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Switchgrass

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22 Switchgrass

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CONTENTS

22.1 INTRODUCTION

Switchgrass (*Panicum virgatum* L.) is a tall, erect, warm-season perennial native to the tall grass prairie, oak savanna, and associated ecosystems of North America. It can be found in prairies, open woodlands, and brackish marshes east of the Rocky Mountains and generally south of 55° north latitude (Hitchcock 1951; Stubbendieck et al. 1991). Less than 1% of these ecosystems exist today, but these prairie and savanna remnants have served as in situ gene banks, preserving a vast amount of genetic diversity within switchgrass and many other plant species. Switchgrass has a diversity of uses as well, including pasture, hay production, biomass for energy production, soil and water conservation, carbon sequestration, and wildlife habitat.

Switchgrass is adapted to a wide range of habitats, climatic conditions, and management strategies. In North America, switchgrass can be found in hardiness zones 3–9, from southern Canada (Manitoba to Newfoundland) to Baja California and the Gulf Coast (central Mexico to central Florida) (Figure 22.1). Switchgrass tolerates drought, extreme heat and cold, and moderately acid soils, and has relatively few major insect or disease pests. Switchgrass can be defoliated a number of times during the growing season, as in a managed grazing system, or infrequently, as in a bioenergy management system with only one or two harvests per season. Timing of harvests is moderately critical, largely to ensure that the plant is allowed to translocate storage carbohydrates to roots for regrowth after harvest and following overwintering. Grazing systems should incorporate adequate rest periods, although hay or bioenergy management systems should avoid harvesting during the last few weeks of the growing season to allow carbohydrate storage.

Switchgrass is a C_4 species with associated anatomical and physiological characteristics (Waller and Lewis 1979). Switchgrass is very slow to establish, largely because establishment-year development is oriented toward extensive root and crown development, often resulting in intense above-ground competition between switchgrass shoots and annual weeds. Both pre- and postemergence herbicides are valuable tools that aid in the establishment of switchgrass, shortening the time required to reach successful establishment and maximal biomass yields.

Interest in switchgrass as a bioenergy feedstock began when the U.S. Department of Energy (DOE) initiated its Bioenergy Feedstock Development Program (BFDP) by selecting switchgrass as the herbaceous model species. The decision was made largely because of consistently high biomass yields relative to other species across a broad geographic landscape, the relative simplicity of switchgrass propagation by seed, and an existing seed industry (McLaughlin and Kzsos 2005; Parrish and Fike 2005; Sanderson et al. 2007). Accomplishments of this program are credited with the approximately 25% increase in biomass yields of switchgrass because of the improved description and deployment of adapted cultivars, improved harvest and fertility management, and the development of new cultivars with higher biomass yield and expanded adaptation ranges (Sanderson et al. 2007).

FIGURE 22.1 Historical range of switchgrass in North America.

22.2 MORPHOLOGY AND TAXONOMY

Switchgrass grows 0.5–3 m tall and most plants are caespitose in appearance, with an occasional rhizomatous plant. Caespitose plants have short rhizomes and can form a sod over time. The inflorescence is a diffuse panicle 15–55 cm long with spikelets toward the end of long branches (Hitchcock 1951; Gould 1975). Spikelets disarticulate below the glumes and are two-flowered with the upper floret perfect and the lower floret either empty or staminate. Spikelets are 3–5 mm long and florets are glabrous and awnless. The lemma of the fertile floret is smooth and shiny. Leaves have rounded sheaths and firm flat blades that can vary from 10 to 60 cm in length. The number of leaves per culm will vary depending on genotype and environment (Redfearn et al. 1997). The ligule is a fringed membrane 1.5–3.5 mm long and consists mostly of hairs. Switchgrass reproduces by seeds, tillers, and rhizomes. It has the Pancoid type of seedling root (Newman and Moser 1988; Tischler and Voigt 1993). Roots of established plants may reach depths of 3 m (Weaver 1954).

Seed consists of the indurate and smooth lemma and palea, which hold tightly to the caryopsis. The margins of the lemma are enrolled over the margin of the palea. Glumes are almost entirely removed by combining and cleaning. On the average there are approximately 850 seeds/g (Wheeler and Hill 1957). Seed weight differences exist within and among cultivars. As an example, genotypic variation in seed mass within the cultivar Sunburst has been reported with a range of 450–850 seeds/g (Vogel 2002). Switchgrass is easily threshed, cleaned, and planted with commercial planting equipment. A switchgrass seed industry has existed for over 50 years and numerous private companies and public crop improvement associations are involved in seed production, distribution, and marketing.

Switchgrass has two distinct ecotypes—upland and lowland (Brunken and Estes 1975). As the names suggest, the lowland ecotype was originally found on flood plains and riparian zones subject to occasional flooding and/or waterlogging. The upland ecotype was originally found in upland areas that were not subject to flooding and often prone to drought. Plants of the upland and lowland ecotypes are morphologically and genetically distinct from each other. Generally, lowland plants have a later heading date, taller plant height, larger and thicker stems, fewer stems per plant, more upright leaf blades, and a more bluish cast than upland plants. Upland and lowland plants can be easily crossed with each other (Martinez-Reyna et al. 2001) and intermediate types exist in nature, suggesting that upland x lowland crosses have occurred in natural ecosystems, despite the large difference in heading date between upland and lowland ecotypes.

22.3 GENETICS

Switchgrass has a basic chromosome number of $x = 9$ (Gould 1975). A wide range of chromosome numbers has been reported in the literature including somatic counts of 18, 36, 54, 72, 90, and 108 chromosomes (Nielsen 1944; Barnett and Carver 1967). Switchgrass has small chromosomes that are difficult to count. Recent studies aided by the use of flow cytometry indicate that most switchgrass cultivars are either tetraploid ($2n = 4x = 36$) or octaploid ($2n = 8x = 72$) (Hopkins et al. 1996; Lu et al. 1998). The tetraploids and octaploids average 3.1 and 6.1 pg $2C^{-1}$ DNA (Lu et al. 1998). The 2C (“C” stands for “constant”) value is the DNA content of a diploid somatic nucleus expressed in pg (picogram or 10^{-12} g) and can be converted to daltons or nucleotide pairs using the formulas: 1 nucleotide pair = 660 Da; 1 pg = 0.965×10^9 nucleotide pairs (Bennett and Smith 1976). To date, all lowland plants appear to be tetraploids on the basis of chromosome counts of mitosis in root tips or flow cytometry analyses, although most upland plants are tetraploids or octaploids. Tetraploid and octaploid plants occur sympatrically in over half of the remnant prairies that were evaluated by Hultquist et al. (1997). They did not report hexaploid plants in remnant prairies. Several researchers have attempted to relate ploidy levels to morphological traits and geographical distribution, but the results were inconclusive (Nielsen 1944, 1947; McMillan and Weiler 1959; Barnett and Carver 1967). There are numerous reports of aneuploidy in switchgrass, particularly at the higher ploidy levels (Costich et al. 2010), but some disagreement as to the frequency and severity of this phenomenon.

Normal bivalent pairing has been reported for tetraploid and octaploid switchgrass plants (Riley and Vogel 1982; Martinez-Reyna et al. 2001). Aneuploid variants and multivalent chromosome associations are more frequent at higher ploidy levels (Barnett and Carver 1967; Brunken and Estes 1975). An analysis of segregation and linkage relationships for random markers distributed across the genome of an upland × lowland tetraploid cross suggested polysomic inheritance (Missaoui et al. 2005a). This conclusion was based on the observed ratios of single- to multiple-dose markers and the observed ratios of loci linked in coupling vs. repulsion phase. Additional analyses, following more complete genomewide marker saturation, clearly identified 18 linkage groups, suggesting an all-tetraploid genome with disomic inheritance (Okada et al. 2010).

The evidence for preferential pairing and disomic inheritance within a polyploid series that ranges from $2n = 2x = 18$ to $2n = 12x = 108$ is surprising. Normally, extensive polyploid series such as this one arise by spontaneous doubling of whole genomes, leading to autopolyploidy (Mable 2003). The evidence for higher frequencies of aneuploid variants and multivalent pairing at higher ploidy levels suggests multiple mechanisms of polyploidization, pairing, and gene inheritance within switchgrass, i.e., apparent allopolyploidy and disomic inheritance at the tetraploid level and possible autopolyploidy and polysomic inheritance at higher ploidy levels. It also raises the intriguing question: If tetraploid switchgrass is an allopolyploid, what are its ancestors and, as a corollary, do upland and lowland switchgrasses have different ancestors? Alternatively, is the polyploid switchgrass genome in the process of diverging into two distinct and duplicate genomes?

Switchgrass is a member of the Paniceae tribe of grasses, which diverged from the Maydeae (maize) tribe approximately 23 Mya. Upland and lowland ecotypes are thought to have diverged from each other sometime between 1 and 2 Mya on the basis of sequences of the nuclear gene encoding plastid acetyl-CoA carboxylase, *Acc-1* (Huang et al. 2003). These authors further speculate that polyploidization events were involved in this divergence, as the *Acc-1* polymorphisms appear to discriminate a "lowland tetraploid" from an "upland octaploid" form. Polymorphisms at the *Acc-1* locus within tetraploid plants of both the upland and lowland ecotypes suggest the possibility of four ancestral diploids (Huang et al. 2003).

