

10-19-2015

Switchgrass Germplasm Resources

Michael D. Casler

USDA-ARS, michael.casler@ars.usda.gov


Kenneth P. Vogel

University of Nebraska-Lincoln, Ken.Vogel@ars.usda.gov

Melanie Harrison

USDA-ARS

Follow this and additional works at: <http://digitalcommons.unl.edu/agronomyfacpub>

 Part of the [Agricultural Science Commons](#), [Agriculture Commons](#), [Agronomy and Crop Sciences Commons](#), [Botany Commons](#), [Horticulture Commons](#), [Other Plant Sciences Commons](#), and the [Plant Biology Commons](#)

Casler, Michael D.; Vogel, Kenneth P.; and Harrison, Melanie, "Switchgrass Germplasm Resources" (2015). *Agronomy & Horticulture -- Faculty Publications*. 843.

<http://digitalcommons.unl.edu/agronomyfacpub/843>

This Article is brought to you for free and open access by the Agronomy and Horticulture Department at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in Agronomy & Horticulture -- Faculty Publications by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.

Switchgrass Germplasm Resources

Michael D. Casler,[★] Kenneth P. Vogel, and Melanie Harrison

ABSTRACT

Switchgrass (*Panicum virgatum* L.) is an important native grass and dominant member of the tallgrass prairie ecosystem. It is used for conservation, restoration, livestock feed production, and bioenergy feedstock production. The purpose of this review is to describe the biological and geographical basis for switchgrass germplasm diversity and to provide a resource for scientists and outreach personnel to find switchgrass germplasm to meet their needs. Upland and lowland ecotypes represent the most important polymorphism in switchgrass, with distinct but overlapping geographic distributions. Variation in ploidy exists within both ecotypes, with $2n = 4x = 36$ the dominant ploidy in the lowland ecotype and $2n = 8x = 72$ the dominant ploidy in the upland ecotype. Ploidy is a strong barrier to gene flow, but ecotype is a weak barrier, with up to 10% of random individuals demonstrating some evidence for upland-lowland hybridization in their ancestry. Latitudinal and, to a lesser extent, longitudinal differentiation exists within each ecotype, such that most wild populations and cultivars are not well adapted more than one hardiness zone from their place of origin. Plant breeding can alter this relationship by creating populations with improved cold tolerance, for example, increasing the adaptation range of an individual cultivar. The USDA National Plant Germplasm System maintains the national switchgrass collection, which is available for research and breeding purposes.

M. Casler, USDA-ARS, U.S. Dairy Forage Research Center, 1925 Linden Dr., Madison, WI 53706-1108; K.P. Vogel, USDA-ARS (retired), Grain, Forage, and Bioenergy Research Unit, 137 Keim Hall, Dep. Agronomy and Horticulture, Univ. of Nebraska-Lincoln, Lincoln, NE 68583-0937; M. Harrison, USDA-ARS, Plant Genetic Resources Conservation Unit, 1109 Experiment Street, Griffin, GA 30223. Received 5 Feb. 2015. Accepted 30 Apr. 2015. [★]Corresponding author (mdcasler@wisc.edu).

Abbreviations: ybp, years before present; GRIN, Germplasm Resources Information Network; M, million; NPGS, National Plant Germplasm System; NRCS, Natural Resources Conservation Service; PMC, Plant Materials Center; PI, Plant Introduction; SCS, Soil Conservation Service.

SWITCHGRASS (*Panicum virgatum* L.) has undergone a significant biological and sociological transformation since 1992 when it was chosen as one of two model species for bioenergy feedstock development. Research, outreach, and education activities on switchgrass have dramatically expanded since 1992, with significant increases in funding, personnel, uses, and geographic range (Sanderson et al., 2007). Conservation and restoration, including habitat restoration and natural resource conservation initiatives, pastures and grazing, hay or silage production, and bioenergy feedstock production represent the most common uses of switchgrass. Elevation to model species status has increased social consciousness of this and related species that includes both scientific and nonscientific segments of society. Increases in funding have resulted in the development of research teams that would not have been possible otherwise, leading to significant biological advancements in the fields of crop production, ecology, soil science, breeding, genetics, and genomics.

Germplasm resources form one of the most fundamental common themes of all switchgrass research, education, and

Published in Crop Sci. 55:2463–2478 (2015).

doi: 10.2135/cropsci2015.02.0076

© Crop Science Society of America | 5585 Guilford Rd., Madison, WI 53711 USA

All rights reserved.

This document is a U.S. government work and is not subject to copyright in the United States.

Table 1. Summary of the most common range of phenotypic values for upland and lowland switchgrass plants grown in direct-comparison experiments in Wisconsin and New Jersey (40 to 42° N latitude) (Casler, 2005; Cortese et al., 2010).

Ecotype	Heading date [†]	Plant height	Flag leaf length	Flag leaf width	Number of tillers	Stem diameter	CIE x-scale color [‡]	CIE y-scale color [‡]
	doy	m	cm	mm	No. plant ⁻¹	mm		
Upland	180–195	0.9–1.7	32–48	9–11	150–300	3–5	x < 0.4	0.4 < y < 0.8
Lowland	200–220	1.9–2.2	50–58	12–14	40–90	5–7	x < 0.2	0.2 < y < 0.4

[†] Heading date = day of year (doy).

[‡] Color reference: McLaren (1976); <http://www.colorbasics.com/CIESystem/>.

outreach activities. Switchgrass germplasm is highly diverse in morphology, physiology, adaptation, and production, and a surprisingly large amount of this diversity has practical, sociological, and/or economic value for one use or another. Choosing an unadapted population or cultivar can have far-reaching consequences for conservation, restoration, livestock feed production, or bioenergy feedstock production. Nearly all of these consequences are negative. The purpose of this review is to describe the biological and geographical basis for switchgrass germplasm diversity and to provide a resource for scientists and outreach personnel to find switchgrass germplasm to meet their needs. The geographical focus of the review is confined to North America, specifically the species' range before fragmentation of the tallgrass prairie and savanna ecosystems, the remnants of which still serve as a living germplasm repository.

WHAT IS SWITCHGRASS?

Switchgrass is one of the dominant grasses of the tallgrass prairie and its associated ecosystems. These associated ecosystems include oak savanna, pine barrens, forest margins, and some wetlands that form transition habitats between the ancient tallgrass prairie and eastern forest ecosystems. Switchgrass can be found in thousands of prairie remnants scattered through much of the original species range (Casler et al., 2012). Many of these remnant ecosystems have been preserved through the foresight of various governmental and nongovernmental organizations and private landowners (Hopkins et al., 1995b). These remnant prairies, scattered throughout much of the area from the Rocky Mountains to the Atlantic Ocean, from Nova Scotia to Florida, and from the Dakotas to Mexico (Stubbendieck et al., 1991), are the source of all switchgrass germplasm. While it is not shown on maps or well documented, there are also additional remnant prairie sites in Mexico, Cuba, and Canada. Most of these remnants are very small, ranging in size from a 0.1 to 10 ha, but a few extensive prairies still survive, for example, the Flint Hills of Kansas, the Osage Prairie of Oklahoma, and the Sand Hills of Nebraska (Vogel, 2004).

Switchgrass is an erect warm-season grass with the C4 photosynthetic pathway (Waller and Lewis, 1979). Most switchgrass plants are caespitose, resulting in formation of bunches or clumps of switchgrass in long-term stands.

Some plants have short rhizomes that can result in formation of sod in the long term. The switchgrass inflorescence is a diffuse panicle, 15- to 55-cm long, with spikelets toward the end of its branches (Gould, 1975; Hitchcock, 1951). Spikelets are two-flowered with a perfect upper flower and a sterile or staminate lower flower. Florets are 3- to 5-mm long, glabrous, and awnless, and the fertile floret has a smooth and shiny lemma. Switchgrass leaves have rounded sheaths and flat blades that are 10- to 60-cm long. Ligules are hairy with fringed membranes, 1.5- to 3.5-mm long. Switchgrass reproduces sexually by seed and vegetatively by tillers or rhizomes.

Switchgrass seed is heavy and smooth, easily harvested, threshed, and cleaned using conventional equipment (Cornelius, 1950; Wheeler and Hill, 1957). A seed consists of a caryopsis, tightly held between an indurate and smooth lemma and palea, with the margins of the lemma rolled over the margins of the palea. Glumes are almost completely removed during threshing and cleaning. Seed size varies considerably among and within cultivars, but 850 seeds g⁻¹ is considered to be an average value (Wheeler and Hill, 1957).

Nearly all these traits show considerable variation within the species. The two main ecotypes, upland and lowland, form the principal morphological and physiological division within switchgrass (Brunken and Estes, 1975; Porter, 1966). Lowland types are found on flood plains and other areas subject to inundation, while upland types are found in upland areas that are not subject to flooding but may be subject to frequent droughts. Lowland switchgrass is taller, later in heading and flowering, has longer leaf blades, fewer tillers per plant, and larger stem diameter than upland switchgrass (Table 1; Fig. 1A). A bluish waxy bloom on leaf sheaths and blades is typically associated with the lowland phenotype, although there can be variation in this trait within some accessions, potentially causing confusion in using this as a diagnostic trait. The wealth of diversity between and within ecotypes is illustrated in Fig. 1B.

Lowland ecotypes are the dominant form in the southern portion of the range, while upland ecotypes are the dominant form in the northern portion of the range, with a transition zone in which both ecotypes are well adapted (Fig. 2). In general, upland ecotypes are well adapted to USDA Hardiness Zones 3 to 7 and lowland ecotypes are well adapted to USDA Hardiness Zones 5 to 9. Exceptions

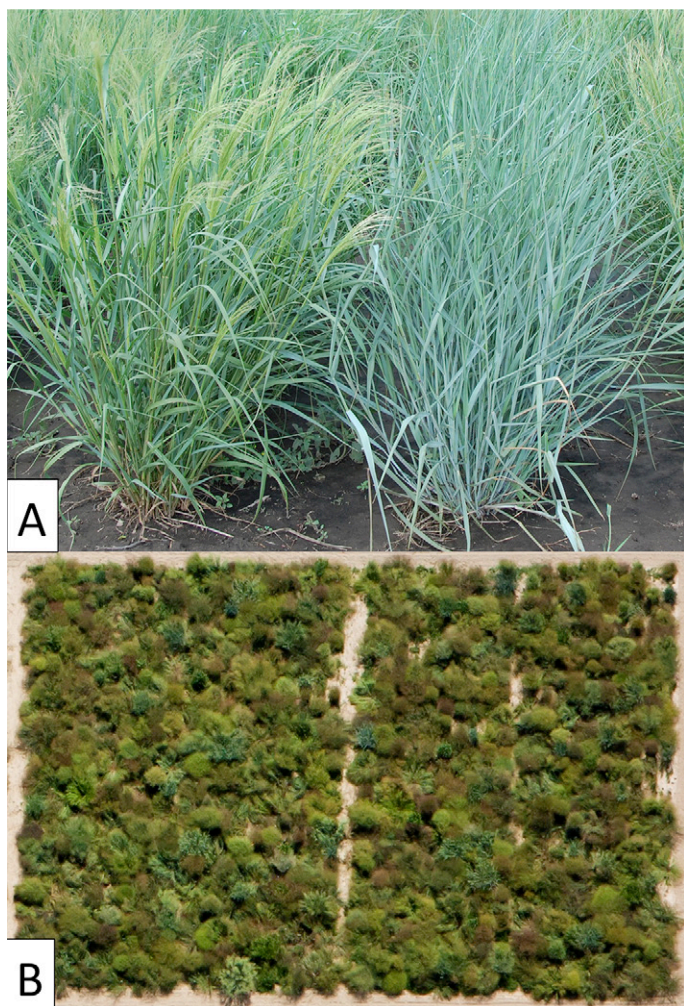


Figure 1. A. Classic upland phenotype on left vs. classic lowland phenotype on right. Photo taken on 1 Aug. 2012 near Arlington, WI (MDC). B. Aerial view of the northern association panel of switchgrass (Lipka et al., 2014) that contains 600 diverse genotypes representing nearly the entire range of switchgrass within the United States. Plants are spaced 0.9-m apart, and the full dimensions of the photo are 40 × 27 m. Photo courtesy of E.S. Buckler, USDA-ARS, Ithaca, NY.

to this derive from microclimate effects due to altitude, soil type, moisture availability, or specific pest problems. Plant breeding has also played a role in expansion of the adaptation range of improved or modified switchgrass populations.

