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16 Switchgrass

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Switchgrass (*Panicum virgatum* L.) is an erect, warm-season perennial whose native habitat originally included the prairies, open woods, brackish marches, and pine-woods (*Pinus* spp.) of most of North America except for the areas west of the Rocky Mountains and north of 55°N lat. (Hitchcock, 1951; Stubbendieck et al., 1991). It is a polymorphic species with two distinct ecotypes, lowland and upland (Brunken and Estes, 1975), and with two major ploidy levels, tetraploid and octaploid (Hopkins et al, 1996; Hultquist et al., 1996, 1997). The ecotypes are cross-fertile when plants with the same ploidy level are intermated (Martinez et al., 2001). Ecotypes and cytotypes of switchgrass are classified as a single species.

TAXONOMIC DESCRIPTION

Switchgrass grows 0.5- to 3-m tall and although most genotypes are caespitose in appearance, some are rhizomatous. The caespitose genotypes have short rhizomes and can form a sod over time. The inflorescence is a diffuse panicle 15- to 55-cm long with spikelets toward the end of long branches (Fig. 16-1) (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 (Fig. 16-1 and 16-2). Spikelets are 3- to 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- to 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^{-1} (Wheeler and Hill 1957). Seed weight differences exist within and among cultivars. As an example, variation in seeds g^{-1} for the cv. Sunburst has been reported to vary from 450 to 850 seeds (Vogel, 2002).

Switchgrass has two distinct ecotypes, lowland and upland (Porter, 1966; Brunken and Estes, 1975). Lowland types are found on flood plains and other areas subject to inundation while upland types occur in upland areas that are not subject to flooding. Lowland types are taller, more coarse, generally more rust (*Puccinia* spp.) resistant, have a more bunch-type growth and may be more rapid growing than upland types.



Fig. 16-1. Illustration of switchgrass plant: culm(center) is 0.5- to 3-m tall with leaves 3- to 15-mm wide and 10- to 60-cm long; panicle inflorescence (left) is 15- to 55-cm long; collar region (lower right) with 1.5- to 3.5-mm long fringed membraneous ligule that is mostly hairs; spikelet (middle right) that is about 3- to 5-mm long; and seed (upper left).

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 that have been evaluated using chromosome counts of mitosis in root tips and flow cytometry analyses were tetraploids while upland plants were tetraploids or octaploids. Tetraploid and octaploid plants were found occurring together 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; McMillian and Weiler, 1959; Barnett and Carver, 1967). Normal bivalent pairing has been reported for tetraploid and octaploid switchgrass plants (Riley and Vogel, 1982; Martinez-Reyna et al., 2001). Frequencies of aneuploid variants and multivalent chromosome



Fig. 16-2. Switchgrass spikelet, lower floret is staminate, upper floret is fertile (from Martinez-Reyna and Vogel, 1998).

associations are more frequent at higher ploidy levels (Barnett and Carver 1967; Brunken and Estes 1975).

Switchgrass is a cross-pollinated species which is enforced by 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. Percentages of self-compatibility as measured by seed set from bagged panicles is typically 1% (Martinez-Reyna and Vogel, 2002; Talbert et al., 1983). A post-fertilization incompatibility system also exists that inhibits intermatings among octaploid and tetraploid plants (Martinez-Reyna and Vogel, 2002). The post-fertilization incompatibility system between ploidy levels in switchgrass appears to be similar to the endosperm balance number system found in other species. The post-fertilization incompatibility system is probably responsible for the lack of hexaploid plants in native prairies. The tetraploid and octaploids plants in native prairies may exist as separate and distinct populations.

Switchgrass has two cytoplasm types, 'L' and 'U' based on a chloroplast DNA (cpDNA) polymorphisms that are associated with the lowland and upland ecotypes, respectively, (Hultquist et al., 1996). The 'L' cytoplasm types are tetraploids while 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 polymorphic molecular marker (RFLP) 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. The genetic diversity among 14 switchgrass cultivars including both upland and lowland ecotypes was assessed by Gunter et al. (1996) using random amplified polymorphic DNA (RAPD) markers. Cluster analysis of 92 polymorphic loci separated the cultivars into two groups that matched the ecotype classification and the cytoplasm type classification of Hultquist et al. (1996). Although they are cross-fertile, the lowland and upland ecotypes are genetically distinct. A molecular map for switchgrass has not been developed to date nor has genetic relationship of switchgrass to other *Panicum* species been determined.