Switchgrass has two cytoplasm types, "L" and "U" that are based on chloroplast DNA (cpDNA) polymorphisms that are associated with the lowland and upland ecotypes, respectively, (Hultquist et al. 1996; Missaoui et al. 2006). The "L" cytoplasm types are tetraploids whereas the "U" types can be either tetraploids or octaploids (Hultquist et al. 1996). Martinez-Reyna et al. (2001) used controlled reciprocal crosses between "Kanlow" ("L" tetraploid) and "Summer" ("U" tetraploid) plants and a restriction fragment length polymorphism (RFLP) marker to demonstrate that the chloroplast DNA of switchgrass is maternally inherited. They also determined that the lowland and upland ecotypes and associated cytoplasm types of switchgrass are completely cross-fertile at the tetraploid level and that there is a high degree of similarity among their nuclear genomes as indicated by normal bivalent pairing during meiosis. This is supported by linkage analyses and homology between "Alamo" ("L" tetraploid) and Summer linkage groups (Missaoui et al. 2005a). Despite their homology, upland and lowland ecotypes are genetically distinct, as demonstrated by cpDNA markers (Hultquist et al. 1996; Missaoui et al. 2006) and random amplified polymorphic DNA (RAPD) markers (Gunter et al. 1996). Extreme differential heading and anthesis dates, combined with physical isolation due to habitat differentiation and fragmentation, are the likely causes of relatively recent genetic isolation of the upland and lowland ecotypes. Upland and lowland ecotypes can occur sympatrically, with differential heading and anthesis dates serving to maintain distinct and isolated germplasm pools (Brunken and Estes 1975).

Ecotypic variation in switchgrass derives largely from the broad geographic distribution of the species, which extends from approximately 15 to 55° north latitude in North America. Photoperiod is one of the principal drivers of ecotypic variation, ranging from 13 to 17 h on the summer solstice at these extreme latitudes. Switchgrass is thought to have survived the Pliestocene Glaciation in three refugia located in the southern United States, perhaps including northern Mexico: a western semimontane (dryland) region, a central humid region with rich, fertile soils, and a southeastern region, perhaps near the Gulf Coast (McMillan 1959). With the retreat of glaciation approximately 11,000 years ago, switchgrass and other members of these prairie remnants rapidly moved north, colonizing a wide range of habitats under increasingly longer day length, but shorter growing seasons. High levels of genetic diversity within these remnant populations allowed natural selection to proceed for traits necessary to survive in northern latitudes, including early flowering and cold tolerance.

As a result of natural selection, switchgrass ecotypes are photoperiod sensitive, requiring short days to induce flowering (Benedict 1941). Photoperiod requirements are based on the latitude-of-origin of individual ecotypes. Flowering is induced by decreases in day length following the summer solstice. In North America, exporting northern ecotypes south exposes them to a shorter-than-normal day length during summer months, which causes early flowering, often drastically reducing their ability to utilize the full growing season because of early senescence (Vogel 2004). The opposite occurs when southern ecotypes are exported north. They remain vegetative for a longer period of time, with a longer photosynthetically active period, often producing more forage than northern ecotypes (Newell 1968a). When grown in the central Great Plains, switchgrasses from the Dakotas (northern ecotypes) flower and mature early and are short in stature whereas those from Texas and Oklahoma (southern ecotypes) flower late and are tall (Cornelius and Johnson 1941; McMillan 1959). This patterned response to photoperiod also occurs for switchgrass cultivars and ecotypes grown in Europe where it is not native (Elbersen et al. 2003).

The photoperiod response also appears to be associated with winter survival and cold tolerance. Southern ecotypes exported too far north will not survive winters because they stay vegetative too late in the fall, lack the ability to store sufficient carbohydrates during winter, and lack sufficient cold/freezing tolerance (Casler et al. 2004, 2007a). As a general rule, switchgrass germplasm should not be exported more than one USDA Plant Hardiness Zone (Cathey 1990) north or south of its area of origin because of these adaptation issues. At this time, the genetic regulation of these latitude-associated traits is unknown.

Switchgrass is a cross-pollinated species with a gametophytic self-compatibility system that is similar to the S-Z incompatibility system found in other Poaceae (Martinez-Reyna and Vogel 2002). Pollen is dispersed by wind. Self-compatibility, as measured by seed set from bagged panicles, is typically less than 1% (Talbert et al. 1983; Martinez-Reyna and Vogel 2002). A postfertilization incompatibility system also exists that inhibits intermatings among octaploid and tetraploid plants (Martinez-Reyna and Vogel 2002). The postfertilization incompatibility system between ploidy levels in switchgrass appears to be similar to the endosperm balance number system found in other species. The postfertilization incompatibility system is probably responsible for the relatively low frequency of hexaploid plants in native prairies. The tetraploid and octaploid plants in native prairies may exist as separate and distinct populations.

As switchgrass migrated north from the glacial refugia, wind pollination and migratory animals that carried seeds, as undigested feed or as hitchhikers in fur or feathers, were likely responsible for considerable genetic mixing along populational boundaries and, perhaps, over large geographic regions. Cross-pollination balanced the effects of natural selection, causing some genetic homogenization across sites and large amounts of genetic variation within sites (Casler et al. 2007b). Even though the tallgrass prairie ecosystem is highly fragmented with only about 1% intact, a vast array of genetic variability has been preserved both within and among prairie remnant sites. Analyses of RAPD markers for plants collected from prairie remnants from the Dakotas to New York suggest that these isolated prairie remnants continue to act as one large remnant population that contains many subpopulations each capable of representing much of the variability present within the population as a whole (Casler et al. 2007b). Although the destruction of the tallgrass prairie and associated ecosystems was nearly complete 100 years ago, self-incompatibility and polyploidy have served to preserve genetic variability within this species.

Because of the effects of photoperiod of flowering and the large temperature differential across the north-south gradient of natural switchgrass populations, latitude is the most important factor determining adaptation of switchgrass ecotypes and cultivars. Differentiation along east-west gradients of switchgrass populations tend to be less obvious than along north-south gradients, most likely because the factors that may cause such differentiation—soil type, historical vegetational succession, and moisture availability—are less important than temperature and day length in generating selection pressures leading to morphological or physiological differentiation (Nixon and McMillan 1964; Casler et al. 2007a). Nevertheless, there is some differentiation between upland switchgrass populations deriving from the tallgrass prairie of the Central Great Plains and the historical Eastern Forest ecosystems (McMillan 1959; Casler et al. 2007a).

The balancing effects of natural selection, creating differentiation among populations and uniformity within populations, and self-incompatibility, which favors homogenization of populations and promotes diversity within populations, suggests that switchgrass germplasm can be classified into relatively few functional gene pools to represent the eastern two-thirds of the United States (Casler et al. 2007a, b). Eight gene pools are proposed to represent four groups of hardiness zones within each of the Great Plains region and Eastern Forest biomes east of the Mississippi River (Figure 22.2). The choice of eight gene pools was somewhat arbitrary and the boundaries between gene pools are fluid to promote flexibility. Some hardiness zones have been combined because it is impractical and unnecessarily reductionist to develop and/or recommend switchgrass germplasm for one hardiness zone. The east-west discrimination of the historical Great Plains and Eastern Forest biomes is based largely on precipitation and humidity, recognizing that eastern germplasm may have reduced drought tolerance relative to western germplasm whereas western germplasm may not have the disease resistance required in the more humid eastern region. For example, 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

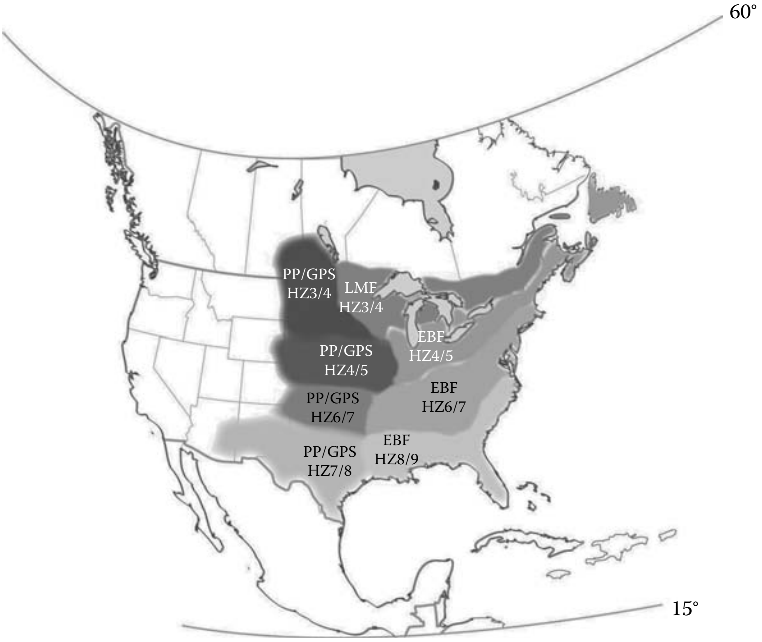

FIGURE 22.2 (See color insert) Proposed gene pools for deployment of regionally adapted switchgrass germplasm and cultivars for use in breeding programs or in conservation and restoration projects. PP, prairie parkland; GPS, Great Plains steppe; LMF, Laurentian mixed forest; EBF, eastern broadleaf forest. (From Bailey, R.G., *Ecoregions: The Ecosystem Geography of the Oceans and Continents,* Springer-Verlag Inc., New York, 1998; Bailey, R. G., *Ecosystem Geography,* 2nd ed, Springer-Verlag Inc., New York, 2009.) HZ, USDA hardiness zone. (From Cathey, H.M., USDA plant hardiness zone map, USDA Misc Pub No 1475. U.S. Department of Agriculture, Washington, DC, 1998; U.S. National Arboretum, 1990. Available at www.usna.usda.gov/Hardzone/ushzmap.html)

reduced relative biomass yields as it is moved east into the historic Eastern Forest biome (Hopkins et al. 1995a; Casler and Boe 2003).