SWITCHGRASS GENETICS

Switchgrass has a base chromosome number of $x = 9$ (Gould, 1975). Chromosome numbers of adult plants have been reported to range from $2n = 2x = 18$ to $2n = 12x = 108$ (Nielsen, 1944; Barnett and Carver, 1967). Switchgrass has small chromosomes that are very difficult to count accurately, and aneuploidy is rampant, particularly at the higher ploidy levels (Costich et al., 2010). Most aneuploidy at the octoploid level derives from genotypes with fewer than the expected number of chromosomes, suggesting that chromosome loss is a frequent occurrence and that there is considerable gene duplication within the species (Costich et al., 2010).

Most plants of switchgrass are tetraploid ($2n = 4x = 36$), octoploid ($2n = 8x = 72$), or aneuploid, with chromosome numbers ranging slightly above or below $2n = 36$ or slightly below $2n = 72$. Flow cytometry can be used to classify switchgrass plants according to their euploid levels (Lu et al., 1998) but is not sufficiently sensitive or repeatable to classify plants according to level of aneuploidy or exact chromosome number (Costich et al., 2010). One diploid plant ($2n = 2x = 18$), more accurately termed “dihaploid” as described below, was reported in the early chromosome investigations of switchgrass (Nielsen, 1944), but that site has since been urbanized (Casler, personal observation, 1996). Additional dihaploids have been recently discovered following two different intensive “dihaploid screens” in two laboratories. Dihaploid screens consisted of “reduced heterozygosity measured by DNA markers” in the USDA-ARS Albany, CA, laboratory (Young et al., 2010) and twin seedlings or polyembryony in the USDA-ARS Madison, WI, laboratory (Price and Casler, unpublished data, 2010). Regardless of the screening method, all dihaploids discovered in this manner were very low in vigor, growth rate, and tillering capacity. Apart from these observations of a small number of dihaploid individuals, there are no known morphological, physiological, or agronomic traits to distinguish switchgrass plants with different ploidy levels. Hexaploids ($2n = 6x = 54$) have been reported in several studies but have not been verified in recent cytological and flow cytometry investigations, except for occasional individuals at very low frequencies (Costich et al., 2010; Narasimhamoorthy et al., 2008). True hexaploids are fairly rare in nature (Vogel, 2004), and many of the putative hexaploids reported in the literature are probably due to errors in chromosome counts or were aneuploids that had lost significant numbers of chromosomes from the octoploid level to give the appearance of stable hexaploids. It is also possible that hexaploids may serve as a bridge for rare gene flow between tetraploid and octoploid levels (Zhang et al., 2011b). The discovery of sympatric tetraploids, hexaploids, and octoploids in two prairie remnants (Sterling Barrens Natural Area, Wisconsin, and Oscar Scherer State Park, Florida) lends credence to this hypothesis (Costich et al., 2010).

Tetraploid switchgrass has 18 linkage groups arranged in two highly homologous genomes (Okada et al., 2010). Chromosome pairing in tetraploids and octoploids is primarily bivalent, suggesting largely preferential pairing within homologous genomes and disomic segregation patterns (Martinez-Reyna et al., 2001; Riley and Vogel, 1982). Tetraploid switchgrass is an allotetraploid that behaves like a functional diploid. It is classified as a diploidized palaeopolyploid with a complex lineage that includes interspecific hybridization between unknown ancestors, polyploidization, whole-genome duplication, and diploidization (Lu et al., 2013; Le Comber et al., 2010;

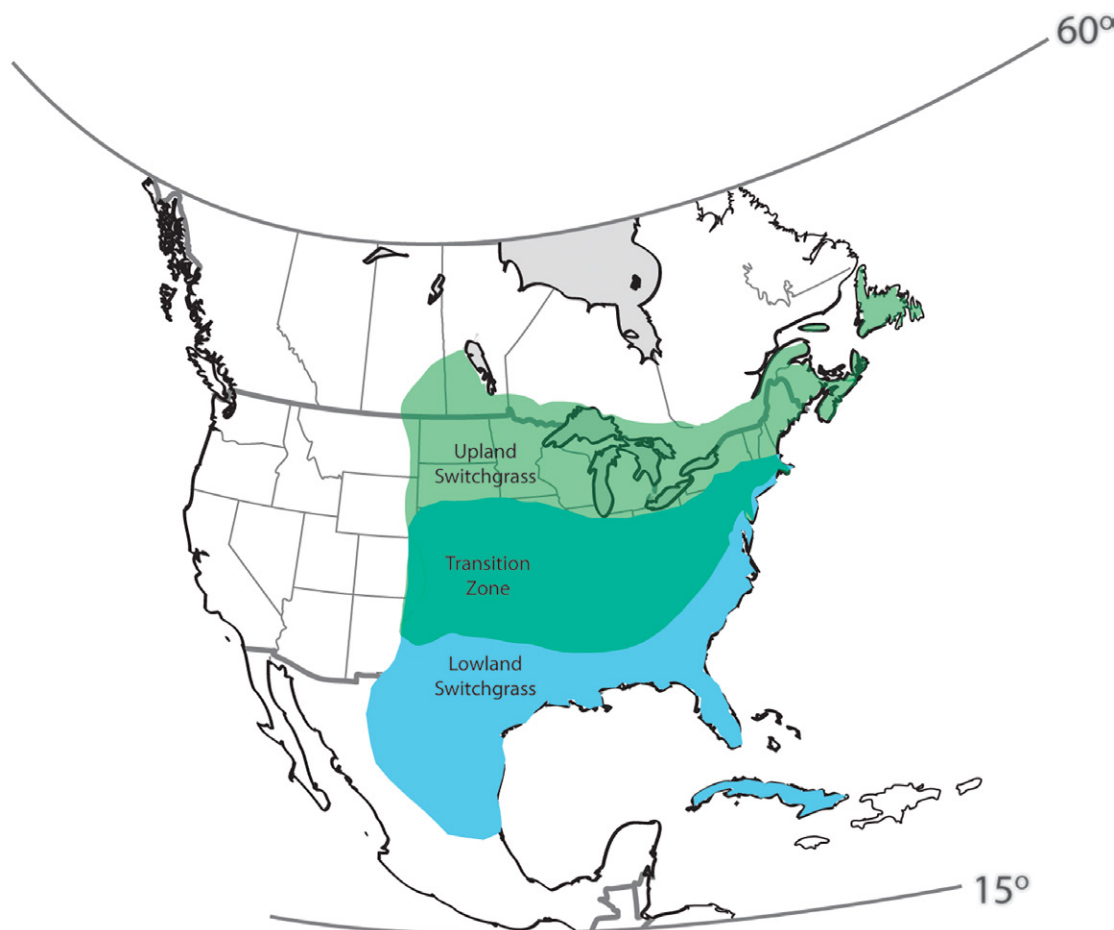


Figure 2. Generalized distribution of upland and lowland switchgrass, including the geographic areas for which each ecotype can be found in remnants of its natural range, and the expected areas of agronomic fitness for cultivated use of each ecotype.

Wolfe, 2001). Because chromosome pairing in octoploids is more complex, with higher frequencies of multivalents than in tetraploids (Barnett and Carver, 1967), octoploids most likely consist of 18 linkage groups in an autotetraploid segregation pattern, although this has yet to be verified by segregation and linkage experiments.

Switchgrass has a strong gametophytic self-incompatibility system similar to the S-Z system within temperate members of the Poaceae (Martinez-Reyna and Vogel, 2002). Pollen is dispersed by wind, and bagging panicles to exclude outside pollen typically results in less than 1% seed set (Martinez-Reyna and Vogel, 2002; Talbert et al., 1983). Despite this general observation, rare genotypes are capable of high rates of self-pollination (Liu and Wu, 2012; Liu et al., 2014), and these genotypes can be used to create inbred lines at least up to the S_3 generation (Sripathi and Casler, unpublished data, 2015).

A postfertilization incompatibility system, similar to the endosperm balance number system in other species, prevents the development of viable seed between tetraploid and octoploid parents (Martinez-Reyna and Vogel, 2002). Vogel (2004) suggested this hybridization barrier is responsible for the rarity of hexaploid plants in native prairies. Many prairie remnant populations possess both

tetraploid and octoploid individuals (Casler et al., 2006; Costich et al., 2010), but these largely represent separate and distinct populations (Vogel, 2004).

Upland and lowland ecotypes of switchgrass have classically been defined by visual assessment of plant traits, such as those listed in Table 1. Early studies of both nuclear DNA markers and cpDNA sequences suggested the presence of consistent discriminatory polymorphisms in both the nuclear and chloroplast genomes. The most consistent and discriminatory of these were a 49-bp indel in the chloroplast intron *trnL* (UAA) (Missaoui et al., 2006) and a restriction fragment length polymorphism within the gene for the large subunit of ribulose-1,5-bisphosphate carboxylase/oxygenase (Hultquist et al., 1996; Martinez-Reyna et al., 2001). These two cpDNA polymorphisms led to the use of the term “cytotype,” or cytoplasm type, as a descriptive moniker for these two races of switchgrass (Hultquist et al., 1996; Vogel, 2004). Because “cytotype” is a confusing and cryptic term to most scientists, the term “ecotype” has been more recently adopted as the descriptive term for the upland and lowland polymorphisms.

Upland and lowland switchgrass ecotypes can be readily hybridized at the tetraploid level. Seed fertility, meiosis, and bivalent chromosome pairing are completely

normal in tetraploid upland \times lowland hybrids, indicating high homology between upland and lowland genomes (Martinez-Reyna et al., 2001). In a survey of upland and lowland accessions that spanned nearly the full range of switchgrass in the United States, Zhang et al. (2011b) found approximately 10% of individuals to have evidence of upland \times lowland hybridization in their ancestry.

BIOGEOGRAPHY SPAWNS DIVERSITY

The diploid progenitors of switchgrass are thought to have diverged from their closest relatives approximately 2 million (M) years before present (ybp) (Huang et al., 2003), but recent evidence suggests these events may have occurred as early as 4 M ybp (Zhang et al., 2011a). Switchgrass originated by polyploidization sometime between 4 and 1.5 M ybp, while the earliest 4x-to-8x polyploidization events and divergence between upland and lowland types occurred between 1.5 and 1 M ybp (Zhang et al., 2011a). Since that time, major continental glaciation events, with distinct interglacial (ice-free) periods, have occurred on approximately a 100,000-yr cycle (Bintanja and van de Wal, 2008). Repeated glaciation of a large portion of North America would have caused massive cyclic migrations of all the major North American ecosystems, including the major grasslands, essentially a repeated cycle of retreat to southern North American and Central American refugia, followed by recolonization of central North America (Deevey, 1949). Both the extinction and recolonization phases would each have required thousands of years because of the slow rate of temperature change and the relatively sessile nature of perennial plants. Repeated exposure to massively extreme climate change favored species with sufficient levels of residual genetic variability to allow successful adaptive shifts during these periods of greatest climate change. Gene duplication from polyploidization, continual genetic recombination due to self-incompatibility and frequent pollen and seed migration, and stabilizing selection during long and stable climate periods have all probably been major forces allowing switchgrass to survive these massive extinction and recolonization cycles of the past million years (Stebbins, 1985). Indeed, as Stebbins (1985) hypothesized, the octoploid form of switchgrass has colonized a significantly broader distribution of native habitats, existing across essentially the entire range of the species, than the tetraploid form, which is fairly rare in the northern portion of the range (Zhang et al., 2011a,b).

