not be trivial (requiring a doubling of the current approximately 600 000 km^2 in corn and soybean production [Robertson et al. 2008, Barney and DiTomaso 2010, Dauber et al. 2010]); indeed, this projected “energy sprawl” (McDonald et al. 2009) of dedicated biofuel feedstocks is expected to result in the largest landscape alteration in the United States and elsewhere since the beginnings of industrial agriculture (Altieri 2009, Raghu et al. 2011).

Reaching renewable biofuel production goals has also prompted and will continue to require conventional, molecular, and transgenic breeding efforts (Gressel 2008, Jakob et al. 2009). The aims of such efforts are to sustainably increase biomass yields, maximize end-fuel output through increased conversion efficiency, and allow for feedstock production under a variety of environmental conditions. Indeed, significant advances

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have been made along these fronts in a number of feedstocks capable of widespread agronomic production (Ray et al. 2010, Fu et al. 2011).

Widespread planting of biofuel feedstock plants and improvements of their traits carry environmental, agribusiness, and regulatory concerns. One concern is that improvement of certain traits (e.g., rapid early-season growth, partitioning of nutrients belowground in the fall, high water-use efficiency) in biofuel feedstocks, which have been shown to be invasive (Buddenhagen et al. 2009, Chimera et al. 2010), will only exacerbate their invasive potential (Raghu et al. 2006). While such "weedy" invasiveness has been a focus of biofuel feedstock environmental concerns, there also exists concern about the movement of biofuel feedstock genes via profuse pollen dispersal into native wild populations, which could have negative consequences for local native population persistence under conditions of outbreeding depression and decreased hybrid fitness (Byrne and Stone 2011). There also exist seed purity concerns in an agribusiness context, in which genes from certain planted cultivars could enter other cultivar "populations" via field-to-field gene flow via pollen and/or seed. It is also possible that genes from wild conspecific or relative populations may enter the agronomic cultivar "populations" (see Lavigne et al. 2002). The purity of hybrid seed sources has long been a subject of scrupulous concern in the agribusiness sector (see Laverack and Turner 1995, Parlivliet 2007, Naresh et al. 2009), and ensuring seed purity in "seed farms" will be necessary. A related concern is the challenge of regulation of potential gene flow of transgenic biofuel feedstocks to nontransgenic crops and wild relatives that is conducted by the USDA APHIS Biotechnology Regulatory Service (see Kausch et al. 2010, Moon et al. 2010, Bagavathiannan et al. 2011). Proceeding with widespread planting of biofuel feedstocks without adequate information on gene flow will prevent estimation of environmental and economic risks, which can carry ecological and economic costs (see Mack et al. 2000) to be borne by a large number of stakeholders (see Lonsdale and FitzGibbon 2011). Hence, detailed knowledge of gene flow of targeted biofuel feedstocks, whether native or not, is of paramount importance for the implementation of sustainable agronomic efforts.

Arguably one of the most "attractive" biofuel feedstocks for which gene flow issues should be of high concern is the perennial bunchgrass, switchgrass (*Panicum virgatum* L.). Interest in switchgrass as a dedicated lignocellulosic biofuel feedstock dates back to research conducted in the 1980s (McLaughlin and Kszos 2005, Wright and Turhollow 2010). In these early efforts, switchgrass outperformed most other potential feedstocks in terms of yields throughout the central and eastern United States (Wright and Turhollow 2010). Later, a study of numerous inputs and outputs associated with representative biofuel crops resulted in switchgrass being viewed favorably (Groom et al. 2008). Lastly, one critical facet regarding switchgrass is that it has been touted from the beginning as a feedstock capable of being grown on lands of marginal quality (see Wright and Turhollow 2010). This last factor set switchgrass apart from most other alternatives, and recent modeling efforts further illustrate its lure as a feedstock-of-choice by projecting high yields across much of the eastern United States, especially in the mid-South (Jager et al. 2010, Wullschleger et al. 2010). While envisioned planting of switchgrass in new settings could assist in carbon sequestration efforts (Skinner and Adler 2010), the unprecedented change in the landscape carries with it potential plant community and ecosystem concerns wherein switchgrass may become invasive or contribute to local native population extinction. In light of current conventional and molecular breeding efforts (see Sanderson et al. 2006, Bouton 2007, Jakob et al. 2009) and successful genetic transformation (Fu et al. 2011) for switchgrass, understanding the invasibility risks—both out of and within the agronomic matrix—will require filling knowledge gaps in our understanding of switchgrass gene flow.

Detailed measures of switchgrass gene flow are lacking. Though switchgrass population genetic structure, especially of agronomic cultivars, has been a subject of interest, inferences of gene flow from such studies have not been suggested. Genetic relatedness of cultivars has been investigated using a variety of molecular markers (Gunter et al. 1996, Narasimhamoorthy et al. 2008, Cortese et al. 2010), and some patterns of geographic structure do exist. Moreover, these studies emphasize that variation observed within populations exceeds that exhibited among populations. This could result from substantial gene flow among populations, or the slow-to-materialize differentiation among populations that were once more continuous. A shortcoming of these works is the lack of sampling from existing native populations (but see Casler et al. 2007); samples typically originate from the Germplasm Resources Information Network and are specific to agronomic cultivars. Though the samples may be representative of original populations in this far-from-domesticated species, there is a need to quantify contemporary measures of gene flow, including those from native populations.