Gene pools are defined so that germplasm originating within any region can be utilized at other sites within that region without concern about lack of adaptation or fear of contaminating local switchgrass populations with exotic genetics (Vogel et al. 2005). The switchgrass gene pool concept is intended to apply to any use of switchgrass germplasm, including development of germplasm pools and breeding populations, parental materials for cultivar development, and deployment of ecotypes and/or natural-track cultivars for use in conservation and restoration projects. The northern gene pools of the United States likely apply to regions of southern Canada that share similar climatic and edaphic conditions, as evidenced by adaptation of numerous switchgrass cultivars in eastern Canada (Madakadze et al. 1998, 1999b).

22.4 PHYSIOLOGY AND GROWTH

The germination and growth of switchgrass seedlings are reduced at soil temperatures less than 20°C (Hsu et al. 1985a, 1985b). Consequently, the recommended seeding dates for switchgrass correspond to those for maize (*Zea mays* L.). Switchgrass seedlings have the panicoid seedling morphology and seedlings emerge by elongation of the mesocotyl or the subcoleoptile internode, which pushes the crown node and the coleoptile, which stays short, to the soil surface (Hoshikawa 1969; Newman and Moser 1988; Tischler and Voigt 1993). When the coleoptile reaches the soil surface, light induces the mesocotyl to stop elongating. Adventitious roots, which are necessary for seedling and plant survival, arise from the crown node at the base of the coleoptile near the soil surface. Planting seed deeper than 1 cm can adversely affect field establishment because more seedling reserves are required for mesocotyl elongation. Dry soil conditions at the soil surface can prevent seedlings from developing adventitious roots to ensure survival, therefore planting dates should be targeted for periods when the probability of rain is high and soil temperatures are sufficiently high for germination (Smart and Moser 1997). Planting too late in the summer will result in stand failures because seedlings will not have adequate time to become established, transition from juvenile to adult phase, and develop the root reserves necessary to become perennial.

Within 6 weeks of emergence several tillers may be produced. Growth of switchgrass in the establishment year depends upon soil moisture, fertility, and competition from weeds and other plants. Switchgrass does not require vernalization to induce flowering. Under optimum conditions, switchgrass will produce seed in the establishment year but flowering occurs several weeks later than in following years. This delay in flowering and seed ripening is likely due to the ineffectiveness of floral induction before the transition from juvenile to adult phase (Poethig 2003). Growth of switchgrass during the establishment year is slow relative to many other grasses, largely because many plant resources are being devoted to development of an extensive root system.

New growth in the spring is initiated from axillary buds on the stem, crown, or rhizomes (Heidemann and Van Riper 1967; Sims et al. 1971; Beaty et al. 1978). The relative amount of new growth from each type of bud varies with ecotype and strain. Bunch types apparently produce new tillers from both crown buds and rhizomes (Heidemann and Van Riper 1967; Sims et al. 1971) but sod-forming plants produce new tillers primarily from rhizomes (Beaty et al. 1978). Depending upon the physiological stage and environmental conditions, new growth may be initiated after harvest from all three types of buds. Plants with short rhizomes produce bunch-type plants, which can be pushed above the soil line by roots, whereas sod-forming plants have longer rhizomes (Beaty et al. 1978). The growth and development of a switchgrass plant depends upon its genotype and the location where it is evaluated. The development of switchgrass is location dependent because flowering depends on photoperiod as discussed previously but also growing-degree-days (GDD) which measure accumulated heat or photosynthesis energy.

The physiological development of switchgrass as determined using a maturity staging system (Moore et al. 1991) is highly correlated to day-of-the-year (DOY) and GDD in temperate climates such as the

Great Plains of the United States (Sanderson and Wolf 1995; Mitchell et al. 1997, 2001). In the Central Great Plains, photoperiod as measured by DOY was more predictive of physiological development than GDD, indicating that photoperiod is the primary determinant of switchgrass development but photosynthesis or heat units can modify the developmental response (Mitchell et al. 1997).

A population of switchgrass plants will have populations of tillers at different stages of development (Mitchell et al. 1997). Genetically broad-based populations will have some plants at anthesis over a 3-week period (Jones and Brown 1951). Florets in an individual panicle will be undergoing anthesis for up to 12 d (Jones and Newell 1946). Peak pollen shedding periods are from 10:00 to 12:00 h or from 12:00 to 15:00 h depending upon environmental conditions (Jones and Newell 1946). Heading dates for cultivars are typically expressed as population means. Because flowering time varies among individual genotypes, the development of ripe seed is also variable within a population or cultivar.

The stem bases, roots, and rhizomes are the primary sites of nonstructural carbohydrate storage. Starch is the primary and most dynamic nonstructural carbohydrate in switchgrass stem bases and rhizomes (Smith 1975). Nonreducing sugars, primarily sucrose, are secondary in importance to starch and fluctuate in a similar manner during the growing season. Total nonstructural carbohydrates (TNC) concentrations in the stem bases of unharvested plants are greatest at the beginning and end of the growing season. Stem base TNC concentrations reach the lowest levels at the time of tiller elongation or when regrowth is initiated following harvest (Smith 1975). A recent fertilization study in which N concentration of biomass was monitored indicates that switchgrass may actively transport N and nonstructural carbohydrates from above ground biomass to stem bases and roots after anthesis but before a killing frost (Vogel et al. 2002a). Harvest time is critical for adequate survival of switchgrass swards, with consistently early harvests reducing switchgrass stands, most likely due to inadequate time for cycling of nitrogen and soluble carbohydrates to storage organs (Casler and Boe 2003).

Switchgrass requires the establishment of a symbiotic relationship with arbuscular mycorrhizal fungi (AMF) in its roots to become established and persist (Brejda et al. 1998). Rhizosphere microflora from numerous native prairies and old seeded stands of switchgrass were effective in enhancing seedling growth of switchgrass in greenhouse trials (Brejda et al. 1998). A field study on two different soils demonstrated that indigenous AMF in cultivated fields of the central Great Plains establish a symbiotic relationship with switchgrass and that inoculation offers little potential to increase switchgrass production unless the soils have been severely degraded (Brejda 1996). Significant interactions between AMF isolates and soil types suggest some differential adaptation of AMF isolates to different soils (Clark et al. 2005).

Switchgrass is relatively drought tolerant with a deep root system likely contributing to its ability to draw water from deep aquifers. Water-use efficiency (WUE) of switchgrass was 1.8–3.6 mg biomass/g water across several soils and nitrogen rates in Pennsylvania (Stout 1992). Switchgrass WUE increased by 30% with an increase in N fertilizer from 0 to 84 kg N/ha. In that study, the WUE of switchgrass was 5.7 times greater than the WUE of orchardgrass (*Dactylis glomerata* L.). In the Great Plains of the United States, the WUE of switchgrass ranged from 3.5 to 5 mg biomass/g water across several locations (Kiniry et al. 2008). The WUE of switchgrass was 1.8–5.0 times greater than the WUE of maize used for grain production, but similar to the WUE of maize biomass production (Kiniry et al. 2008).

22.5 MANAGEMENT

22.5.1 Establishment

Recommended seeding rates are 200–400 pure live seeds (PLS) per m^2 (Vogel 1987). Establishment-year stands with 20 or more plants/m^2 will produce harvestable forage the year of establishment if weeds are controlled and can be in full production the year after establishment (Vogel 1987; Vogel and Masters 2001). Establishment-year stands of 10 plants/m^2 are adequate but will require one or more years to achieve full production yields. Stands of less than 10 plants/m^2 may need to be overseeded or re-seeded. An on-farm study indicated that establishment-year stands of 40% or greater, determined by a frequency grid, can be considered adequate for successful establishment (Schmer et al. 2006).

The minimal germination temperature for switchgrass is 10°C (Hsu et al. 1985a). Temperature-gradient-table studies with several switchgrass cultivars and seedlots demonstrated that near-maximal germination was obtained from 19 to 36°C and optimal germination was between 27 and 30°C (Dierberger 1991). Optimum germination temperatures for switchgrass may be lower than those for seedling development (Panciera and Jung, 1984). Seedling growth of switchgrass at 20°C is much slower than at 25 or 30°C (Hsu et al. 1985b). Although seedlings develop slowly, planting in early spring may be advantageous even though the soil is cold if the seed lot being used has dormant seed. The cold soil may aid in breaking dormancy. Best stands in Iowa were obtained when planted at early to mid-spring (Vassey et al. 1985). In the northeastern United States, a planting window of 3 weeks before and 3 weeks after the recommended maize planting date has been suggested (Panciera and Jung 1984). This general guideline for time of planting would be suitable in most areas where switchgrass is adapted. In some areas "dormant plantings" are made very late in the fall, late enough that the seed will not germinate. The seed remains dormant during winter and the cool moist spring conditions result in a natural cold stratification. Switchgrass should not be planted in late summer because it may not have time to develop sufficient cold tolerance before onset of winter.

Planting seed too deeply often leads to seeding failures with switchgrass and other small seeded warm-season grasses. Switchgrass requires a firm seedbed, allowing the drill to plant the seed approximately 1–2 cm deep. No-till seeding into crop residues or chemically killed sods is often very effective (Samson and Moser 1982). Corrective applications of P or K should be made before seeding but N applications are generally not made until the grass is established because it will stimulate excessive weed growth during the seeding year.