The last of these glaciation events, the Pleistocene Glaciation, ended 14,000 to 12,000 ybp (Berger et al., 1987). Fossil evidence, based on grassland and forest ecosystem pollen, suggests that tallgrass prairie ecosystems did not become stable until 9000 to 5000 ybp (Clark et al., 2001; Jacobson and Grimm, 1986; Kelley et al., 2006). Switchgrass is thought to have survived the Pleistocene Glaciation

in three refugia located in the southern United States, including parts of northern Mexico and Cuba, which was then connected by land bridge to Florida. McMillan (1959) described these refugia as: a western semi-montane region; a central humid region with rich, fertile soils; and a southeastern region, perhaps along the northern and eastern edges of the Gulf of Mexico. Upland switchgrass originated largely from the western montane and western Gulf Coast refugia, while lowland switchgrass originated from throughout the Gulf Coast region (Zhang et al., 2011a,b).

As the glaciers retreated and the continent warmed, switchgrass and many other members of these ecosystems rapidly moved north, recolonizing grasslands and many other associated habitats. Because this process was repeated many times since the origin of the diploid progenitors and the polyploidization events that created modern switchgrass, genetic variation for a wide range of adaptive phenotypes has existed for hundreds of millennia and was likely preserved in these glacial refugia. Furthermore, the existence of natural upland \times lowland hybrids and backcrosses of switchgrass (Zhang et al., 2011b) suggests that significant hybridization and mixing has occurred between populations derived from different refugia. Because switchgrass is sessile, it was forced to rely on birds and mammals as vectors to transport seeds from southern refugia to reestablish northern prairies (Ernst et al., 1992; Ocumpaugh et al., 1996; Pakeman, 2001; Webb, 1986). As such, multiple introduction events were likely for any given site, creating the distinct possibility that both ploidy and ecotypic polymorphisms were introduced into individual prairie sites. Thus, hybridization and gene flow between upland and lowland ecotypes and between ploidy levels was likely most frequent during glacial maxima but did not completely die out after the glaciers retreated. As scientists, our bias is often to think of switchgrass from a single prairie site as fairly uniform, likely sharing common ancestry, but this is often not the case. Sterling Barrens Natural Area in northern Wisconsin is a prominent example, with two distinct forms of switchgrass, an early-flowering tetraploid upland type and a late-flowering octoploid upland type (Lu et al., 2013).

Both upland and lowland switchgrass have distinctive eastern and western clades, the eastern clade associated with ancient broadleaf forest margins, savanna, and wetlands and the western clade associated with tallgrass prairie and semi-dryland habitats (Zalapa et al., 2011; Zhang et al., 2011a). Numerous DNA marker diversity studies on switchgrass have led to several consistent observations: (i) upland and lowland ecotypes form the principal taxonomic division within the species; (ii) ploidy defines the secondary taxonomic division within both upland (4x vs. 8x) and lowland (4x vs. the rare 8x) ecotypes; (iii) geography (eastern vs. western clades) forms the tertiary taxonomic division with switchgrass; (iv) natural populations

of switchgrass are highly diverse, containing as much as 80 to 90% of marker variation, largely owing to their high level of outcrossing; and (v) most alleles are shared across many populations and a fairly broad physical landscape, suggesting migration of pollen, seed, or both as a significant source of genetic variability (Casler et al., 2007a; Cortese et al., 2010; Gunter et al., 1996; Lu et al., 2013; Missaoui et al., 2006; Narasimhamoorthy et al., 2008; Young et al., 2010; Zalapa et al., 2011; Zhang et al., 2011a).

Before fragmentation of the tallgrass prairie and its associated ecosystems during the 20th century, migration of pollen and seed appeared to maintain incredibly large effective population sizes for switchgrass across a very broad landscape, likely on a scale of hundreds of kilometers. High winds, especially on the relatively flat plains, dominated by tallgrass prairie, would have promoted genetic homogenization of switchgrass across a very broad landscape. Birds and mammals are capable of transmitting viable switchgrass seeds through their gut, likely contributing to migration between adjacent populations, maintenance of genetic diversity across a broad landscape, and some degree of genetic homogenization between adjacent populations.

Despite the significant role of migration in maintaining genetic diversity and promoting genetic homogeneity on a regional basis, selection played a very strong historical role in genetic differentiation within switchgrass. The upland-lowland polymorphism represents the oldest known genetic differentiation event within tetraploid switchgrass, occurring between 0.8 and 0.5 Mybp (Young et al., 2011). Within the tetraploid upland group, additional polyploidization events, from 4x to 8x and 8x to the very rare 12x form, occurred during the past 0.5 M years. Following those polyploidization events, genetic differentiation on a geographic level was the dominant force driving changes in allele frequencies and phenotype, constantly tempered, of course, by the homogenizing effects of migration.

Phenotypic differentiation of switchgrass occurs on both latitudinal and longitudinal clines (Sanderson et al., 1999; Casler et al., 2004, 2007b). Latitudinal variation is by far the most obvious and significant of the two, likely originating from a combination of temperature and photoperiod gradients. Switchgrass is highly photoperiodic with a range in heading and flowering dates as great as 8 wk for natural populations from locations as distant as North Dakota and Texas, evaluated in common experiments in southern Wisconsin (Casler, unpublished data, 1998 to 2010). Flowering is induced by reduced daylength following the summer solstice (Benedict, 1941). Switchgrass does not require vernalization to flower, but establishment-year flowering time is significantly delayed relative to flowering time in subsequent years. This may be due to an extraordinarily long juvenility period during which floral induction cannot occur. At higher latitudes, such as southern to central Wisconsin (42 to 45° N), development of ripe seed

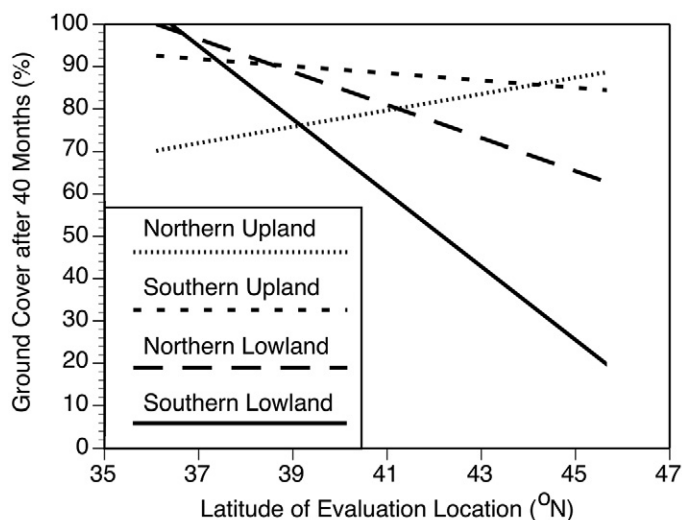


Figure 3. Linear regressions of ground cover (survival percentage) on latitude of evaluation location for four distinct ecotype groups of switchgrass, based on data from Casler et al. (2004, 2007b). Slopes are: $b = +1.9$ for northern upland, $b = -0.8$ for southern upland, $b = -3.9$ for northern lowland, and $b = -8.7$ for southern lowland.

is very rare during the establishment year, regardless of genotype. Photoperiodism and differentiation in flowering time have severely restricted gene flow on a latitudinal cline. Gene flow is unlikely to be a significant factor in homogenization or maintenance of genetic variability for natural populations separated by more than two hardiness zones, that is, across a broad latitudinal gradient.

Accessions from southern locations are later in heading and flowering, taller, and generally have higher biomass yield than northern accessions when evaluated in common experiments, regardless of the latitude of evaluation (Casler et al., 2004, 2007b). When evaluated across a sufficiently wide range of latitudes, all switchgrass populations show differential survival (Fig. 3). Populations of the upland ecotype are more northern adapted, while populations of the southern ecotype are more southern adapted (Fig. 4). Furthermore, within both ecotypes, germplasm can be classified as more southern vs. northern adapted, depending on its origin. Lowland accessions from central Texas can survive in the central Great Plains but suffer increasing mortality and stand loss as they are moved further north. This effect is much more severe moving lowland germplasm north than moving upland germplasm south, suggesting that cold-related stresses are the most dominant group of stresses regulating long-term survival of switchgrass, as suggested by Casler et al. (2002).

Adaptation is one of the most important factors limiting human-facilitated migration of switchgrass populations and cultivars. At northern sites, nearly all mortality in switchgrass swards occurs during the winter (Fig. 4), suggesting that cold hardening, cold tolerance, and/or freezing tolerance regulate the adaptation of switchgrass in cold-winter climates (Casler et al., 2004, 2007b). Moving switchgrass



Figure 4. Field evaluation of switchgrass cultivars at Hancock, WI, after two winter seasons. The 1.5- × 1.8-m sward plot in the center was planted to Kanlow, a lowland cultivar from northern Oklahoma, surrounded by locally adapted upland cultivars. Note the presence of approximately 15 surviving plants out of 1800 seeds planted approximately 2 yr before the photograph was taken. Photo from May 2010 (MDC).

populations north of their origin provides a “silver bullet” toward increasing biomass yields, with longer days prolonging the vegetative growth period, sometimes to the extent of preventing completion of the sexual cycle (Vogel, 2004). This practice is limited to geographical distances within the zone of adaptation of the population or cultivar. Switchgrass populations or cultivars should generally not be moved north or south of their origin by more than one hardiness zone (Casler et al., 2007b, 2012).

This raises the interesting question of whether or not switchgrass breeders might be able to capitalize on this phenomenon, selecting germplasm from the Deep South at northern locations, shipping plants back to a southern location for intercrossing and seed production, then using the progeny for biomass production at northern locations. Such a breeding scheme would require close collaboration and long-term funding for two breeding locations—a northern and a southern location, with the practical benefit of an improved cultivar likely realized only in the north. Provided an incentive exists for both collaborators, such a scheme is feasible, because there are typically a few to moderate number of survivors following the first winter or two for most southern accessions grown at northern locations (Fig. 4; Casler et al., 2004, 2007b). Extremely late-flowering cultivars for northern locations would represent decidedly nonlocal germplasm but should not raise the typical objections of the ecological community of contaminating local gene banks because of the extreme differential flowering times compared with true local germplasm.

Longitude also has a significant, albeit smaller, effect on phenotypic and genotypic differentiation of switchgrass populations, largely owing to available moisture and soil type (Casler et al., 2007b; McMillan, 1959). Biomass yields of ‘Cave-in-Rock’ tend to be reduced relative to that of other cultivars as this cultivar is moved west of its origin, particularly as moisture becomes limiting (Hopkins et al., 1995a; Casler and Boe, 2003; Berdahl et al., 2005). Conversely, ‘Sunburst’, originating in the northern Great Plains, tends to have reduced relative biomass yields as it is moved east into the historic Eastern Forest biome of the Upper Mississippi River watershed (Hopkins et al., 1995a; Casler and Boe, 2003). The experiments have yet to be conducted to determine if there are any differential adaptive responses between the central and eastern United States.

On the basis of these results and conclusions, Casler et al. (2012) proposed eight gene pools for switchgrass in North America (Fig. 5). The gene pools are a refinement of the “Plant Adaptation Regions” proposed by Vogel et al. (2005), which combined USDA hardiness zones (temperature and photoperiod gradients) with Bailey’s ecoregions (Bailey, 1998; based on soil type, moisture, and historical vegetation classes) into a single classification system. The eight proposed gene pools are intended largely as fluid guidelines for driving collection of germplasm with specific adaptation characteristics, synthesis of regionally adapted populations, and cultivar or population deployment for conservation and restoration. The size, dimensions, and number of proposed gene pools is based on generalizations drawn from Casler et al. (2004, 2007b) and many other published studies cited in those two papers, combined with the general observations that (i) populations are broadly adapted to no more than one hardiness zone north or south of their origin and (ii) adaptation of cultivars and wild populations is driven principally by latitude (temperature and photoperiod) and secondarily by longitude (humidity, soil moisture, and disease resistance). This gene pool concept is intended to be a compromise between a desire within the restoration community to create narrowly defined “localities” for germplasm deployment vs. the seed industry’s need for large-scale cultivar deployment and economy of scale, which will be discussed in more detail in the next section.