DISTRIBUTION AND ADAPTION

Switchgrass in native stands was most abundant east of 100° W long in North America. Switchgrass ecotypes, germplasm accessions, and cultivars are adapted to the ecoregions and the Plant Hardiness Zones in which they or their parental germplasm evolved. Switchgrasses are photoperiod sensitive and require short days to induce flowering (Benedict, 1941). Their photoperiod requirement is based on the latitude where they evolved. In nature, flowering is induced by decreasing day length during early summer. In North America, moving northern ecotypes south provides them a shorter than normal daylength during summer months and they flower early. The opposite occurs when southern ecotypes are moved north. They remain vegetative longer and produce more forage than northern strains

moved south (Newell, 1968a). When grown in the central Great Plains, switchgrasses from the Dakotas (northern ecotypes) flower and mature early and are short in stature while those from Texas and Oklahoma (southern ecotypes) flower late and are tall (Cornelius and Johnson, 1941; McMillian, 1959). The photoperiod response also appears to be associated with winter survival. Southern types moved too far north will not survive winters because they stay vegetative too late in the fall. As a general rule, switchgrass germplasm should not be moved more than one USDA Plant Hardiness Zone (Cathey, 1990) north of its area of origin because of the possibility of stand losses from winter injury. Adaptation range varies with cultivar.

In addition to photoperiod, the other factor that determines specific adaptation is response to precipitation and the associated humidity. Cultivars from the more arid Great Plains states may be more susceptible to foliar diseases when grown in the more humid eastern USA. Cultivars developed from eastern germplasm may not be as well adapted to drought stress as those based on western germplasm. Switchgrass tolerates a wide range of soil conditions. It grows on sands to clay loam soils. Although much of the prairie and grasslands in North America that were once occupied by tallgrass prairie species such as switchgrass were plowed and converted into cropland, remnant prairie sites still exist in most areas and are an invaluable germplasm resource (Hopkins et al., 1995b). Some extensive native prairies still exist, notably the Flint Hills in Kansas, the Osage Prairie in Oklahoma, and the Sandhills of Nebraska.

PHYSIOLOGY AND GROWTH

Switchgrass is a C_4 species (Waller and Lewis, 1979) and has the anatomical and physiological characteristics of C_4 grasses. The germination and growth of switchgrass seedlings are reduced at soil temperatures $<20^\circ\text{C}$ (Hsu et al., 1985a,b). 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 needed 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 warm enough to germinate the seed (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 and develop the root reserves necessary to become perennial.

Within 6 wk 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. Under optimum conditions, switchgrass will pro-

duce seed the establishment year but flowering occurs several weeks later than in following years.

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 genotypes 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. Genotypes with short rhizomes produce bunch-type plants which can be pushed above the soil line by roots while sod-forming genotypes 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 USA (Sanderson and Wolf, 1995a; Mitchell et al., 1997, 2001). In the central Great Plains, photoperiod as measured by DOY was more predictive of physiological development than GDD (Fig. 16–3) indicating the 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 (Fig. 16–4) (Mitchell et al., 1997). Genetically broad-based populations will have some plants at anthesis over a 3- wk period (Jones and

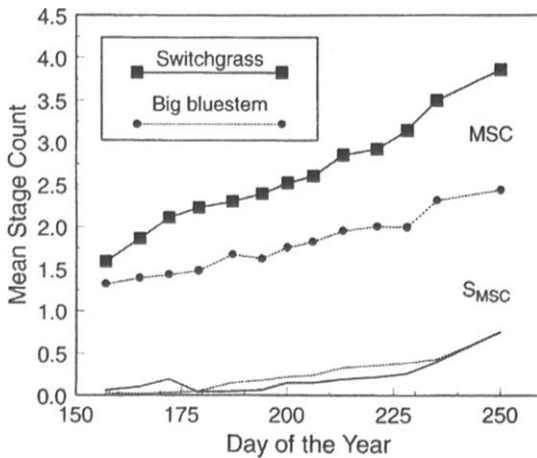


Fig. 16–3. Mean stage count (MSC) and its standard deviation of switchgrass and big bluestem grown near Mead, NE (from Mitchell et al., 1997). The staging system of Moore et al. (1991) was used to classify the vegetation by growth stage. Stage 1.0 indicates the emergence of the first leaf, 2.0 is the onset of stem elongation, 3.0 is the boot stage, 4.0 is the post-fertilization seed development stage, 4.9 is the ripe seed stage.