Physiological seed dormancy of some cultivars and seedlots of switchgrass can result in seeding failure. Although alive, dormant seed will not germinate under normally suitable conditions. Simple dormancy will be broken if the seed is aged long enough or if it is given cold treatments or cold stratified to break dormancy (Zheng-Xing et al. 2001). The normal germination test carried out according to Association of Official Seed Analysts procedures (AOSA 1988) includes a period of cold stratification where seed are allowed to imbibe water and are chilled at 4°C for 2–4 weeks to break dormancy. The germination percentage on the seed tag represents the percentage of viable seed but does not represent the actual amount of seed that will germinate upon planting because of dormancy. Producers should conduct a germination test without chilling if they suspect dormant seed and want to determine the percentage of seed that will germinate when planted. With time, much of the dormancy will be broken if seed is stored for 1 year at room temperatures. Seed stored for 3 or more years at room temperature may result in poor stands due to decreased vigor (Vogel 2002). Dormancy of switchgrass seed can be broken by stratification by wet chilling, but drying can cause some of the seed to revert to a dormant condition (Zhang-Xing et al. 2001). Extended stratification (>42 days) significantly reduced the percentage of switchgrass seed that reverted to a dormant condition after drying (Zhang-Xing et al. 2001). It must be emphasized that switchgrass seed should have high germination (>75%) and should not be older than 3 years to ensure successful establishment. Old seed can have good laboratory germination but may have poor seedling vigor and fail to produce acceptable stands under field conditions.

Variation exists among and within cultivars for seed size. Smart and Moser (1999) graded switchgrass seed into lots differing in seed weight and evaluated the seed lots in field plantings. Seedlings from the heavy seed had greater germination, earlier shoot and adventitious root growth than seedlings from light seed but growth and development were similar 8–10 weeks after emergence.

Weed competition is one of the major reasons for stand failure of switchgrass. Seedlings do not develop rapidly until conditions are warm, which is also the same time that annual weeds develop.

Most dicot weeds can be controlled with 2,4-D (2,4-dichlorophenoxyacteic acid). Generally, 2,4-D should be applied after switchgrass seedlings have approximately four to five leaves. Atrazine [6-chloro-*N*-ethyl-*N*′-(1-methylethyl)-1,3,5-triazine-2,4-diamine] has been used to improve establishment of switchgrass by controlling broadleaf weeds and C_3 weedy grasses (Martin et al. 1982; Bahler et al. 1984). Switchgrass can metabolize atrazine (Weimer et al. 1988). Acceptable stands of switchgrass could be established at a reduced seeding rate of 107 pure live seed per m^2 when weed interference was reduced following atrazine application at time of planting (Vogel 1987). Imazethapyr {2-[4,5-dihydro-4-methyl-4-(1-methylethyl)-5-oxo-1H-imidazol-2-yl]-5-ethyl-3-pyridine carboxylic acid}, applied at 70 g ai/ha before the grass seedlings emerged, provided excellent weed control and enabled excellent stands of switchgrass to be obtained within 1 year of planting (Masters et al. 1996). The postplant, pre-emergence application of a tank mix of quinclorac (Paramount®; 3,7-dichloro-8-quinolinecarboxylic acid) at 1.1 kg ai/ha plusatrazine at 1.12 kg ai/ha has provided excellent weed control in switchgrass seedlings in Nebraska, North Dakota, and South Dakota (Mitchell, unpublished data). This herbicide treatment controlled broadleaf weeds and weedy grasses and resulted in acceptable stands and high biomass yields. Application of imazapic {2-[4,5-dihydro-4-methyl-4-(1-methylethyl)-5-oxo-1H-imidazol-2-yl]-5-methyl-3-pyridine carboxylic acid} on switchgrass, although effective in some trials, has resulted in significant stand reductions in other tests. The labeled use of imazethapyr and quinclorac on switchgrass as a pre- or postemergent herbicide varies with state or region and year. The efficacy of these herbicides does not change, only the regulations. Maize has been successfully used as a cover crop for switchgrass (Hintz et al. 1998). Atrazine is applied for weed control after both crops are planted. Corn is harvested for grain and is the primary crop the year of establishment. Herbicides should be used only in geographical regions and applications for which they are labeled.

In addition to herbicides that can be used during establishment, other herbicides are available for use on established stands of switchgrass. Switchgrass stands are not affected by metolachlor [2-chloro-*N*-(2-ethyl-6-methylphenyl)-*N*-(2-methoxy-1-methylethyl)acetamide] applied at rates needed to control annual weedy grasses (Masters et al. 1996). Commercial products containing both atrazine and metolachlor are labeled for use in seed production in some regions. Metasulfuron (methyl 2-[[[[(4-methoxy-6-methyl-1,3,5-trizin-2-yl)-amino]carbonyl]-amino]sulfonyl]benzoate) and clopyralid (3,6-dichloro-2-pyridinecarboxylic acid) plus 2,4-D can be used for weed control in established stands (Anonymous 2002).

22.5.2 FERTILITY

Switchgrass can tolerate low fertility conditions but it responds to fertilizer (Rehm et al. 1976; Jung et al. 1988). It responds to N fertilization with significant increases in forage and biomass yield (McMurphy et al. 1975; Rehm et al. 1976, 1977; Perry and Baltensperger 1979; Hall et al. 1982; Rehm 1984; Madakadze et al. 1999a; Sanderson et al. 1999; Vogel et al. 2002a). Recommended N fertilization rates vary with location and are primarily dependent upon precipitation, cultivar, and harvest management. In the eastern Great Plains and the Midwest, United States, recommended annual rates of N vary from 90 to 110 kg/ha when switchgrass is managed for hay or pasture whereas further west, where there is less precipitation, rates of 45–70 kg/ha are used. When switchgrass is managed for optimal biomass production in the Midwest, approximately 10–12 kg/ha N needs to be applied for each Mg/ha of biomass yield (Vogel et al. 2002a). At fertility rates above this level, nitrates accumulated in the soil profile. In South Dakota Conservation Reserve Program (CRP) lands dominated by switchgrass, the application of 56 kg N/ha increased total biomass, but there was no benefit to applying more N (Mulkey et al. 2006). Switchgrass may respond to P fertilization if the availability of P in the soil is low (Rehm et al. 1976; Rehm 1984). Switchgrass and other C_4 grasses should be fertilized in late spring when they are initiating growth. Early spring fertilization will stimulate invasion by C_3 grasses and forbs (Rehm et al. 1976). Nitrogen fertilization increases the herbage protein concentration (Rehm et al. 1977; Perry and Baltensperger 1979; Rehm 1984; Vogel et al. 2002a) and in vitro dry matter digestibility (IVDMD) of switchgrass (Perry and Baltsenberger 1979; George et al. 1990).

Fertilizer application rates for switchgrass should be based on the difference between the requirements of the crop and available soil N. However, time of harvest will have a significant impact on the nutrients removed in the harvested biomass. For example, harvesting a switchgrass field at anthesis that produces 11 Mg/ha of DM with a N concentration 1.2% N will remove about 130 kg of N/ha, whereas material harvested after a killing frost may remove only half of that amount of N/ha. Harvesting after a killing frost may reduce N application by 30–40%. Sampling soils to determine available N for switchgrass production must be taken to a depth of 1.5–2 m because of the soil mineralization potential of some soils, atmospheric N deposition, residual soil N from previous crops that may be distributed deep in the soil profile, and the deep rooting capability of switchgrass (Mitchell et al. 2008).

On a strongly acid (pH 4.3–4.9), low P soil, unfertilized switchgrass and big bluestem (*Andropogon gerardii* Vitman) produced 50% as much forage as that receiving a low level of nutrients (Jung et al. 1988). When P declined from 35 to 5 mg/kg, switchgrass yields declined 12% compared to C_3 grasses which declined 35% (Panciera and Jung 1984). On acidic, low water-holding capacity soils, first-cut switchgrass yields were two to three times greater, and four times greater than for tall fescue on sites with N and without N, respectively. Nitrogen-use efficiency was greater for switchgrass than for tall fescue (Staley et al. 1991). The timing of N application is critical in the maintenance of switchgrass stands. If N is applied too early in the spring or in the previous autumn, cool-season plants will utilize it because switchgrass is not active. The stimulated C_3 invaders will increase rapidly and utilize the soil moisture. Later, during the period of switchgrass growth, soil moisture will be depleted and the vigor of switchgrass plants will decline and stands will be invaded by additional C_3 plants which can result in the conversion of a switchgrass pasture into a mixed species cool-season pasture.

22.5.3 HARVEST TIMING AND FREQUENCY

Cellulosic biomass of herbaceous plants can be used as a feedstock for the production of liquid fuels such as ethanol (Lynd et al. 1991) and switchgrass has been identified as a promising species for development into a herbaceous biomass fuel crop in the United States (Vogel 1996; Sanderson et al. 2007). Switchgrass has an array of desirable energy, conservation, environmental, and economic attributes for its use as a bioenergy crop (McLaughlin et al. 2002). These include broad adaptation, high yields on marginal and erosive croplands, harvestability with conventional forage equipment, a very positive energy balance, and relatively easy seed processing.

Several trials have been conducted in the United States and other countries to optimize harvest timing and frequency. In general, a single harvest when switchgrass is fully headed gives the highest yields (Madakadze et al. 1999a, b; Sanderson et al. 1999; Christian et al. 2002; Vogel et al. 2002a). Biomass yield continues to increase up to anthesis, after which biomass yield decreases up to 10–20% before killing frost (Vogel et al. 2002a). There are circumstances, some cultivars at some locations, in which two harvests provide higher biomass yields than one harvest, but the extra fossil fuels required to conduct two harvests may not warrant a two-harvest management system. Harvests after a killing frost usually result in decreased biomass yields but may require lower inputs of N fertilizer, because the plant is able to utilize N mobilized into roots for storage during winter and recovery the following spring. Depending on location and cultivar, biomass yields of the best-adapted cultivars ranged from 10 to more than 20 Mg/ha.