The notable exception to this concept of regional gene pools occurs when plant breeders design screens to capture genetic variation for adaptive traits and selection results in a significant change in the fundamental adaptive qualities of a population. A summary of 23 cultivar evaluation experiments, conducted from Texas to Wisconsin, showed a clear linear decline in the biomass-yield advantage of lowland switchgrass over upland switchgrass as mean minimum winter temperatures declined with increasing latitude (Fig. 6). Substitution of five later experiments for the two experiments in which the

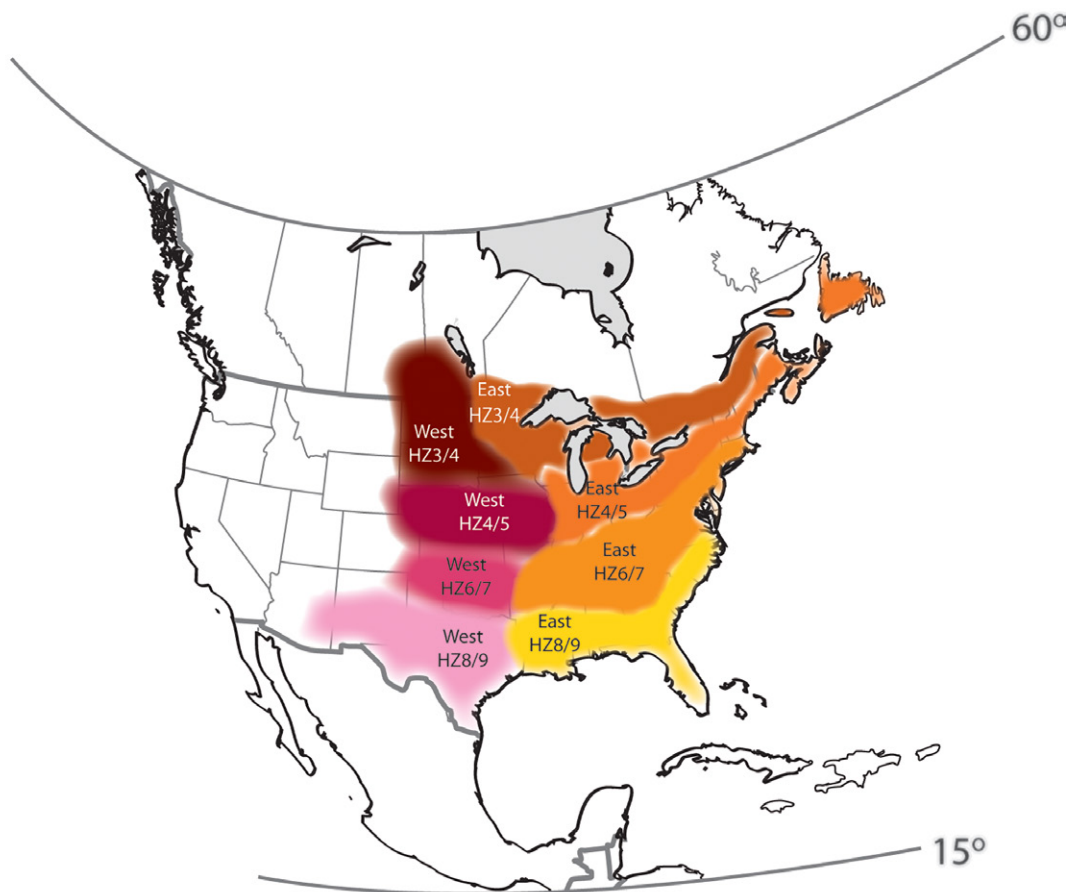


Figure 5. Proposed gene pools for deployment of regionally adapted switchgrass germplasm and cultivars for use in conservation and restoration projects (adapted from Casler et al., 2012); HZ = USDA Hardiness Zone (Cathey, 1990).

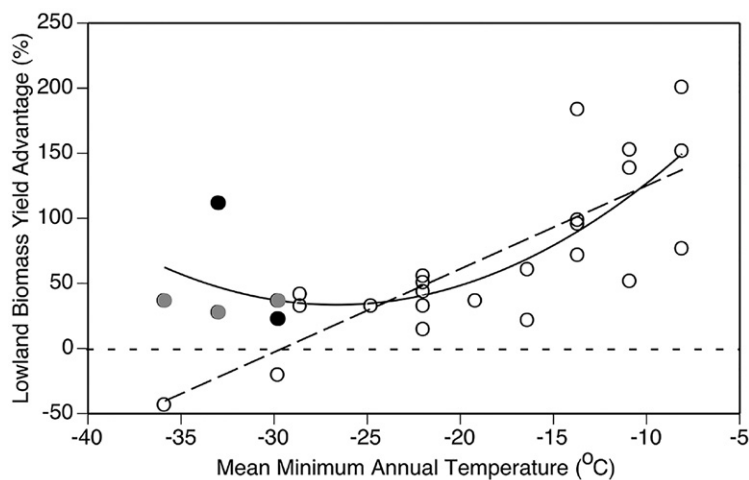


Figure 6. Relationship between lowland-ecotype biomass-yield advantage and mean minimum annual temperature (<http://planthardiness.ars.usda.gov/PHZMWeb/>, accessed 15 Aug. 2015) for 28 cultivar-evaluation trials conducted under varying climatic conditions in the United States. Each point represents a mean of at least two upland and two lowland cultivars, and the difference is expressed as a percentage of the upland mean. Open circles and dashed line ($Y = 184 + 6.32X$, $R^2 = 0.64$, $P < 0.0001$) represent unimproved prairie-remnant lowland populations. Data taken from Casler et al., 2004 (Arlington and Spooner, WI; Mead, NE; Manhattan, KS; Stillwater, OK); Cassida et al., 2005 (Hope, AR; College Station, Dallas, and Stephenville, TX); Fike et al., 2006 (Princeton, KY; Raleigh, NC; Jackson and Knoxville, TN; Blacksburg and Orange, VA; Morgantown, WV); Lemus et al., 2002 (Chariton, IA); and Sanderson et al., 1999 (Beeville, College Station, Dallas, Stephenville, and Temple, TX). Black circles represent the first lowland population selected for improved survivorship under northern climates (Casler, 2014), and gray circles represent late-flowering populations derived from upland × lowland hybrids (Casler and Vogel, 2014). The overall regression, including improved northern populations but excluding the two negative Y values, was: $Y = 272 + 17.94X + 0.34X^2$, $R^2 = 0.54$, $P < 0.0001$ (solid curve).

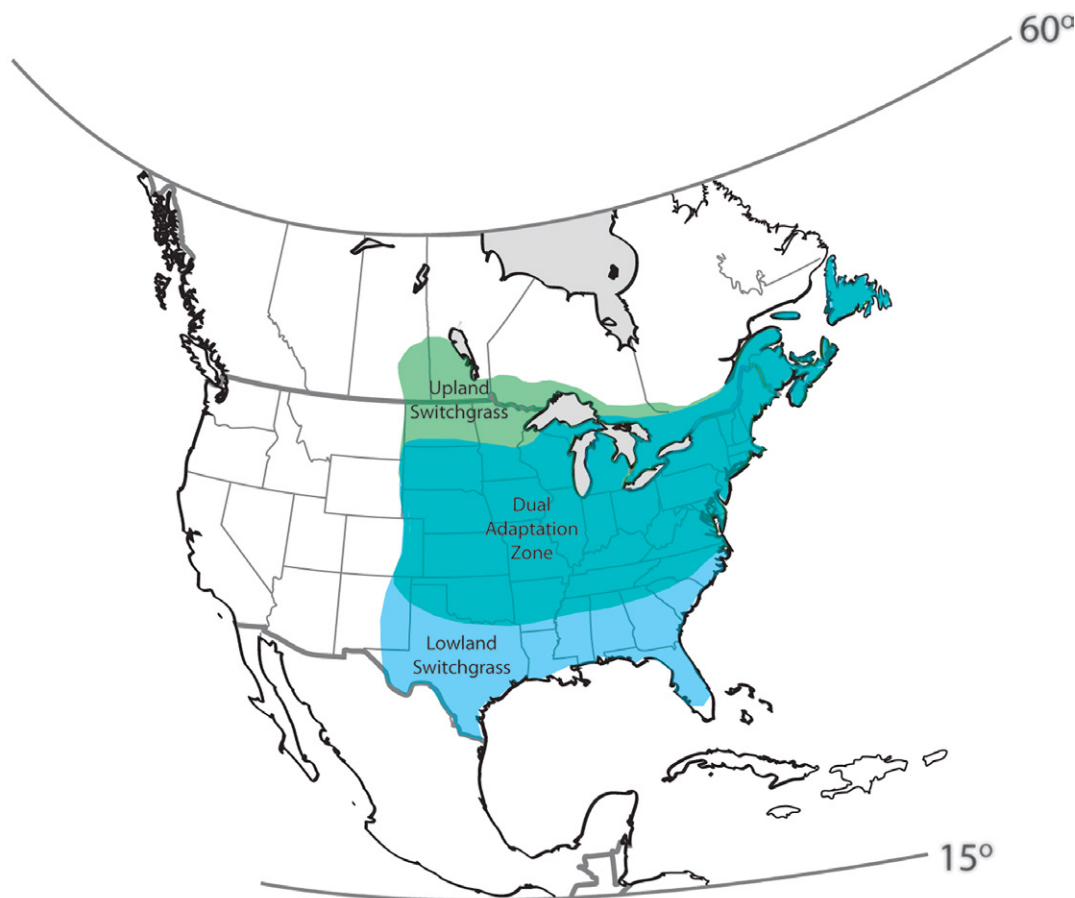


Figure 7. Modified adaptation range for commercial deployment of cultivars representing upland and lowland switchgrass ecotypes, following the gains made in developing lowland and mixed-parentage populations adapted to USDA Hardiness Zones 3 and 4, as shown in Fig. 6.

upland ecotype had the biomass-yield advantage, which included either lowland populations or hybrid-derived populations selected for improved cold tolerance, resulted in a significant alteration of this relationship. Essentially, breeding lowland types and upland \times lowland hybrids for increased cold tolerance in northern climates have “bent” this relationship upward at the most northern locations, represented by USDA Hardiness Zones 3, 4, and 5. This observation drives home the point of the breeder’s axiom, “You get what you select for.” As a direct result of these efforts (Casler and Vogel, 2014; Casler, 2014), the potential commercial range of lowland switchgrass has been greatly expanded to include USDA Hardiness Zones 3 and 4 (Fig. 7, compare to Fig. 2).

WHAT IS A CULTIVAR?

The term “cultivar” is a contraction of the phrase “cultivated variety,” which implies some application and usage under cultivation or some form of agriculture. Given that, most switchgrass cultivars, including those in Table 2, are cultivars in name only. Beginning in the early 20th century, numerous collections were made of switchgrass and its congeners, covering a wide range of climatic regions and habitats. Many of these switchgrass accessions were evaluated in small experiments or demonstration plots at

a common location or based on feedback from producers that had grown switchgrass originating from a particular remnant prairie site. Following the droughts of the 1930s, increased demand for switchgrass seed fueled a need to develop an efficient seed delivery and deployment system; the USDA Natural Resources Conservation Service (NRCS) and its predecessor, the Soil Conservation Service (SCS), were the leaders of this effort. Desirable switchgrass accessions were labeled with place names to signify their origin and to simplify seed marketing and distribution (Table 2). These cultivars represent completely wild germplasm with little or no refinement by breeding and selection, with the exception of a few instances of culling nonvigorous plants from the original seed production nursery, or in the elimination of agronomically undesirable accessions. As such, unimproved cultivars are direct representatives of natural germplasm from prairie remnants.