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 1000 to 1200 h or from 1200 to 1500 h depending upon environmental conditions (Jones and Newell, 1946). Heading dates for cultivars are typically population means. Because flowering is variable, 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 aboveground biomass to stem bases and roots after anthesis but before a killing frost (Vogel et al., 2002a).

BREEDING HISTORY

Much of the initial breeding work in switchgrass involved collecting a large array of native accessions (ecotypes or strains) from a specific geographic region, screening them in a common nursery for various agronomic traits, selecting one or more of these accessions for testing in additional environments, and based on these

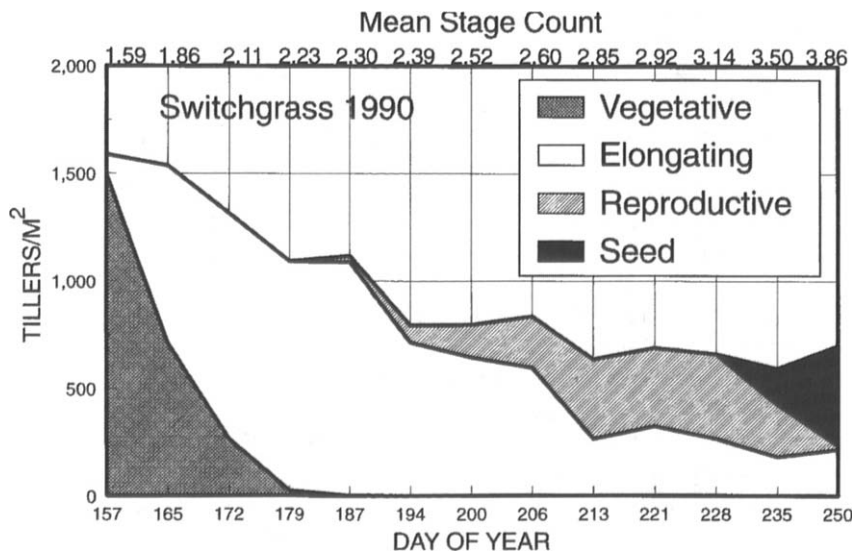


Fig. 16-4. Tiller demographics of a ‘Trailblazer’ switchgrass population grown near Mead, NE during the 1990 growing season (from Mitchell et al., 1997).

tests, directly increasing the most desirable accession for release as a cultivar. This procedure was used by state experiment stations and the Plant Material Centers (PMC) of the Soil Conservation Service (SCS), USDA, in developing the initial switchgrass varieties for different geographical regions of the USA. Several switchgrass cultivars including 'Blackwell' and 'Nebraska 28' were developed by this procedure. Nebraska 28 was the first switchgrass cultivar for which certified seed was produced. Eberhart and Newell (1959) and Hopkins et al. (1995b) evaluated an array of endemic strains or accessions in eastern Nebraska and found significant genetic variability among strains for all traits evaluated. The basic breeding procedure used to develop the initial switchgrass cultivars capitalized on the between strain or population genetic variability. The superior strains identified by this procedure formed the germplasm base for further switchgrass improvement by breeding.

Genetic studies in Nebraska, North Carolina, Oklahoma, and other locations have demonstrated that there is also significant genetic variability within strains or accessions for most traits that have been evaluated including forage yield, *in vitro* dry matter digestibility (IVDMD) protein concentration, plant height, seed yield, rust resistance, and maturity (Newell and Eberhart, 1961; Vogel et al., 1981; Talbert et al., 1983; Hopkins et al., 1993; Taliaferro et al., 1999). In these studies, heritability estimates, genetic correlations, and responses to selection were determined. Heritability estimates quantify the proportion of phenotypic plant-to-plant variation for a trait that is due to genetic differences among plants. Genetic correlations express the genetic relationship among traits. These studies determined that it should be possible to exploit the within-strain genetic variability of switchgrass as well as the between-strain variability to develop improved switchgrass cultivars. Since switchgrass is a cross-pollinated species, breeding procedures that have been developed for other cross-pollinated crops are used (Vogel, 2000; Vogel and Pedersen, 1993; Vogel and Burson, 2004, this publication). Because switchgrass has two main ploidy levels, tetraploid and octaploid, that are largely cross incompatible (Martinez-Reyna and Vogel, 2002), plants in a breeding population must be the same ploidy level. Population improvement breeding procedures are the primary breeding methods that have been used to develop new cultivars. Controlled matings for genetic studies can be made using the procedure described by Martinez-Reyna and Vogel (1998). All released switchgrass cultivars (Table 16–1) are improved populations or synthetics. Released cultivars have been developed for use in most areas of North America where switchgrass is adapted (Table 16–1).