In the literature, switchgrass is typically characterized as an obligate outcrosser. Thus, pollen must travel from one genetic individual to another for sexual reproduction to take place. The blanket statement regarding switchgrass's status as an obligate outcrosser is most likely based on Talbert et al.'s (1983) work wherein they found that bagged inflorescences produced $<1\%$ as many seeds as open-pollinated inflorescences (more thoroughly confirmed by Martinez-Reyna and Vogel [2002]). The self-incompatibility (and hence "required" cross-pollination) in switchgrass's breeding system has been utilized in the development of agronomic hybrids exhibiting heterosis for certain traits (e.g., biomass yield;

Martinez-Reyna and Vogel 2008, Vogel and Mitchell 2008). Successful crossing in switchgrass also requires equivalent numbers of chromosomes and ploidy levels (see Martinez-Reyna and Vogel 2002). Like other Panicums, and grasses in general, switchgrass exhibits various levels of ploidy (e.g., tetraploid and octaploid); ploidy levels are related to the two major ecotypes (lowland cultivars tend to be tetraploid; upland cultivars tend to be octaploid), though exceptions do occur (see Narasimhamoorthy et al. 2008, Zalapa et al. 2011).

The potential invasion of agronomic switchgrass into non-agronomic-field portions of the landscape matrix could occur in two primary ways. First, introgression into existing wild or feral switchgrass populations would, by definition, require pollination (typically via crop pollen) and subsequent backcrossing events (Rieseberg and Wendel 1993). Herein, the following prerequisites must be satisfied: the pollen recipient must flower in synchrony with the donor cultivar, be in close enough proximity (currently of unknown distance for switchgrass) to receive viable wind-dispersed pollen, and, must also share the same ploidy level. Because switchgrass is native in much of eastern North America where it is being considered as a dedicated biofuel feedstock, this avenue of invasion is indeed possible (see Simberloff 2008). While molecular evidence for such crop-to-wild introgression (nontransgenic and transgenic) is rare among plant species (Kwit et al. 2011), it is feasible (see Ellstrand 2003). The fitness of hybrids and subsequent backcrossed hybrids will ultimately influence whether invaded populations will experience population growth or decline. Ultimately, seeds with genes from agronomic cultivars would need to be dispersed into new locations, from which founder populations could spread for invasion to take place. Having gravity-dispersed seeds lacking any fruiting characteristics promoting long-distance seed dispersal, this avenue of invasion is likely limited; though escape and establishment in roadside locations along transport roads are a possibility (see Garnier et al. 2006, Knispel and McLachlan 2010). Interestingly, despite the multiple non-biofuel uses of planted switchgrass throughout the landscape in the United States (e.g., forage crop mix, conservation, erosion control, horticultural trade; see Heaton et al. [2004]), evidence of spread from these locations is lacking in the literature. This could change, however, with the utilization of select, improved, and transgenic biofuel cultivars, which could also be exacerbated by new, large-scale switchgrass cultivation.

The mechanism for the mixing of genes of multiple agronomic cultivars from separate agronomic fields ultimately relies upon successful hybridization. In this case, as long as flowering synchrony and ploidy levels matched, the only additional requirements entail the first steps of introgression—successful cultivar × cultivar crossing (via pollination) and viable seed set—and subsequent (and perhaps unknowing) use of hybrid seed. Pure seed collection efforts from a particular cultivar planted in a particular field may be compromised by adventitious presence of genes from other cultivars planted in nearby fields; seeds from this scenario could not be sold as pure seed from the maternal cultivar. Ensuring seed purity would depend on obtaining sufficient biological data to estimate isolation distances, a practice utilized when releasing transgenic crops (e.g., Luna V. et al. 2001).

A number of important aspects of switchgrass gene flow necessary to ascertain environmental and economic risks have yet to be determined, and hence constitute areas of needed research. From a pollination standpoint, little is known about pollen viability (how long pollen can survive post-anthesis), and no published studies exist regarding switchgrass pollen flow distances. Recent work places switchgrass pollen viability in the same range as those of other agronomic grasses (half life of approximately 2 h under ideal conditions [Ge et al. 2011]); no other published information is currently available on this subject. Sophisticated modeling efforts have been conducted on pollen flow in other biofuel crops (Wang and Yang 2010), and are arguably needed for switchgrass. Though it may be expected that switchgrass would be incapable of crossing with close relatives in the genus *Panicum* (see Spellenberg 1970), there are no published data to this effect, despite existing and well-accepted *Panicum* phylogenies (see Aliscioni et al. 2003) that could be used to identify closest relatives in particular locations. Neither have there been published studies on the ability for agronomic cultivars of switchgrass to cross with or introgress into wild switchgrass populations, or the characteristics of their putative F_1 hybrids. No published work has substantiated vertebrate-mediated seed dispersal probabilities or distances. While switchgrass seeds are assumed to be depredated by rodents (Haught and Myster 2008) and seed-eating birds, both types of animals are capable of moving some amount/proportion of viable seeds to new locations in the landscape. Last, to help document gene flow involving agronomic switchgrass, discovery of molecular markers diagnostic for specific cultivars will be needed. In the case of switchgrass, the search for molecular markers has been relegated to finding those (e.g., SSR, STS, and SNP markers) associated with marker-assisted selection for traits of interest (Okada et al. 2010).

Switchgrass is but one of countless candidate species for biofuel feedstocks that could become larger parts of a 21st-century agronomic landscape in the United States. With continued research and development, and future incentives, switchgrass could expand further into the bioenergy sector through processes such as co-firing with coal for electricity (Qin et al. 2006, Aravindhakshan et al. 2010, Khanna et al. 2011). Given its status as a leading bioenergy feedstock, it is imperative that gaps in our understanding of switchgrass gene flow are filled to better formulate risk management plans. Similar scrutiny may be needed for risk assessment and mitigation plans for other candidate biofuel feedstocks (see Cousens 2008, Davis et al. 2010, Byrne and Stone 2011), and the process of gene flow needs to be better incorporated into discussions of sustainable bioenergy and environmental risk management.

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