These cultivars are sometimes termed “natural track” cultivars (Aubry et al., 2005). Natural track cultivars of switchgrass are generally source-identified populations originating from a single collection site, in some cases, for example Blackwell, originating from a single plant (Alderson and Sharp, 1994). Most of these collections accurately reflect the genotypic composition of the larger switchgrass population from a region, but some of these populations,

Table 2. Source-identified and unimproved switchgrass cultivars originating from various habitats in the central and eastern United States, largely representing local ecotypes with minimal or no selection for plant traits.

Cultivar	PI no. [†]	Ecotype	Ploidy	Year	Origin	HZ [‡]	Seed source [#]
Alamo	422006	Lowland	4x	1978	Southern Texas	6, 7, 8, 9	NRCS-PMC, Knox City, TX
Kanlow	421521	Lowland	4x	1963	Northern Oklahoma	6, 7	NRCS-PMC, Manhattan, KS
Pangburn	414065	Lowland	4x	NA [§]	Arkansas	6, 7	GRIN [†]
Penn Center		Lowland	NA [§]	2010	Coastal South Carolina	8	NRCS-PMC, Americus, GA
Stuart	422001	Lowland	4x	1996	Southern Coastal Florida	9, 10	NRCS-PMC, Brooksville, FL
Miami	421901	Up/Low [‡]	4x	1996	Southern Florida	9, 10	NRCS-PMC, Brooksville, FL
Wabasso	422000	Up/Low [‡]	4x	1996	Southern Coastal Florida	9, 10	NRCS-PMC, Brooksville, FL
Dacotah	537588	Upland	4x	1989	Southern North Dakota	2, 3, 4	NRCS-PMC, Bismarck, ND
Falcon	642190	Upland	4x	1963	New Mexico	5, 6, 7	GRIN [†]
Grenville	414066	Upland	8x	1940	Northeastern New Mexico	5, 6, 7	NRCS-PMC, Los Lunas, NM
High Tide		Upland	NA	2007	Northeastern Maryland	5, 6, 7	NRCS-PMC, Cape May, NJ
KY1625	431575	Upland	4x	1987	Southern West Virginia	5, 6, 7	NRCS-PMC, Alderson, WV
Blackwell	421520	Upland	8x	1944	Northern Oklahoma	5, 6, 7	NRCS-PMC, Manhattan, KS
Caddo	476297	Upland	8x	1955	Central Oklahoma	6, 7	GRIN [†]
Carthage	421138	Upland	8x	2006	North Carolina	5, 6, 7	NRCS-PMC, Cape May, NJ
Cave-in-Rock	469228	Upland	8x	1973	Southern Illinois	5, 6, 7	NRCS-PMC, Elsberry, MO
Central Iowa	657660	Upland	NA	2000	Central Iowa	4, 5	NRCS-PMC, Elsberry, MO
Forestburg	478001	Upland	8x	1987	Eastern South Dakota	3, 4	NRCS-PMC, Bismarck, ND
Nebraska 28	477003	Upland	8x	1949	Northeast Nebraska	3, 4	GRIN [†]
Shelter	430240	Upland	8x	1986	Central West Virginia	4, 5, 6	NRCS-PMC, Big Flats, NY
Southlow	642395	Upland	NA	2003	Southern Michigan	4, 5, 6	NRCS-PMC, East Lansing, MI

[†] Plant introduction (PI) number for accessions stored in the USDA National Plant Germplasm System and accessible to anyone who requests seed via GRIN, the Germplasm Resources Information Network, <http://www.ars-grin.gov/> (accessed 17 Aug. 2015). Empty cells indicate that a cultivar is not available through GRIN.

[‡] Upland cytoplasm, but lowland phenotype and nuclear DNA, suggesting an ancient hybrid origin (Zalapa et al., 2011).

[§] NA = year of release or ploidy information is not available.

[‡] USDA Hardiness Zones (HZ) are defined in approximately 5°C increments of mean annual minimum temperature (<http://planthardiness.ars.usda.gov/PHZMWeb/>, accessed 17 Aug. 2015).

[#] NRCS-PMC, Natural Resource Conservation Service Plant Materials Center (<http://www.nrcs.usda.gov/wps/portal/nrcs/main/plantmaterials/pmc/>, accessed 17 Aug. 2015).

for example Carthage from central North Carolina, have been identified as human-facilitated migrants that do not represent the local genotypes (Zhang et al., 2011a). Carthage and another accession from near Albany, NY, were most likely inadvertently introduced to these areas by the U.S. Army; both are representative of the Central Great Plains octoploid type, most likely originating from northwest Nebraska (Zhang et al., 2011a).

Multiple-origin polycrosses (Jones, 2003) are becoming increasingly recognized as useful for restoration and conservation efforts. Switchgrass and other prairie plants are not static in either remnant or restored prairies. Rather, they undergo constant evolutionary change in response to climate, pests, and herbivores. Mortality takes out unfit plants, leaving behind plants that have superior fitness to one or more stresses, while seedling recruitment and tillering of adult plants allow new plants with improved fitness to become viable members of the population and to contribute gametes and genes to future generations (Benson and Hartnett, 2006; Jones and Monaco, 2009). The power of in situ selection within perennial grass sods was illustrated by rapid evolution of SO₂ tolerance associated with increasing atmospheric SO₂ pollution in Manchester, UK, during the 1960s, followed by loss of tolerance as SO₂ pollution was markedly decreased in subsequent years (Wilson

and Bell, 1985). With predicted drastic changes in global surface temperature expected during this century (Hansen et al., 2010), populations of switchgrass that are adapted to a narrow temperature range or are being grown at the southern limit of their range will require genetic variation for heat tolerance to be capable of evolving and adapting to climate change. Rapid changes in climate will challenge local and native populations to cope with temperature changes that may be beyond the limits of their genetic variability (Root et al., 2003). While the ancient prairie and savanna were vast ecosystems, characterized by large effective population sizes and large-scale migration of pollen and seed (Casler et al., 2007a; Zhang et al., 2011a,b), fragmentation to less than 1% of the original land area for each habitat has reduced both effective population sizes and the potential for migration to enhance local genetic variability. The usual mechanisms that allow individual populations to adapt to environmental change, for example, selection, mutation, recombination, and migration, may not be sufficient to allow existing prairie remnants or newly established prairie restorations to withstand environmental stresses for decades, as they have done in the past (Davis and Shaw, 2001; Sgrò et al., 2011). Nevertheless, switchgrass has survived at least 15 warming and cooling cycles during its life history (Zhang et al., 2011a,b). The broad range of stress tolerances

Table 3. Improved switchgrass cultivars representing significant breeding and selection activities.

Cultivar	PI No. [†]	Ecotype	Ploidy	Year of release	Principal traits selected during cultivar development [§]	USDA HZ	Seed source [#]
EG2101		Upland	8x	2009	Biomass yield, rust resistance	5, 6, 7	Blade Energy Crops
Pathfinder	642192	Upland	8x	1967	Biomass yield and vigor	4, 5	UNL ARDC Husker Genetics
Shawnee	591824	Upland	8x	1996	IVDMD, biomass yield	5, 6, 7	UNL ARDC Husker Genetics
Sunburst	598136	Upland	8x	1998	Large seed size and mass	3, 4, 5	SDSU Foundation Seed Stocks
Trailblazer	549094	Upland	8x	1984	IVDMD, biomass yield	4, 5	UNL ARDC Husker Genetics
Summer	642191	Upland	4x	1963	Earliness, rust resistance	4, 5	SDSU Foundation Seed Stocks
Liberty	669371	Mixed [‡]	4x	2013	Biomass yield & quality	3, 4, 5, 6, 7	UNL ARDC Husker Genetics
BoMaster	645256	Lowland	4x	2006	IVDMD, biomass yield	6, 7, 8	Ernst Conservation Seeds, Inc.
Cimarron		Lowland	4x	2008	Biomass yield	6, 7, 8	Oklahoma Foundation Seed Stocks
Colony	658520	Lowland	4x	2009	IVDMD, biomass yield	6, 7, 8	Ernst Conservation Seeds, Inc.
EG1101	658530	Lowland	4x	2009	Biomass yield, rust resistance	8, 9, 10	Blade Energy Crops
EG1102	658531	Lowland	4x	2009	Biomass yield, rust resistance	6, 7, 8	Blade Energy Crops
Espresso		Lowland	4x	2014	Reduced seed dormancy	6, 7, 8	Prairie Creek Farms, Newbern, AL
Performer	644818	Lowland	4x	2006	IVDMD, biomass yield	6, 7, 8	Ernst Conservation Seeds, Inc.
TEM-LoDorm	636468	Lowland	4x	2007	Reduced seed dormancy	6, 7, 8	GRIN [†]
Timber Germplasm		Lowland	4x	2009	Biomass yield	6, 7, 8	NRCS-PMC, Cape May, NJ

[†] Plant introduction (PI) number for accessions stored in the USDA National Plant Germplasm System and accessible to anyone who requests seed via GRIN, the Germplasm Resources Information Network, <http://www.ars-grin.gov/> (accessed 17 Aug. 2015). Empty cells indicate that a cultivar is not available through GRIN.

[‡] Product of two generations of random mating and one generation of selection within upland × lowland F₁ hybrids (Vogel et al., 2014).

[§] IVDMD = in vitro dry matter digestibility.

^{||} USDA Hardiness Zones (HZ) are defined in approximately 5°C increments of mean annual minimum temperature (<http://planthardiness.ars.usda.gov/PHZMWeb/>, accessed 17 Aug. 2015).

[#] UNL ARDC Husker Genetics (<http://www.ardc.unl.edu/seed.shtml/>, accessed 17 Aug. 2015); Oklahoma Foundation Seed Stocks (<http://www.oklahomaseed.com/>, accessed 17 Aug. 2015); SDSU Foundation Seed Stocks (<http://www.sdstate.edu/ps/sdfssd/>, accessed 17 Aug. 2015); Ernst Conservation Seeds, Inc. (<http://www.ernstseed.com/>, accessed 17 Aug. 2015); Blade Energy Crops (<http://www.bladeenergy.com/SwitchProducts.aspx>, accessed 17 Aug. 2015); NRCS-PMC, Natural Resource Conservation Service Plant Materials Center (<http://www.nrcs.usda.gov/wps/portal/nrcs/main/plantmaterials/PMC/>, accessed 17 Aug. 2015).

that allow the species to thrive from the Gulf Coast to the northern reaches of the tallgrass prairie can likely be used to develop environmentally resilient cultivars.

Because they possess greater amounts of genetic variation than single-source-identified accessions, multiple-origin polycrosses are an additional mechanism that practitioners can use to cope with environmental change and increase the expected longevity of perennial plants. Switchgrass corresponds to Scenario #2 of Weeks et al. (2011; Fig. 1), a species with high internal genetic variation but originating from highly fragmented natural habitats. Their recommendation for this scenario is to sample from the entire target distribution in creating resilient and adaptable multiple-origin polycrosses. Populations that are more resilient can tolerate a greater magnitude of disturbance before losing function or moving to a different state of nature (Carpenter et al., 2001). Existing multiple-origin polycrosses—for example, Southlow, representing the southern half of Lower Michigan; Central Iowa, representing 41.5 to 42.5° N latitude and about one-third of Iowa (Table 2); and MSPMT-PAV2, representing the entire state of Mississippi (Zhang et al., 2011b; Table 1)—are too geographically narrow to meet the challenge of global climate change (Sgrò et al., 2011). Furthermore, a proliferation of narrowly adapted populations places unneeded pressure on seed production professionals, requiring the community to support seed maintenance and multiplication of an

unnecessarily large number of duplicative populations. As such, target distributions for switchgrass and similar species should be more broadly defined, taking into account both functional diversity and the practical requirements associated with seed production, using the gene pool model shown in Fig. 5, or something similar.