Optimal harvest management for switchgrass use in combustion conversion systems may require delaying harvest until spring when most of the minerals have leached from the plant. Biomass yield reductions during the winter averaged 40% in Pennsylvania (Adler et al. 2006), but this management system may be capable of utilizing some internal N cycling, helping to reduce the N fertilizer requirements (Lowenberg-DeBoer and Cherney 1989). Most of the yield reduction associated with spring harvest was due to harvest losses during baling, suggesting that improvements in harvest machinery could reduce these losses. Losses in plant biomass during late autumn and winter are generally associated with translocation of nitrogenous compounds, soluble carbohydrates, and minerals into underground storage structures and may result in a long-term benefit in a one-harvest biomass production system, promoting a balance between maximal biomass yield and stand longevity while providing a more favorable product for energy from combustion.

22.5.4 Seed Production

Management of switchgrass for seed production is based on practices initially recommended by Cornelius (1950) for the Great Plains, subsequent research in other areas of the United States, and on anecdotal results of seed producers. Cornelius (1950) reported that cultivated seed production fields produce more and higher quality seed than from native prairies; row plantings produce more seed than solid stands; fertilization and weed control are necessary for good seed production; and spring burning of seed fields usually improves seed yields. In the central Great Plains where most of the commercially available switchgrass seed is produced, the seed fields are usually planted in rows spaced about 1 m apart, and are fertilized each spring with 50–110 kg/ha N after the fields are burned and cultivated to maintain the grass in rows. In Iowa, Cave-in-Rock had higher seed yields when grown in narrow rows spaced 20 cm apart than in wider rows spaced 1 m apart (Kassel et al. 1985). In contrast, the cultivars Blackwell and Pathfinder had higher seed yields in wide rows. Nitrogen fertilizer significantly increases seed yields in Iowa (George et al. 1990). Phosphorus should be applied when soil tests indicate available soil P is low. Some seed producers irrigate, but many seed fields in the eastern Great Plains are not irrigated. Switchgrass seed, in contrast to seed of many native grasses, is heavy and smooth and is easily combined and cleaned with conventional combines and cleaning equipment (Cornelius, 1950; Wheeler and Hill 1957). Seed is usually harvested by direct combining. Grazing switchgrass seed fields early in the season reduced seed yields in the Midwest United States (George et al. 1990; Brejda et al. 1994). Seed yields in an Iowa study ranged 200–1,000 kg/ha (Kassel et al. 1985). In Missouri, seed yields ranged from 460 to 700 kg/ha (Brejda et al. 1994). The difference in cultivar response was due to differences in lodging.

22.6 CARBON, ENERGY, AND ECONOMIC BUDGETS

The sustainability of switchgrass for bioenergy crops will be determined using carbon, energy, and economic budgets of the feedstock. Feedstocks must be profitable, have high net energy yields, and be either neutral or positive with respect to the environment to be viable and sustainable (Casler et al. 2009).

22.6.1 Carbon Sequestration

Switchgrass has the potential to extract carbon dioxide from the atmosphere and sequester it in soil. Frank et al. (2004) reported that soil C increased at a rate of 1.01 kg C/m^2 per year, and switchgrass plantings in the northern Great Plains have the potential to store significant quantities of soil organic carbon (SOC). Liebig et al. (2005) reported that switchgrass grown in North Dakota stored 12 Mg/ha more SOC in the 30- to 90-cm depth than a cropland paired field experiment. They concluded that switchgrass effectively stores SOC not just near the soil surface, but at greater depths where C is less susceptible to mineralization and loss. Lee et al. (2007) reported that switchgrass grown in South Dakota CRP lands stored SOC at a rate of 2.4–4 Mg/ha per year at the 0- to 90-cm depth. In a 5-year field study conducted on 10 farms in Nebraska, South Dakota, and North Dakota, SOC increased significantly at 0–30 cm and 0–120 cm soil depths, with an average increase in SOC of 1.1 and 2.9 Mg C/ha per year, respectively (Liebig et al. 2008). However, they noted that change in

SOC varied across sites and ranged from −0.6 to 4.3 Mg C/ha per year for the 0- to 30-cm depth. For example, on four farms in Nebraska, change in SOC for the 0- to 120-cm depth averaged 2.9 Mg C/ha per year. The variation in SOC change reiterated the importance of long-term environmental monitoring sites in major agro-ecoregions.

In addition to increasing soil C, growing switchgrass may increase wildlife habitat, increase landscape and biological diversity, increase farm revenues, and return marginal farmland to production (Sanderson et al. 1996; McLaughlin and Walsh 1998; McLaughlin et al. 2002; Roth et al. 2005). Not harvesting some switchgrass each year would increase the habitat value for grassland bird species that require tall, dense vegetation structure (Roth et al. 2005).

22.6.2 Energy Balance

Energy produced from renewable carbon sources is held to a different standard than energy produced from fossil fuels, in that renewable fuels must have highly-positive energy values. The energy efficiency and sustainability of ethanol produced from grains and cellulosics has been evaluated using net energy value (NEV), net energy yield (NEY), and the ratio of the biofuel output to petroleum input [petroleum energy ratio (PER)] (Schmer et al. 2008) An energy model using estimated agricultural inputs and simulated biomass yields predicted switchgrass could produce greater than 700% more output than input energy (Farrell et al. 2006). These modeled results were validated in a multifarm, field-scale research in the central and northern Great Plains, United States. Switchgrass fields on ten farms in Nebraska, South Dakota, and North Dakota produced 540% more renewable fuel (NEV) than nonrenewable fuel consumed over a 5-year period (Schmer et al. 2008). The estimated on-farm NEY was 60 GJ/ha per year (Schmer et al. 2008), which was 93% greater than human-made prairies and 652% greater than low-input switchgrass grown in small plots in Minnesota (Tilman et al. 2006). The 10 farms and five production years had a PER of 13.1 MJ of ethanol for every MJ of petroleum input, and produced 93% more ethanol per ha than human-made prairies and 471% more ethanol per ha than low-input switchgrass in Minnesota (Schmer et al. 2008). Average greenhouse gas (GHG) emissions from switchgrass-based ethanol in this study were 94% lower than estimated GHG emissions from gasoline (Schmer et al. 2008). In simulated production trials in Wisconsin, switchgrass produced the most net energy, followed by an alfalfa-corn rotation and then continuous corn (Vadas et al. 2008). Producing switchgrass for bioenergy is an energetically positive and environmentally sustainable production system for the central Great Plains and Midwest.

The implementation of switchgrass-based bioenergy production systems will require the conversion of marginal land from annual row crops to switchgrass production and could exceed 10% in some regions depending on the yield potential of the switchgrass strains. In a 5-year study in Nebraska, the potential ethanol yield of switchgrass averaged 3474 L/ha and was equal to or greater than the potential ethanol yield of no-till corn (grain + stover) on a dry-land site with marginal soils (Varvel et al. 2008). Removing an average of 51% of the corn stover each year reduced subsequent corn grain yield, stover yield, and total biomass yield. Growing switchgrass on these marginal sites will likely enhance ecosystem services more rapidly and significantly than on more productive sites.

22.6.3 Economics

Switchgrass is an economically feasible source for cellulosic ethanol. A field-scale study using known farm inputs and actual harvested switchgrass yields conducted on 10 farms over 5 years in Nebraska, South Dakota, and North Dakota determined switchgrass could be delivered at the farm gate for $54/Mg (Perrin et al. 2008). They concluded that the development of new cultivars improved production practices, and an expanded market for switchgrass may reduce the farm-gate cost by as much as 20% (Perrin et al. 2008). Large quantities of switchgrass could be delivered at the farm gate for $40–45/Mg (Perrin et al. 2008). Assuming a switchgrass farm-gate cost of $40–54/Mg and conversion of 0.329 L ethanol/kg of switchgrass, the farm-gate feedstock cost would range from $0.12 to 0.16/L.

22.7 BREEDING AND SELECTION

22.7.1 Ecotypic Variation

The presence of obvious ecotypic variation has been a strong driver of many switchgrass activities because many of the original collections were made from prairie remnant plants. Although the upland and lowland types form an obvious visual dimorphism, there is a wealth of ecotypic variation within both upland and lowland types. Early plant collectors recognized morphological variations among remnant prairies and sought to collect accessions that would capture much of this variation. Many of the early switchgrass cultivars were simple seed increases of random plants collected from a single source-identified prairie remnant, what are today termed "natural-track" cultivars. A modest amount of selection occurred in determining which of these accessions would be elevated to cultivar status and released to the public. This was accomplished by common-garden experiments in which numerous accessions were evaluated for many years, sometimes followed by more extensive testing at multiple locations. In a few cases, some selection within the strain occurred for vigorous plants and/or traits that would allow for adequate seed production.

These early selection efforts utilized genetic variability among accessions or strains of switchgrass, which is relatively easily observed in replicated experiments (Eberhart and Newell 1959; Hopkins et al. 1995b; Casler 2005). Taken together, these natural-track cultivars provide a fairly effective representation of the morphological and physiological diversity associated with the diverse geography and climates found in the eastern two-thirds of the United States (Table 22.1). Obvious from Table 22.1 and from investigation of switchgrass germplasm resources, such as those present in the USDA National Plant Germplasm System, Germplasm Resources Information Network (GRIN; http://www.ars-grin.gov/npgs/index.html) is the relative difference in frequency of upland vs. lowland accessions, the latter being relatively rare in prairie remnants (Hultquist et al. 1997; Casler 2005).