SWITCHGRASS IMPROVEMENT

Finally, bred cultivars constitute a small, but growing, list of populations that represent one or more distinct agronomic improvements (Table 3). Most breeding objectives and improvements have been based on forage or biomass yield, forage or biomass quality, disease resistance, and seed size or reduced seed dormancy. Because switchgrass is still a very wild species, possessing huge amounts of heterozygosity and a polyploid genome, bred cultivars do not generally represent a distinct domestication of the species. Rather, they represent small and incremental improvements, ranging from 1 to 5% change in a desired trait per generation of selection and breeding (Vogel, 2004). Most cultivars represent no more than three to five generations of selection removed from wild germplasm collected in prairie remnants. There are two notable exceptions that may represent an obvious departure from the “wild” state of the species. Liberty is a third-generation selection from upland × lowland hybrids, with a phenotype intermediate between upland and lowland ecotypes (Vogel et al., 2014).

The combination of upland and lowland genomes appears to have been responsible for maintenance of high biomass yields across a wide range of hardiness zones (Table 3), resulting from a partial breakdown of the classic genotype \times environment interaction that is typical across a latitudinal gradient (Casler et al., 2004; 2007b). Liberty combines the late-flowering and high-biomass yield of the lowland ecotype with the extreme cold tolerance of the upland ecotype. Espresso is the result of several generations of selection for reduced seed dormancy (rapid germination), representing a significant improvement in one of the classic traits that often defines an undomesticated species.

As of this writing, there were 14 switchgrass breeding programs in North America. Public or nonprofit programs are located in the following states or provinces: Alabama, Georgia, Mississippi, Nebraska, New Jersey, New York, Oklahoma, Quebec, South Dakota, Tennessee, and Wisconsin. The breeding programs in Quebec and South Dakota are focused on improving the upland ecotype, the USDA-ARS programs in Nebraska and Wisconsin are split between upland and lowland ecotypes, while the other eight programs are focused exclusively on the lowland ecotype. Two commercial companies have had significant switchgrass breeding activity between 2000 and 2015, one located in Texas and one in Pennsylvania (Table 3; Blade Energy Crops and Ernst Conservation Seeds). There is a continual demand for switchgrass seed for use in conservation plantings and in pasture mixtures in the Great Plains and the midwestern United States, which is being met by established independent seed companies, many of which are family owned. Currently there is limited demand for switchgrass seed to plant biomass production fields, with the exception of the pellet industry in the eastern United States and Canada (Bailey-Stamler et al., 2006; Cherney, 2006; Samson et al., 2007).

Because germplasm is the foundation of all efforts to improve switchgrass through selection and breeding, adequate germplasm resources are critical for the long-term improvement of the species to help meet future energy demands (U.S. Department of Energy, 2011). Unfortunately, germplasm resources of switchgrass are highly fragmented, and there is no comprehensive plan or oversight for exploration, collection, multiplication, and maintenance of germplasm that encompasses all public collections.

The USDA-ARS is responsible for the national switchgrass collection, maintained within the National Plant Germplasm System (NPGS) and accessible through the Germplasm Resources Information Network (GRIN, <http://www.ars-grin.gov/>, accessed 17 Aug. 2015). There are currently 413 accessions of switchgrass in the NPGS, 96 of which are available for distribution at the time of this writing (Fig. 8). When requested for research purposes, a sample of 200 seeds per accession will be distributed with the exception of two clonally maintained accessions, plant

introduction (PI 671956 (AP13) and PI 671957 (VS16), which are parents of a mapping population distributed as live plant material. Much of the material has been recently collected (2008 through 2014) and requires regeneration before the material is available for public access. It is anticipated that the majority of this material will be regenerated and available for distribution sometime after 2017. Another large subset of unavailable material represents half-sib populations originally donated in the early 1970s from South Dakota. This material has been consolidated into two accessions, PI 672984 and PI 672985. The original individual accessions can still be requested by contacting the warm-season grass curator directly (coauthor MH). Material protected by intellectual property rights are also maintained by the NPGS, but the material is not available for distribution until the terms of the contract have expired (e.g., 'Bomaster' PI 645256).

The NPGS switchgrass collection relies heavily on the interest and input of community members to (i) propose and participate in collection expeditions (e.g., Hopkins et al., 1995b) and (ii) donate collections to the GRIN system. Recent collection efforts in 2008 to 2014, funded by the USDA-ARS Plant Exchange Office, have focused on collecting in the Gulf Coast states and south Atlantic states, with extra effort spent on collecting in Florida. These efforts have resulted in the collection of 113 new accessions. Another 83 accessions were donated by the NRCS Big Flats Plant Material Center (Corning, NY), originating from the northeastern United States, primarily Pennsylvania, New York, and the New England states. Future acquisition efforts will focus on filling gaps in the collection where native populations occur but are not conserved in the collection. One of the main areas targeted will be the New England portion of the United States. Despite these efforts, there are still some very significant gaps in the collection. For example, Michigan and Iowa are represented by only one accession each, but both of those are bulked accessions that represent large portions of each state. The greatest value to the community of germplasm users is derived by donation of individual source-identified accessions before bulking across multiple and diverse collection sites. While bulked samples are highly useful from a commercial point of view, they are essentially useless for genetic and ecological studies. Any individuals who possess collections that could help to fill in some of the gaps shown in Fig. 8 are encouraged to donate seed samples and passport data to NPGS for inclusion in the collection by contacting the curator (MH).

Outside of acquiring new material, the main obstacle in providing available switchgrass germplasm is the need for regeneration. Preferred regeneration protocols require isolation of accessions by a minimum of 25 m (Johnson et al., 1996), which limits the number of accessions regenerated each year. Additionally, reduced germination and

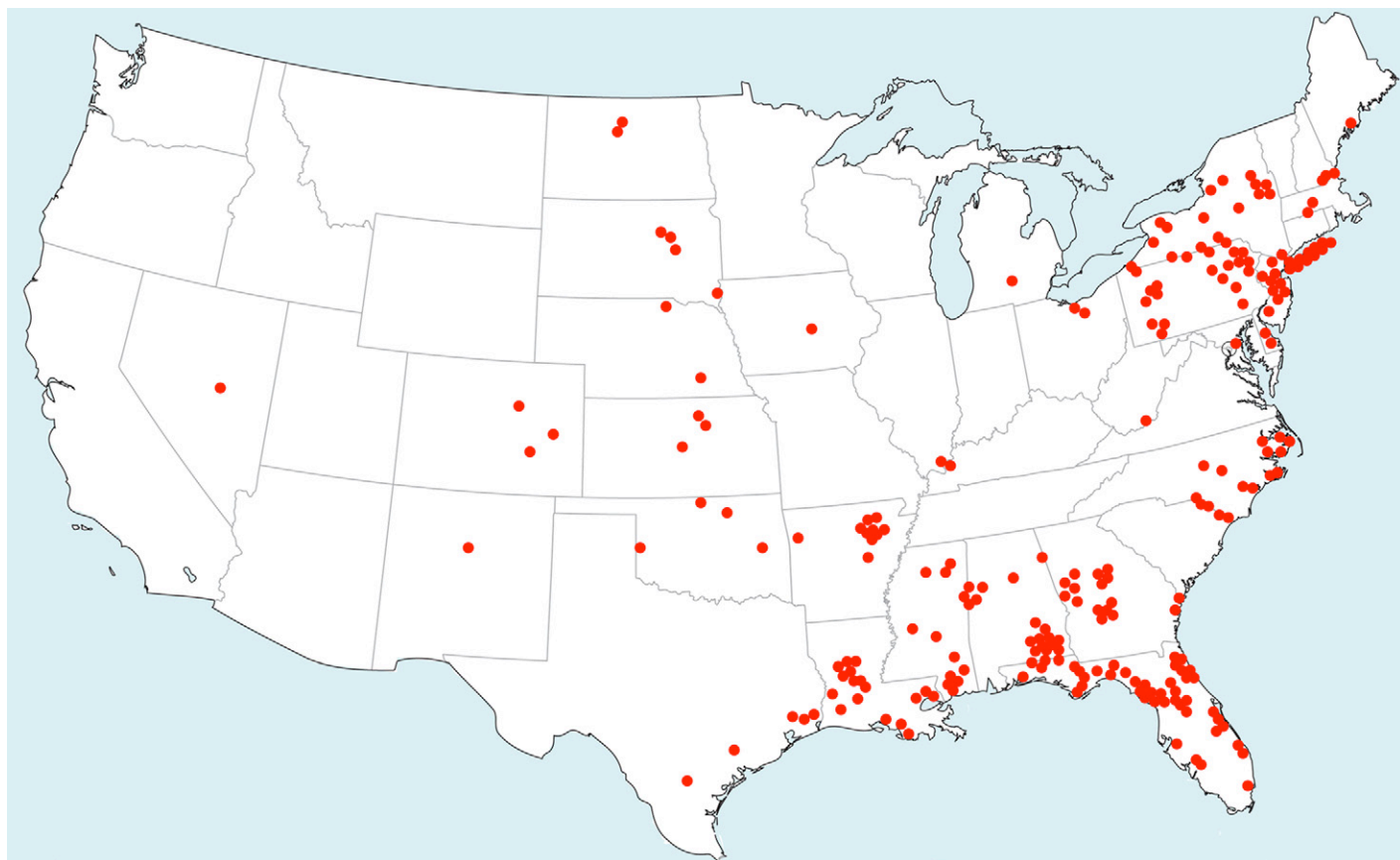


Figure 8. Map of the United States, showing the locations of switchgrass accessions collected by or donated to the USDA National Plant Germplasm System. Each dot represents an individual collection site or a group of collection sites in the case of a small number of bulked accessions. Collection site locations were mapped according to coordinates or locality data supplied by the collector or by approximation in cases where there was not sufficient passport data.

lack of adequate initial seed quantities typical of native collections make regeneration further challenging. In the past several years, collaboration with private seed companies and USDA–ARS researchers has allowed for greater regeneration opportunities. A set of 57 northeastern accessions has been regenerated by the senior author and should be available for distribution in late 2015. Ernst Seed, Inc., has regenerated a large portion of the Gulf Coast and south Atlantic germplasm. In addition to acquiring and conserving native populations, the NPGS recognizes the need for maintaining material used as genetic tools such as recombinant inbred lines (RILs) and parents of mapping populations. This material will be handled on a case-by-case basis and can be arranged by contacting the warm-season grass curator. Typically, RILs are maintained for a set period of time or when seed quantities are depleted (whichever comes first), and there will be no responsibility for regeneration of the material by the NPGS. Inbred lines, up to the S_3 generation, are currently under development at the USDA–ARS in Madison, WI, and at Oklahoma State University, although they are not yet available for donation to NPGS or distribution to the public.

The USDA–NRCS has 27 Plant Materials Centers (PMCs), 12 of which have been actively involved

in collecting, maintaining, multiplying, and releasing switchgrass germplasm for public use (Table 2). Collection, maintenance, and multiplication of germplasm within NRCS are decentralized, with each PMC representing a distinct geographical service area. Public accessibility of PMC germplasm is largely limited to named germplasms or cultivars that are listed under the heading “Conservation Plants” on the website for each individual PMC (<http://www.nrcs.usda.gov/wps/portal/nrcs/main/plant-materials/pmc/>, accessed 17 Aug. 2015). Most PMCs have additional switchgrass accessions that represent a range of environments within their service area, but public access to these accessions is highly limited and variable. Some of these accessions have been entered into the GRIN system and can be identified by the PMC 7-digit number beginning with the numeral 9, for example, GRIN PI numbers 659341 through 659346. In some cases, PMC personnel have created multiple-origin polycrosses to represent a defined region, as discussed above, for example, Southlow, central Iowa, and MSPMT-PAV2.

Finally, numerous collections exist within other public organizations, for example, University of Wisconsin, University of Texas, University of Connecticut, University of Tennessee, University of Georgia, Oklahoma State

University, and the USDA–ARS Research Units at Lincoln, NE, and Madison, WI. Donation of a portion of these collections to the NPGS would allow public access to support a wide range of research activities. Germplasm donations to GRIN should balance the need to preserve a wide array of germplasm, representing all climates and habitats that harbor remnant switchgrass populations vs. the need to limit the NPGS collection to a manageable size, such that maintenance and multiplication can be accomplished within the budget. For example, a collection of 25 upland accessions representing most of Wisconsin was relatively uniform in both phenotype and genotype (Casler, 2005; Casler et al., 2007a; Zhang et al., 2011a,b), indicating that a single multiple-origin polycross would adequately represent the entire region. Conversely, 10 accessions from Florida and Georgia were highly variable, displaying variation far in excess of expectations for such a small sample size (Zhang et al., 2011a,b). In this case, pooling, bulking, or polycrossing would result in massive loss of information and likely lead to significant loss of rare and interesting alleles due to drift and selection (Sackville-Hamilton and Chorlton, 1997). The MSPMT-PAV2 multiple-location polycross is an example of pooling a group of accessions that represented more diversity than a single population can maintain. This population originated as 97 accessions collected throughout Mississippi, representing USDA Hardiness Zones 7 through 9, both upland and lowland ecotypes, and both tetraploid and octoploid chromosome numbers (Zhang et al., 2011b). Maintenance of this level of diversity and any semblance of population integrity through generations of seed multiplication will be impossible. Even narrow source-identified accessions, such as Alamo, have resulted in detectable and significant divergence among seed lots produced in different locations (Gunter et al., 1996).

The best germplasm available for immediate use by breeding programs are the cultivars that have already been released. These cultivars are basically improved populations that still possess significant amounts of genetic diversity. They represent the best of many previous germplasm collection and evaluation programs, and most have been extensively tested so their adaptation regions are well known. Plants from these cultivars can be used in both population-improvement breeding programs and in making controlled crosses to develop improved populations, specific narrow-based cultivars, and hybrid populations.

References

- Alderson, J., and W.C. Sharp. 1994. Grass varieties in the United States. Agric. Handb. 170. Soil Conserv. Serv. USDA, Washington, DC.
- Aubry, C., R. Shoal, and V. Erickson. 2005. Grass cultivars: Their origins, development, and use on national forests and grasslands in the Pacific Northwest. USDA Forest Service, Native Seed Network, Corvallis, OR. http://svinet2.fs.fed.us/wildflowers/Native_Plant_Materials/documents/cultivars_maindoc_040405_appendices.pdf (accessed 1 Sept. 2015).
- Bailey, R.G. 1998. Ecoregions: The ecosystem geography of the oceans and continents. Springer-Verlag Inc., New York. <http://www.fs.fed.us/land/ecosysmgmt/> (accessed 12 Dec. 2013).
- Bailey-Stamler, S., R. Samson, and C. Ho Lem. 2006. Biomass resource options: Creating a BIOHEAT supply for the Canadian greenhouse industry. REAP-Canada, Ste. Anne de Bellevue, Quebec. <http://www.reap-canada.com/> (accessed 17 Aug. 2015).
- Barnett, F.L., and R.F. Carver. 1967. Meiosis and pollen stainability in switchgrass, *Panicum virgatum* L. Crop Sci. 7:301–304. doi:10.2135/cropsci1967.0011183X000700040005x
- Benedict, H.M. 1941. Effect of day length and temperature on the flowering and growth of four species of grasses. J. Agric. Res. 61:661–672.
- Benson, E.J., and D.C. Hartnett. 2006. The role of seed and vegetative reproduction in plant recruitment and demography in tallgrass prairie. Plant Ecol. 187:163–177. doi:10.1007/s11258-005-0975-y
- Berdahl, J.D., A.B. Frank, J.M. Krupinsky, P.M. Carr, J.D. Hanson, and H.A. Johnson. 2005. Biomass yield, phenology, and survival of diverse switchgrass cultivars and experimental strains in western North Dakota. Agron. J. 97:549–555. doi:10.2134/agronj2005.0549
- Berger, W.H., J.S. Killingley, and E. Vincent. 1987. Time scale of the Wisconsin/Holocene transition: Oxygen isotope record in the Western Equatorial Pacific. Quat. Res. 28:295–306. doi:10.1016/0033-5894(87)90068-8
- Bintanja, R., and R.S.W. van de Wal. 2008. North American ice-sheet dynamics and the onset of 100,000-year glacial cycles. Nature 454:869–872. doi:10.1038/nature07158
- Brunken, J.N., and J.R. Estes. 1975. Cytological and morphological variation in *Panicum virgatum* L. Southwest. Nat. 19:379–385. doi:10.2307/3670396
- Carpenter, S., B. Walker, J.M. Anderies, and N. Abel. 2001. From metaphor to measurement: Resilience of what to what? Ecosystems 4:765–781. doi:10.1007/s10021-001-0045-9
- Casler, M.D. 2005. Ecotypic variation among switchgrass populations from the northern USA. Crop Sci. 45:388–398. doi:10.2135/cropsci2005.0388
- Casler, M.D. 2014. Heterosis and reciprocal-cross effects in tetraploid switchgrass. Crop Sci. 54:2063–2069. doi:10.2135/cropsci2013.12.0821
- Casler, M.D., and A.R. Boe. 2003. Cultivar × environment interactions in switchgrass. Crop Sci. 43:2226–2233. doi:10.2135/cropsci2003.2226
- Casler, M.D., D.R. Buxton, and K.P. Vogel. 2002. Genetic modification of lignin concentration affects fitness of perennial herbaceous plants. Theor. Appl. Genet. 104:127–131. doi:10.1007/s001220200015
- Casler, M.D., R.B. Mitchell, and K.P. Vogel. 2012. Switchgrass. In: C. Kole et al., editors, Handbook of bioenergy crop plants. Vol. 2. Taylor and Francis, New York. p. 563–590.
- Casler, M.D., C.A. Stendal, L. Kapich, and K.P. Vogel. 2007a. Genetic diversity, plant adaptation regions, and gene pools for switchgrass. Crop Sci. 47:2261–2273. doi:10.2135/cropsci2006.12.0797
- Casler, M.D., and K.P. Vogel. 2014. Selection for biomass yield in upland, lowland, and hybrid switchgrass. Crop Sci. 54:626–636. doi:10.2135/cropsci2013.04.0239
- Casler, M.D., K.P. Vogel, and A.C. Beal. 2006. Registration of WS4U and WS8U switchgrass germplasms. Crop Sci. 46:998–999. doi:10.2135/cropsci2005.04-0020

- Casler, M.D., K.P. Vogel, C.M. Taliaferro, N.J. Ehler, J.D. Berdahl, E.C. Brummer, R.L. Kallenbach, C.P. West, and R.B. Mitchell. 2007b. Latitudinal and longitudinal adaptation of switchgrass populations. *Crop Sci.* 47:2249–2260. doi:10.2135/cropsci2006.12.0780
- Casler, M.D., K.P. Vogel, C.M. Taliaferro, and R.L. Wynia. 2004. Latitudinal adaptation of switchgrass populations. *Crop Sci.* 44:293–303.
- Cassida, K.A., J.P. Muir, M.A. Hussey, J.C. Read, B.C. Venuto, and W.R. Ocumpaugh. 2005. Biomass yield and stand characteristics of switchgrass in south central U.S. environments. *Crop Sci.* 45:673–681. doi:10.2135/cropsci2005.0673
- Cathey, H.M. 1990. USDA plant hardiness zone map. USDA Misc. Publ. No. 1475. U.S. Natl. Arboretum, USDA-ARS, Washington, DC. <http://planthardiness.ars.usda.gov/PHZMWeb/> (accessed 12 Dec. 2013).
- Cherney, J.H. 2006. USA history of grasses for biofuel. Bioenergy Information Sheet #3. Cornell Univ. Coop. Ext., Ithaca, NY. <http://www.grassbioenergy.org/> (accessed 17 Aug. 2015).
- Clark, J.S., E.C. Grimm, J. Lynch, and P.G. Mueller. 2001. Effects of Holocene climate change on the C₄ grassland/woodland boundary in the Northern Plains, USA. *Ecology* 82:620–636.
- Cornelius, D.R. 1950. Seed production of native grasses. *Ecol. Monogr.* 20:1–27. doi:10.2307/1943521
- Cortese, L.M., J. Honig, C. Miller, and S.A. Bonos. 2010. Genetic diversity of twelve switchgrass populations using molecular and morphological markers. *Bioenerg. Res.* 3:262–271. doi:10.1007/s12155-010-9078-2
- Costich, D.E., B. Friebe, M.J. Sheehan, M.D. Casler, and E.S. Buckler. 2010. Genome-size variation in switchgrass (*Panicum virgatum*): Flow cytometry and cytology reveal rampant aneuploidy. *Plant Gen.* 3:130–141. doi:10.3835/plantgenome2010.04.0010
- Davis, M.B., and R.G. Shaw. 2001. Range shifts and adaptive responses to Quaternary climate change. *Science* 292:673–679. doi:10.1126/science.292.5517.673
- Deevey, E.S., Jr. 1949. Biogeography of the Pleistocene: Part I: Europe and North America. *Geol. Soc. Am. Bull.* 60:1315–1416. doi:10.1130/0016-7606(1949)60[1315:BOTP]2.0.CO;2
- Ernst, W.H.O., E.M. Veenendaal, and M.M. Kebakile. 1992. Possibilities for dispersal in annual and perennial grasses in a savanna in Botswana. *Vegetatio* 102:1–11. doi:10.1007/BF00031700
- Fike, J.H., D.J. Parrish, D.D. Wolf, J.A. Balasko, J.T. Green, Jr., M. Rasnake, and J.H. Reynolds. 2006. Switchgrass production for the upper southeastern USA: Influence of cultivar and cutting frequency on biomass yields. *Biomass Bioenergy* 30:207–213. doi:10.1016/j.biombioe.2005.10.008
- Gould, F.W. 1975. The grasses of Texas. Texas A&M Univ. Press, College Station.
- Gunter, L.E., G.A. Tuscan, and S.D. Wullshleger. 1996. Diversity of switchgrass based on RAPD markers. *Crop Sci.* 36:1017–1022. doi:10.2135/cropsci1996.0011183X003600040034x
- Hansen, J., R. Ruedy, M. Sato, and K. Lo. 2010. Global surface temperature change. *Rev. Geophys.* 48:RG4004. doi:10.1029/2010RG000345
- Hitchcock, A.S. 1951. Manual of the grasses of the US. USDA Misc. Publ. 200. 2nd ed. U.S. Govt. Printing Office, Washington, DC.
- Hopkins, A.A., K.P. Vogel, K.J. Moore, K.D. Johnson, and I.T. Carlson. 1995a. Genotype effects and genotype by environment interactions for traits of elite switchgrass populations. *Crop Sci.* 35:125–132. doi:10.2135/cropsci1995.0011183X003500010023x
- Hopkins, A.A., K.P. Vogel, K.J. Moore, K.D. Johnson, and I.T. Carlson. 1995b. Genetic variability and genotype \times environment interactions among switchgrass accessions from the midwestern USA. *Crop Sci.* 35:565–571. doi:10.2135/cropsci1995.0011183X003500020047x
- Huang, S., X. Siu, R. Haselkorn, and P. Gornicki. 2003. Evolution of switchgrass (*Panicum virgatum* L.) based on sequences of the nuclear gene encoding plastic acetyl-CoA carboxylase. *Plant Sci.* 164:43–49. doi:10.1016/S0168-9452(02)00327-8
- Hultquist, S.J., K.P. Vogel, D.J. Lee, K. Arumuganathan, and S. Kaeppler. 1996. Chloroplast DNA and nuclear DNA content variations among cultivars of switchgrass, *Panicum virgatum* L. *Crop Sci.* 36:1049–1052. doi:10.2135/cropsci1996.0011183X003600040039x
- Jacobson, G.T., and E.C. Grimm. 1986. A numerical analysis of Holocene forest and prairie vegetation in central Minnesota. *Ecology* 67:958–966. doi:10.2307/1939818
- Johnson, R.C., V.L. Bradley, and R.P. Knowles. 1996. Genetic contamination by windborne pollen in germplasm-regeneration plots of smooth brome grass. *Plant Genet. Resour. Newsl.* 106:30–34.
- Jones, T.A. 2003. The restoration gene pool concept: Beyond the native versus non-native debate. *Restor. Ecol.* 11:281–290. doi:10.1046/j.1526-100X.2003.00064.x
- Jones, T.A., and T.A. Monaco. 2009. A role for assisted evolution in designing native plant materials for domesticated landscapes. *Front. Ecol. Environ.* 7:541–547. doi:10.1890/080028
- Kelley, D.W., S.A. Brachfeld, E.A. Nater, and H.E. Wright, Jr. 2006. Sources of sediment in Lake Pepin on the Upper Mississippi River in response to Holocene climate changes. *J. Paleoclim.* 35:193–206. doi:10.1007/s10933-005-8686-x
- Le Comber, S.C., M.L. Ainouche, A. Kovarik, and A.R. Leitch. 2010. Making a functional diploid: From polysomic to disomic inheritance. *New Phytol.* 186:113–122. doi:10.1111/j.1469-8137.2009.03117.x
- Lemus, R., E.C. Brummer, K.J. Moore, N.E. Molstad, C.L. Burras, and M.F. Barker. 2002. Biomass yield and quality of 20 switchgrass populations in southern Iowa, USA. *Biomass Bioenergy* 23:433–442. doi:10.1016/S0961-9534(02)00073-9
- Lipka, A.E., F. Lu, J.H. Cherney, E.S. Buckler, M.D. Casler, and D.E. Costich. 2014. Accelerating the switchgrass (*Panicum virgatum* L.) breeding cycle using genomic selection approaches. *PLoS ONE* 10:1371/journal.pone.0112227.
- Liu, L., S.L. Thames, and Y. Wu. 2014. Lowland switchgrass plants in populations set completely outcrossed seeds under field conditions as assessed with SSR markers. *BioEnergy Res.* 7:253–259. doi:10.1007/s12155-013-9367-7
- Liu, L., and Y. Wu. 2012. Identification of a selfing compatible genotype and mode of inheritance in switchgrass. *BioEnergy Res.* 5:662–668. doi:10.1007/s12155-011-9173-z
- Lu, F., A.E. Lipka, J. Glaubitz, R. Elshire, J.H. Cherney, M.D. Casler, E.S. Buckler, and D.E. Costich. 2013. Switchgrass genomic diversity, ploidy, and evolution: Novel insights from a network-based SNP discovery protocol. *PLoS Genet.* 9(1):e1003215. doi:10.1371/journal.pgen.1003215
- Lu, K., S.M. Kaeppler, K.P. Vogel, K. Arumuganathan, and D.J. Lee. 1998. Nuclear DNA content and chromosome numbers in switchgrass. *Great Plains Res.* 8:269–280.
- Martinez-Reyna, J.M., and K.P. Vogel. 2002. Incompatibility systems in switchgrass. *Crop Sci.* 42:1800–1805. doi:10.2135/cropsci2002.1800