Lowland ecotypes of switchgrass tend to be more southern adapted than upland ecotypes, as a group. Because of their late heading and ability to maintain photosynthetically active tissue through the longer growing season, lowland ecotypes generally have higher biomass yield than upland ecotypes at southern locations located in USDA hardiness zones 6–9 (Sanderson et al. 1999; Fike et al. 2006b). Lowland ecotypes had 44% higher biomass yield than upland ecotypes under a one-harvest management, whereas this advantage was reduced to 13% under a two-cut management (Fike et al. 2006b). The upland ecotypes used in this study were more closely matched in phenology to the photoperiods of these test locations. Because they were near anthesis at the time of first harvest, there was sufficient time to allow a second period of vegetative development, unlike the lowland ecotypes for which first harvest occurred before their first period of vegetative development was completed (Fike et al. 2006b). Even though the lowland ecotypes had the highest biomass yields, their use in a geographic region considerably north and east of their origin is likely responsible for their more inconsistent responses to harvest management and other increased inputs compared to upland ecotypes (Fike et al. 2006a).

With the recent expansion of breeding and selection activities on switchgrass in the United States, upland-lowland intermediate types have been found with increasing frequency. The exact origin and nature of these accessions is not known. In some cases, they occur sympatrically with obvious upland ecotypes, suggesting their possible hybrid origin (Hultquist et al. 1997). Cave-in-Rock appears to be an intermediate ecotype, sharing traits of both classic upland and lowland phenotypes. Interestingly, Cave-in-Rock is an octaploid, suggesting a fairly complex genetic history if it indeed arose as a hybrid between tetraploid upland and lowland plants. Analysis of DNA from "Miami" switchgrass also provides conflicting data for classification, with cpDNA suggestive of the

TABLE 22.1

Switchgrass Cultivars Representing Various Habitats in the Central and Eastern United States, Largely Representing Local Ecotypes with Minimal Selection for Plant Traits

Cultivar	Ecotype	Ploidy	Year	Origin	Adapted to USDA Hardiness Zones
Alamo	Lowland	4x	1978	Southern Texas	6, 7, 8, 9
Kanlow	Lowland	4x	1963	Northern Oklahoma	6, 7
Miami	U/L[a]	4x	1996	Southern Florida	9, 10
Pangburn	Lowland	4x	NA	Arkansas	6, 7
Dacotah	Upland	4x	1989	Southern North Dakota	2, 3, 4[a]
Falcon	Upland	4x	1963	New Mexico	4, 5, 6
Grenville	Upland	NA	1940	Northeastern New Mexico	4, 5, 6
High Tide	Intermediate[b]	NA	2007	Northeastern Maryland	5, 6, 7
KY1625	Upland	4x	1987	Southern West Virginia	5, 6, 7
Blackwell	Upland	8x	1944	Northern Oklahoma	5, 6, 7
Caddo	Upland	8x	1955	Central Oklahoma	6, 7
Carthage	Upland	NA	2006	North Carolina	5, 6, 7
Cave-in-Rock	Upland	8x	1973	Southern Illinois	5, 6, 7
Forestburg	Upland	8x	1987	Eastern South Dakota	3, 4
Nebraska 28	Upland	8x	1949	Northeast Nebraska	3, 4
Shelter	Upland	8x	1986	Central West Virginia	4, 5, 6

NA, information not available.

[a] Classified as upland on the basis of chloroplast DNA markers and lowland on the basis of nuclear DNA markers. (Gunter, L.E., Tuscan, G.A., and Wullshcleger, S.D., *Crop Sci.*, 36, 1017–1022, 1996.)

[b] Intermediate type on the basis of a mixture of phenotypic traits of upland and lowland ecotypes Unequivocal classification is not possible at this time.

upland type and nuclear DNA suggestive of the lowland type (Gunter et al. 1996). As of this writing, only a tiny fraction of switchgrass germplasm collected in prairie remnants has been characterized for phenotypic traits that distinguish upland from lowland phenotypes, DNA content for ploidy classification, or DNA markers that would help to elucidate origins, genetic nature, and potential breeding value of these putative intermediate types.

In contrast to the cultivars that derive from seed increases of prairie remnant populations or that have undergone very little interplant selection (Table 22.1), there are relatively few cultivars derived from intensive breeding and selection (Table 22.2). Despite their improvement status, bred cultivars of switchgrass are generally no more than three to four cycle or generations of selection removed from wild germplasm. As such, DNA marker profiles of prairie remnant populations and bred cultivars are remarkably similar, showing no separation or discrimination (Figure 22.3). Switchgrass is still a wild and undomesticated plant.

22.7.2 BREEDING METHODS

Switchgrass breeding originates within populations that are direct targets for improvement, relying on genetic variability for target traits within the population of interest. Because switchgrass has two main ploidy levels, tetraploid and octaploid, that are largely cross incompatible (Martinez-Reyna and Vogel 2002), breeding populations should be developed from plants on a uniform ploidy level. Breeding populations can be defined broadly or narrowly, depending on the breeder's objective. Because there is generally so much genetic variability within populations from a single native prairie

TABLE 22.2
Improved Switchgrass Cultivars Representing Significant Breeding and Selection Activities

Cultivar	Ecotype	Ploidy	Year	Principal Traits Selected during Cultivar Development	Adapted to USDA Hardiness Zones
Pathfinder	Upland	8*x*	1967	Biomass yield and vigor	4, 5
Shawnee	Upland	8*x*	1996	IVDMD, biomass yield	5, 6, 7
Sunburst	Upland	8*x*	1998	Heavy seeds	3, 4, 5
Trailblazer	Upland	8*x*	1984	IVDMD, biomass yield	4, 5
Summer	Upland	4*x*	1963	Earliness, rust resistance	4, 5
BoMaster	Lowland	4*x*	2006	IVDMD, biomass yield	6, 7, 8
Performer	Lowland	4*x*	2006	IVDMD, biomass yield	6, 7, 8

IVDMD, in vitro dry matter digestibility.

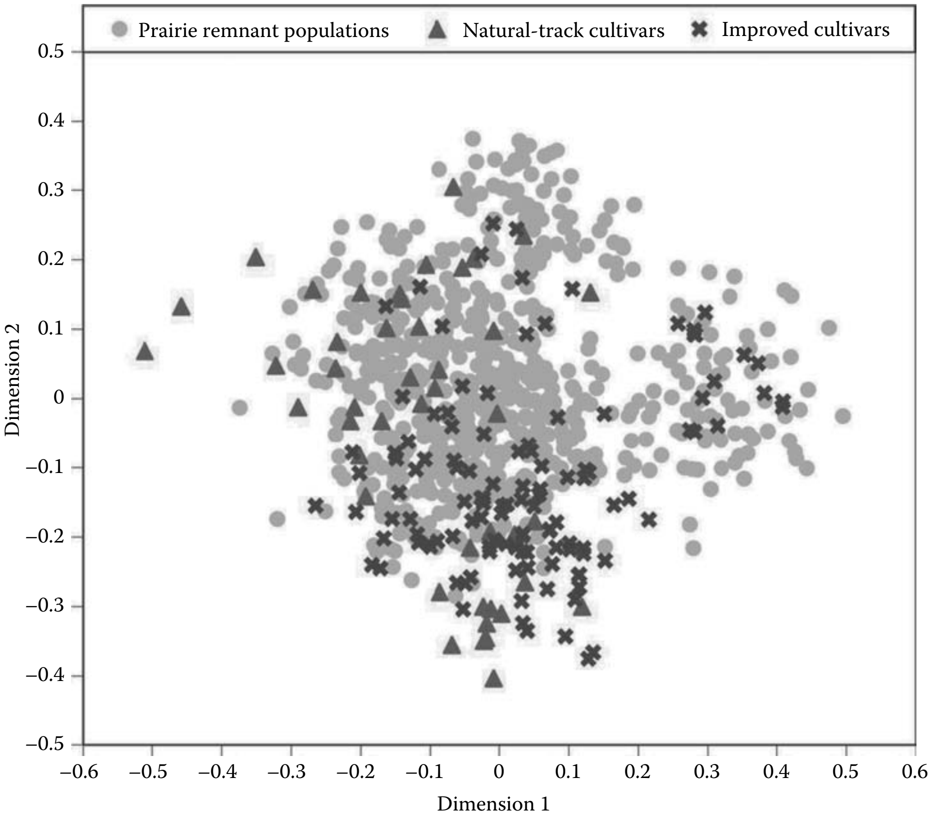

FIGURE 22.3 (See color insert) Multidimensional scale plot of 818 switchgrass plants representing collections made in remnant prairies, public cultivars derived as random seed increases from remnant prairies (natural track), and cultivars improved by selection and breeding, based on random amplified polymorphic DNA (RAPD) markers (From Casler, M.D. et al., *Crop Sci*, 47, 2261–2273, 2007b.)

remnant, populations derived from seed or plants collected at a single site may serve as breeding populations. In this regard, Cave-in-Rock, an accession deriving from one collection site, served as the breeding population for 'Shawnee' (Vogel et al. 1996). Other cultivars, such as Pathfinder, were developed by selection within broader germplasm pools created as composites or synthetics from seed collected at multiple sites that define a target region of interest (Newell 1968b). Multisite composites or synthetics are often thought to have a broader genetic base capable of sustaining genetic gains for more generations of selection and to buffer new cultivars against the possibility of pests or abiotic stresses. DNA marker diversity studies in switchgrass (Casler et al. 2007b; Narasimhamoorthy et al. 2008) and selection experiments in another grass (Burton 1974) suggest that this perception by breeders may not be accurate. Germplasm pools perceived to be either narrow or broad in their genetic diversity are both capable of allowing sustained genetic gains. The polyploid nature of switchgrass serves as a reservoir, storing large amounts of genetic variability.