- Martinez-Reyna, J.M., K.P. Vogel, C. Caha, and D.J. Lee. 2001. Meiotic stability, chloroplast DNA polymorphisms, and morphological traits of upland \times lowland switchgrass reciprocal hybrids. *Crop Sci.* 41:1579–1583. doi:10.2135/cropsci2001.4151579x
- McLaren, K. 1976. The development of the CIE 1976 (L*a*b*) uniform colour space and colour-difference formula. *J. Soc. Dyers Colorists.* 92:337–338. doi:10.1111/j.1478-4408.1976.tb03300.x
- McMillan, C. 1959. The role of ecotypic variation in the distribution of the central grassland of North America. *Ecol. Monogr.* 29:285–308. doi:10.2307/1942132
- Missaoui, A.M., A.H. Paterson, and J.H. Bouton. 2006. Molecular markers for the classification of switchgrass (*Panicum virgatum* L.) germplasm and to assess genetic diversity in three synthetic switchgrass populations. *Genet. Resour. Crop Evol.* 53:1291–1302. doi:10.1007/s10722-005-3878-9
- Narasimhamoorthy, B., M.C. Saha, T. Swaller, and J.H. Bouton. 2008. Genetic diversity in switchgrass collections assessed by EST-SSR markers. *BioEnergy Res.* 1:136–146. doi:10.1007/s12155-008-9011-0
- Nielsen, E.L. 1944. Analysis of variation in *Panicum virgatum*. *J. Agric. Res.* 69:327–353.
- Ocuppaugh, W.R., S. Archer, and J.W. Stuth. 1996. Switchgrass recruitment from broadcast seed vs. seed fed to cattle. *J. Range Manage.* 49:368–371. doi:10.2307/4002599
- Okada, M., C. Lanzatella, M.C. Saha, J.H. Bouton, R. Wu, and C.M. Tobias. 2010. Complete switchgrass genetic maps reveal subgenome collinearity, preferential pairing, and multilocus interactions. *Genetics* 185:745–760. doi:10.1534/genetics.110.113910
- Pakeman, R.J. 2001. Plant migration rates and seed dispersal mechanisms. *J. Biogeogr.* 28:795–800. doi:10.1046/j.1365-2699.2001.00581.x
- Porter, C.L. 1966. An analysis of variation between upland and lowland switchgrass *Panicum virgatum* L. in central Oklahoma. *Ecology* 47:980–992. doi:10.2307/1935646
- Riley, R.D., and K.P. Vogel. 1982. Chromosome numbers of released cultivars of switchgrass, indiangrass, big bluestem, and sand bluestem. *Crop Sci.* 22:1081–1083. doi:10.2135/cropsci1982.0011183X002200050047x
- Root, T.L., J.T. Price, K.R. Hall, S.H. Schneider, C. Rosenzweig, and J.A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. *Nature* 421:57–60. doi:10.1038/nature01333
- Sackville-Hamilton, N.R., and K.H. Chorlton. 1997. Regeneration of accessions in seed collections: A decision guide. *Intl. Plant Genetic Res. Inst., Rome.* 75 p.
- Samson, R., S. Bailey, and C. Ho Lem. 2007. The emerging agropellet industry in Canada. REAP-Canada, Ste. Anne de Bellevue, Quebec. <http://www.reap-canada.com/> (accessed 17 Aug. 2015).
- Sanderson, M.A., P.R. Adler, A.A. Boateng, M.D. Casler, and G. Sarath. 2007. Switchgrass as a biofuels feedstock in the USA. *Can. J. Plant Sci.* 86:1315–1325. doi:10.4141/P06-136
- Sanderson, M.A., R.L. Reed, W.L. Ocuppaugh, M.A. Hussey, G. Van Esbroeck, J.C. Read, C.R. Tischler, and F.M. Hons. 1999. Switchgrass cultivars and germplasm for biomass feedstock production in Texas. *Bioresour. Technol.* 67:209–219. doi:10.1016/S0960-8524(98)00132-1
- Sgrò, C.M., A.J. Lowe, and A.A. Hoffmann. 2011. Building evolutionary resilience for conserving biodiversity under climate change. *Evol. Appl.* 4:326–337. doi:10.1111/j.1752-4571.2010.00157.x
- Stebbins, G.L. 1985. Polyploidy, hybridization, and the invasion of new habitats. *Ann. Mo. Bot. Gard.* 72:824–832. doi:10.2307/2399224
- Stubbendieck, J., S.L. Hatch, and C.H. Butterfield. 1991. *North American range plants.* Univ. of Nebraska Press, Lincoln.
- Talbert, L.E., D.H. Timothy, J.C. Burns, J.O. Rawlings, and R.H. Moll. 1983. Estimates of genetic parameters in switchgrass. *Crop Sci.* 23:725–728. doi:10.2135/cropsci1983.0011183X002300040029x
- U.S. Department of Energy. 2011. U.S. billion-ton update: Biomass supply for a bioenergy and bioproducts industry. R.D. Perlack and B.J. Stokes (Leads), ORNL/TM-2011/224. Oak Ridge National Laboratory, Oak Ridge, TN. 227 p.
- Vogel, K.P. 2004. Switchgrass. In: L.E. Moser, L. Sollenberger, and B. Burson, editors, Warm-season (C₄) grasses. ASA-CSSA-SSSA Monograph, Madison, WI. p. 561–588.
- Vogel, K.P., R.B. Mitchell, M.D. Casler, and G. Sarath. 2014. Registration of ‘Liberty’ switchgrass. *J. Plant Reg.* 8:242–247. doi:10.3198/jpr2013.12.0076crc
- Vogel, K.P., M.R. Schmer, and R.B. Mitchell. 2005. Plant adaptation regions: Ecological and climatic classification of plant materials. *Rangeland Ecol. Manag.* 58:315–319. doi:10.2111/1551-5028(2005)58[315:PAREAC]2.0.CO;2
- Waller, S.S., and J.K. Lewis. 1979. Occurrence of C3 and C4 photosynthetic pathways of North American grasses. *J. Range Manage.* 32:12–28. doi:10.2307/3897378
- Webb, S. 1986. Potential role of passenger pigeons and other vertebrates in the rapid Holocene migrations of nut trees. *Quat. Res.* 26:367–375. doi:10.1016/0033-5894(86)90096-7
- Weeks, A.R., C.M. Sgrò, A.G. Young, R. Frankham, N.J. Mitchell, K.A. Miller, M. Byrne, D.J. Coates, M.D.B. Eldridge, P. Aunnucks, M.F. Breed, E.A. James, and A.A. Hoffmann. 2011. Assessing the benefits and risks of translocations in changing environments: A genetic perspective. *Evol. Appl.* 4:709–725. doi:10.1111/j.1752-4571.2011.00192.x
- Wheeler, W.A., and D.D. Hill. 1957. *Grassland seeds.* D. Van Nostrand Co., Inc., Princeton, NJ.
- Wilson, G.B., and J.N.B. Bell. 1985. Studies on the tolerance to SO₂ of grass populations in polluted areas. III. Investigations on the rate of development of tolerance. *New Phytol.* 100:63–77. doi:10.1111/j.1469-8137.1985.tb02758.x
- Wolfe, K.H. 2001. Yesterday's polyploids and the mystery of diploidization. *Nat. Rev. Genet.* 2:333–341. doi:10.1038/35072009
- Young, H.A., B.J. Hernlem, A.L. Anderton, C.L. Lanzatella, and C.M. Tobias. 2010. Dihaploid stocks of switchgrass isolated by a screening approach. *Bioenergy Res.* 3:305–313. doi:10.1007/s12155-010-9081-7
- Young, H.A., C.L. Lanzatella, G. Sarath, and C.M. Tobias. 2011. Chloroplast genome variation in upland and lowland switchgrass. *PLoS ONE* 6(8):e23980. doi:10.1371/journal.pone.0023980
- Zalapa, J.E., D.L. Price, S.M. Kaeppler, C.M. Tobias, M. Okada, and M.D. Casler. 2011. Hierarchical classification of switchgrass genotypes using SSR and chloroplast sequences: Ecotypes, ploidies, gene pools, and cultivars. *Theor. Appl. Genet.* 122:805–817. doi:10.1007/s00122-010-1488-1
- Zhang, Y., J. Zalapa, A.R. Jakubowski, D.L. Price, A. Acharya, Y. Wei, E.C. Brummer, S.M. Kaeppler, and M.D. Casler. 2011a. Post-glacial evolution of *Panicum virgatum*: Centers of diversity and gene pools revealed by SSR markers and cpDNA sequences. *Genetica (The Hague)* 139:933–948.
- Zhang, Y., J. Zalapa, A.R. Jakubowski, D.L. Price, A. Acharya, Y. Wei, E.C. Brummer, S.M. Kaeppler, and M.D. Casler. 2011b. Natural hybrids and gene flow between upland and lowland switchgrass. *Crop Sci.* 51:2626–2641. doi:10.2135/cropsci2011.02.0104