Genetic variability exists within both broad and narrow gene pools of switchgrass, related to a wide range of traits, including seedling tiller number (Smart et al. 2003a, 2003b, 2004); cell wall composition and forage quality (Vogel et al. 1981; Godshalk et al. 1988); plant height, vigor, and biomass production (Newell and Eberhart 1961; Talbert et al. 1983; Hopkins et al. 1993; Das et al. 2004; Missaoui et al. 2005b; Rose et al. 2007); photoperiod-related traits such as earliness and phytomer number (Van Esbroeck et al. 1998; Boe and Casler 2005; Casler 2005); and biotic or abiotic stress tolerances (Hopkins and Taliaferro 1997; Vogel et al. 2002b; Gustafson et al. 2003). The risk associated with selection for a trait for which little or no genetic variation exists within a population is illustrated by P concentration in Alamo (Missaoui et al. 2005c). P uptake by switchgrass could be improved only by selection for increased biomass yield because of lack of genetic variation for P concentration.

Vogel and Pedersen (1993) and Vogel and Burson (2004) reviewed breeding procedures used to improve switchgrass. Most breeding programs heavily utilize spaced plants as the selection units, in which seeds are germinated in the glasshouse and plants with 3–6 tillers are transplanted to the field on spacings that range from 0.3 to 1.1 m. In most cases, random plants are selected from a bag of seed representing the population to be improved. This is phenotypic selection, sometimes referred to as restricted recurrent phenotypic selection (RRPS) which refers to a number of modifications designed to improve efficiency and the rate of genetic gains (Vogel and Pedersen 1993). Some of these restrictions or modifications include selection for seedling vigor in the glasshouse, removal of some environmental variation in the field using a grid system, and intercrossing selected plants as early and rapidly as possible using excised tillers in the glasshouse (Burton 1974).

One particular aspect of Burton's RRPS, planting extra seedlings in the glasshouse and conducting some form of seedling selection before establishment of field nurseries, may be particularly useful in switchgrass recurrent selection programs. Smart et al. (2003a) demonstrated that seedling tiller number is moderately heritable, creating Cycle-2 populations with mean tiller numbers of 1.2 and 2.0 compared to the base population of 1.6 tillers per plant. Although seedling tiller number did not affect establishment of switchgrass in the field (Smart et al. 2003b), differences in seedling tiller number translated directly to differences in adult-plant tiller numbers (80 vs. 119 tillers per plant). Furthermore, the single-tiller population had a 28% greater leaf elongation rate, 60% more mass per tiller, and 24% higher biomass yield per plant (Smart et al. 2004). Selection of switchgrass seedlings with a single tiller at a defined length of time postgermination appears to be an effective mechanism to improve the efficiency of a field-based recurrent selection program. This is supported by additional studies of adult plants that indicated cultivars with fewer tillers, but more phytomers per tiller and a higher proportion of reproductive tillers, have the highest biomass yield potential (Boe and Casler 2005).

Family selection or genotypic selection methods have also been used for switchgrass improvement. Family selection may involve the use of spaced plants and similar or identical selection protocols as phenotypic selection. In this case, spaced plants are generally arranged in rows where each row represents a family and plants within a row are generally half-sibs of each other, i.e., they each derive from one maternal parent (Vogel and Pedersen 1993). The efficiency of family selection is greatly enhanced by two-stage selection in which the best families are selected based on row means and the best plants are selected from the best rows based on individual-plant observations, i.e., among-and-within-family selection (Vogel and Pedersen 1993; Casler and Brummer 2008). Alternatively, family or genotypic selection may utilize seeded sward plots if family matings allow sufficient seed for plot testing. This breeding method has been rarely utilized in switchgrass breeding at the time of this writing. Implementation of among-and-within-family selection is more challenging when families are seeded into sward plots, because it is impossible to visually distinguish individual genotypes for the second stage of selection. Furthermore, it is not clear that selection of surviving plants from sward plots is advantageous, as it may be relatively inefficient for some species (Casler 2008). As switchgrass swards age, genotypes are lost to interplant competition, stress susceptibilities, and perhaps random mortality. The relative importance of these factors, the rate of genotype loss in switchgrass swards, and the relative fitness of surviving plants (relative to mortal plants) are all important determinants of the efficiency of among-and-within-family selection on sward plots (Casler and Brummer 2008) and all are current unknowns for switchgrass.

Spaced plants are an extremely effective method of collecting data on individual plants and ensuring that the best genotypes can be found and saved for intercrossing once they are identified in the data analysis phase of selection. Spaced plantings are an extremely effective tool for selection based on traits that have moderate to high heritability and are relatively insensitive to interplant competition. Examples include in vitro dry matter digestibility (IVDMD) (Vogel et al. 1981; Casler et al. 2002) and heading date (Van Esbroeck et al. 1998). Conversely, more complex traits that may be highly sensitive to interplant competition, such as biomass yield, may have less predictable selection responses from spaced plants. Selection for increased biomass yield of spaced plants was effective when progeny populations were evaluated as spaced plants (the same trait) (Rose et al. 2007) or as sward plots (a different trait) (Missaoui et al. 2005b). In the case of Rose et al. (2007), selection was more effective under low-input conditions (no supplemental fertilizer or water) compared to high-input conditions. Missaoui et al. (2005b) attributed their gains in biomass yield to a fairly sophisticated approach to controlling interplant competition and spatial variation—use of a honeycomb planting design combined with statistical adjustment for neighbor effects. Selection for increased spaced-plant vigor was also effective for increasing sward-plot biomass yield in WS4U switchgrass, largely by the elimination of unadapted and low-yielding genotypes (Casler 2010). Alternatively, selection for increased biomass yield was ineffective in the EY × FF switchgrass population, due either to lack of genetic variation for forage yield or to a low genetic correlation between forage yield of spaced plants and sward plots (Hopkins et al. 1993).

22.7.3 Breeding Objectives

Breeding for improved forage digestibility as measured by IVDMD (Tilley and Terry, 1963) is an effective way to increase switchgrass productivity as measured by beef cattle (*Bos taurus*) production per unit land area (Vogel et al. 1993). Divergent selection was used to develop strains differing in IVDMD from the same base populations. These strains were evaluated in both small plot and grazing trials (Vogel et al. 1981, 1984; Anderson et al. 1988; Ward et al. 1989). On the basis of these trials the high IVDMD strain was released as the cultivar "Trailblazer" (Vogel et al. 1991). In comparison to the control cultivar "Pathfinder" which had similar forage yield and maturity, the single breeding cycle for high IVDMD resulted in the following genetic increases: IVDMD concentration of 40 g/kg, daily live weight gains by beef cattle of 0.15 kg, beef cattle production of 67 kg/ha, and profit of U.S.$59/ha (Casler and Vogel 1999). On the basis of certified seed production, the area seeded to Trailblazer from 1986 to 1997 was over 63,000 ha. The principal area of adaptation for Trailblazer is the central Great Plains of the United States and similar ecoregions. "Shawnee" switchgrass was developed by a single cycle of selection for high IVDMD and high yield from "Cave-in-Rock" (Vogel et al. 1996). It was higher in IVDMD than the parent cultivar with similar biomass yield. Trailblazer and Shawnee are the only switchgrass cultivars developed with improved forage quality.

Three cycles of phenotypic selection for high IVDMD resulted in a linear increase in IVDMD of +1.7%/cycle and an associated linear decrease of –3.3%/cycle in lignin concentration (Casler et al. 2002). Because IVDMD is not a plant trait per se, but defined only by an anaerobic interaction between plant tissue and enzymes secreted by rumen microbes (Tilley and Terry 1963), it is likely that selection acted largely upon lignin concentration and composition. Low-lignin, high-digestibility genotypes tended to also have lower ratios of *p*-coumaric/ferulic acid than high-lignin, low-digestibility genotypes (Sarath et al. 2008). Reductions in lignin concentration appear to have resulted from reductions in cortical fibers and secondary wall thickenings in switchgrass stems (Sarath et al. 2005).

Selection for increased IVDMD has also resulted in a significant decrease in winter survival (Casler et al. 2002). Some families in the high IVDMD populations continue to have high winter survival rates indicating that this apparent genetic correlation may be broken with selection, allowing simultaneous improvements in IVDMD and winter survival (Vogel et al. 2002b). Genetic correlations of forage yield and IVDMD indicate that it should be possible to improve both traits simultaneously (Talbert et al. 1983). The breeding research on improving IVDMD and forage yield demonstrate the need for multiyear evaluation of breeding nurseries in the environments in which the plant materials will be used to ensure that selected plants are exposed to stresses present in normal production environments (Casler et al. 2002; Vogel et al. 2002b).

22.7.4 SWITCHGRASS HYBRIDS

All current cultivars of switchgrass are either open-pollinated seed increases of prairie remnants or synthetic populations of superior plants selected for agronomic performance. In both cases, random intermating occurs among large numbers of plants and there is little opportunity to utilize structural or genomic information that would lead to improved performance, such as hybrid vigor. The partial genetic isolation between upland and lowland ecotypes of switchgrass is reminiscent of complementary heterotic gene pools in maize (*Zea mays* L. ssp. *mays*). Maize breeders created these heterotic gene pools by choosing parental lines simply based on their observed heterotic patterns (Tracy and Chandler 2006). Many generations of selection reinforced and solidified these patterns. Initial crosses of upland × lowland switchgrass have demonstrated an average of 19% midparent heterosis for biomass yield of spaced plants, whereas upland × upland and lowland × lowland hybrids of similar genetic origin showed no heterosis for biomass yield (Martinez-Reyna and Vogel 2008). When evaluated as sward plots, upland × lowland hybrids averaged 30–38% high-parent heterosis (Vogel and Mitchell 2008). There appears to be some natural genetic complementation between upland and lowland ecotypes that results in significant heterosis of these hybrids. These results suggest the need for breeding and selection methods that incorporate efficient methods of evaluating and selecting parents for combining ability. If these results follow the maize model, selection for combining ability could strengthen what already appears to be significant hybrid vigor between upland and lowland ecotypes.

Commercial production of F_1 hybrid switchgrass cultivars will require a mechanism to propagate parental clones in the thousands or tens of thousands. Efficient and repeatable methods for regenerating switchgrass plants from in vitro cultured cells and tissues have been developed (Denchev and Conger 1994; Alexandrova et al. 1996a, b) including a method for regenerating switchgrass plants from cells in suspension culture (Dutta and Conger 1999). Thousands of plants can be transplanted into alternating rows of two parental clones using existing transplanting technologies for horticultural crops. In many cases, this equipment is unused for much of the year and switchgrass hybrid seed production fields can be transplanted at times of the year when vegetable-transplanting equipment is not in use. Use of two heterotic parental clones and physical isolation from other switchgrass will ensure that nearly 100% of the seed harvested from the entire seed production field will be hybrid seed. Because switchgrass is a long-lived perennial and seedling transplants can be planted on spacings that eliminate or minimize interplant competition and the possibility of genetic shifts, hybrid seed production fields can be used for many years, perhaps even the lifetime of a hybrid cultivar.

22.7.5 TRANSGENIC SWITCHGRASS

Transgenic switchgrass plants have been created using bombardment with tungsten-coated particles or Agrobacterium-mediated procedures (Richards et al. 2001; Somleva et al. 2002). Transgenes for herbicide resistance and reporter genes have both been expressed in transgenic switchgrass plants. Controlled crosses between transgenic and nontransgenic plants resulted in the expected expression of both genes in T_1 plants. So far, the greatest limitation to transformation of switchgrass comes from the limited number of genotypes that are capable of plantlet regeneration from tissue culture. Because of this limitation, Alamo is the only switchgrass cultivar that has been successfully transformed and regenerated from culture (Denchev and Conger 1994; Alexandrova et al. 1996a, 1996b; Dutta Gupta and Conger 1999; Richards et al. 2001; Somleva et al. 2002; Mazarei et al. 2008). Because of the climatic limitations of Alamo, deployment of transgenic switchgrass into upland genotypes and to geographic regions to which Alamo is not adapted becomes complicated by the need to transfer transgenes from Alamo to other genotypes. Transfer of transgenes from Alamo to other genotypes will necessarily include large chromosome segments that may be deleterious to northern strains of switchgrass and reduce genetic complementation between upland × lowland hybrids.

Deployment of transgenes in commercial switchgrass cultivars for use in North America will likely require the use of a hybrid system that prevents the introduction of transgenes into wild or natural switchgrass populations. Such a system could be based on the hybrid seed production scheme of Martinez-Reyna and Vogel (2008) in which two parental clones are increased by somatic embryogenesis and transplanted into alternating rows. Using this system, the transgenic parent must be utilized as the female and the nontransgenic parent utilized as the male. In addition, the female transgenic parent must have a sterility system, such as cytoplasmic male sterility, such that the parental clone itself and all of its progeny are male sterile, incapable of releasing transgenic pollen into the wild. Such a system could borrow from the maize hybrid model in which there are fewer rows of male parents relative to female parents, to avoid large increases in seed production costs associated with lack of hybrid seed production on the male parents.

22.7.6 DNA MARKER SELECTION

Development of efficient DNA marker systems and identification of associations between DNA markers and quantitative trait loci (QTL) has been hampered in switchgrass because of the complexity of its genome organization. Existence of diploid ($2n = 2x = 18$) plants would greatly simplify the discovery of efficient and inexpensive markers and the association of those markers with QTL. Only one diploid accession has ever been reported, originating near Chippewa Falls, Wisconsin (Nielsen 1944). In 1996, the site at which this accession was originally collected had been developed into an urban landscape, destroying all native switchgrass, illustrating just how important habitat loss and fragmentation may be to preservation of switchgrass germplasm. More recently, diploid switchgrass plants have been discovered and confirmed, resulting from haploidy in tetraploid seed stocks (Casler and Price 2010, unpublished data; Young et al. 2010).

Although RAPD markers were used for some of the earlier germplasm diversity research, most current efforts are focused on development of expressed sequence tag (EST) markers or EST-SSR (simple sequence repeat) markers (Tobias et al. 2005, 2006; Narasimhamoorthy et al. 2008). Expressed sequence tag markers hold great promise as tools for selection because many EST markers can be traced to functional genes that can be associated with target plant traits and they are amenable to development of single nucleotide polymorphism (SNP) markers.

Strategies for use of DNA markers as selection tools rely on development of predictable and reliable associations between markers and traits that may take on one of several forms. First and simplest would be a SNP marker located within a functional gene or EST combined with phenotypic evaluations of plants containing alternate forms of the polymorphism identifying which allele is favorable. In this case, one nucleotide polymorphism within one gene is focused on one trait, analogous to the brown-midrib genetic mutations involved in the phenylpropanoid pathway and their effect on lignin (Vignols et al. 1995). Second, QTL discovery, using either linkage mapping or association mapping, would identify random DNA markers flanking a QTL of interest. Selection would be based on the flanking markers associated with favorable phenotype, and (hopefully) a small probability of crossover between the flanking markers and the QTL of interest. Third, selection could target several genes for one or more traits, seeking to pyramid multiple favorable genes together into a population using multiple SNP markers. Fourth, marker-assisted recurrent selection (MARS) expands the DNA markers used as selection tools to a broader genomic coverage focused on regions of the genome known to contain QTL of interest, typically based on linkage or association mapping (Johnson 2001, 2004). Least squares and/or maximal likelihood statistical methods are used to develop a marker selection index that is related to plant phenotype in a predictive capacity. Fifth, genome-wide selection goes one step further to saturate the genome with markers, and using best linear unbiased prediction (BLUP) methods to develop a marker index predictive of plant phenotype (Bernardo and Yu 2007).

Any of the above marker selection strategies can be effectively combined with existing selection methodology to implement marker selection for specific plant traits in switchgrass. For phenotypic selection, markers and traits are measured on the same plants to develop the BLUP equations. Plants selected in the first generation are intercrossed to create a new generation for marker evaluation and BLUP selection, eliminating the need for phenotyping in every generation. For among-and-within-family selection, marker scores or indices would be used as the within-family selection criterion on an individual plant basis, whereas biomass yield or other field-based phenotypic traits would be used as the among-family selection criterion.

22.8 SWITCHGRASS AS A BIOENERGY CROP

Designation of switchgrass as an herbaceous model species for bioenergy feedstock development has transformed this species from obscurity to celebrity status. Before the BFDP, switchgrass was used principally for conservation and restoration of tallgrass prairie habitats and livestock production, the latter largely restricted to the Great Plains region of the United States. With the increase in research activity during the BFDP and subsequent USDA-ARS and U.S.-DOE research programs (Bouton 2007; Sanderson et al. 2007), interest in switchgrass research has grown to many public institutions in North America, Europe, and Asia and to some very high-profile commercial research efforts. In 1992, switchgrass breeding was conducted by the USDA-ARS in Lincoln, Nebraska and by South Dakota State University in Brookings, South Dakota. During the BFDP, Oklahoma State University, University of Georgia, and University of Wisconsin (combined with USDA-ARS) initiated new switchgrass breeding programs targeted to different regions and hardiness zones within the United States. During this period, a switchgrass breeding program was also initiated in the private sector near Ottawa, Canada, and a research program focused on molecular genetics was initiated at the University of Tennessee. Since the completion of the BFDP and the rapid expansion of feedstock research in 2005–2008, new breeding and genetics initiatives have been established at Iowa State University, University of Illinois, Texas A&M University, and the Noble Foundation, Ardmore, OK, whereas new private breeding programs have been established at Auburn, AL, and Bryan, TX.

The boom in switchgrass research can be viewed as a double-edged sword. One side of the sword cuts in favor of creating a vast database on basic biology, genetics, and production information to reduce production costs and improve conversion efficiency of switchgrass feedstock to various forms of energy. Vast amounts of funding have brought basic and applied scientists together and formed partnerships between public and private organizations, all working toward the goal of improving production and conversion efficiency. For a plant that, 20 years ago, was little more than an ecofriendly native prairie plant with some applications in livestock agriculture, this represents a social phenomenon on an unprecedented scale. But that brings us to the other side of that sword, which represents all of the other species that are being ignored or have been relegated to "underfunded" status. Meeting societal needs and governmental goals for bioenergy production (Perlack et al. 2005) will require many different crop species and feedstocks, grown on a wide range of soils, habitats, and climatic conditions. Switchgrass cannot, and should not, be the only focus of a feedstock development program for cellulosic bioenergy. There are many other potential candidates for feedstock development that could become as or more important than switchgrass on a regional, habitat-specific, or management-specific basis. Switchgrass is an interesting and amazing plant species that, together with other potential plant species, has huge potential for helping to wean the human race from dependence on fossil fuels.

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