The primary objectives of switchgrass breeding programs have been improving establishment capability, forage yield and quality, and insect and disease resistance. Breeding for persistence is achieved by the use of adapted germplasm in a breeding program. Breeding work on improving establishment targeted increased seed size (Boe and Johnson, 1987) and seedling growth per se (Smart et al., 2003a, 2003b), or both. Sunburst switchgrass is a cultivar with improved establishment because of its large seed (Boe and Ross, 1998). Because switchgrass is a very good seed producer, little emphasis has been placed on breeding for improved seed yield. Hopkins and Taliaferro (1997) demonstrated that while switchgrass seedlings have good tolerance to acid soils, there was little genetic variation in the germplasm they evaluated. Breeding for disease resistance has occurred by eliminating diseased strains and plants from breeding programs. Diseases that can cause

Table 16-1. Principal cultivars of switchgrass and their primary areas of adaptation.

Cultivar	Origin of germplasm	Type†	Adapted USDA hardiness zones	Reference
Dacotah	North Dakota	Upland tetraploid	2, 3, upper 4	Alderson and Sharp (1994); Barker et al. (1990)
Forestburg	South Dakota	Upland octaploid	3, 4	Alderson and Sharp (1994)
Sunburst	South Dakota	Upland octaploid	3, 4, 5	Boe and Ross (1998)
Nebraska 28	Nebraska	Upland octaploid	3, 4	Alderson and Sharp (1994)
Summer	Nebraska	Upland tetraploid	4,5	Alderson and Sharp (1994)
Shelter	West Virginia	Upland octaploid	4, 5, 6	Alderson and Sharp (1994)
Pathfinder	Nebraska, Kansas	Upland octaploid	4, 5	Alderson and Sharp (1994); Newell (1968b)
Trailblazer	Nebraska, Kansas	Upland octaploid	4, 5	Alderson and Sharp (1994); Vogel et al. (1991)
Blackwell	Oklahoma	Upland octaploid	lower 5, 6, 7	Alderson and Sharp (1994)
Cave-in-Rock	Southern Illinois	Upland octaploid	5, 6, 7	Alderson and Sharp (1994)
Shawnee	Southern Illinois	Upland octaploid	5, 6, 7	Vogel et al. (1996)
Caddo	Oklahoma	Upland octaploid	6,7	Alderson and Sharp (1994)
Kanlow	Oklahoma	Lowland tetraploid	6, 7	Alderson and Sharp (1994)
Alamo	Texas	Lowland tetraploid	7, 8, 9	Alderson and Sharp (1994)

† From Hultquist et al. (1996).

severe losses to switchgrass include rusts caused by *Uromyces graminicola* Burn.(Cornelius and Johnston 1941), panicum mosaic caused by the panicum mosaic virus (Sill and Pickett 1957), and Helminthosporium spot blotch caused by *Helminthosporium sativa* Pam., King, and Bakke (Zeiders, 1984). There is genetic variability ranging from resistance to tolerance to these diseases.

Emphasis has been and is being placed on breeding for increased forage or biomass yield. Released cultivars typically are higher yielding than germplasm accessions originating from the same geographical area or ecoregion (Hopkins et al., 1995b). These gains have been achieved by selecting and intermating the highest yielding or most vigorous plants from the highest yielding and vigorous accessions. Gains in yield can be made by selecting strains originating up to 300 to 500 km south of the intended area of use and then releasing them for use in areas north of their origin. Additional breeding for increased yield within a maturity group will be required if switchgrass yields are to be further increased. Restricted Recurrent Phenotypic Selection (Vogel and Burson, 2004, this publication), which has been used successfully to improve the yield of several perennial grasses (Burton, 1974), has not been effective in increasing forage or biomass yield of switchgrass (Hopkins et al., 1993; Taliaferro et al., 1999). Between and within half-sib family breeding procedures are currently being used to breed for improved forage or biomass yield. There is potential to produce hybrid cultivars using genetic self-incompatibility. In general, switchgrass cultivars are stable for yield and quality traits over years and locations in the geographical region where they are adapted (Hopkins et al., 1995a).

Research in Nebraska has indicated that 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 cv. Trailblazer (Vogel et al., 1991). In comparison to the control cv. 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⁻¹, daily liveweight gains by beef cattle of 0.15 kg, beef cattle production of 67 kg ha⁻¹, and profit of U.S. \$59 ha⁻¹ (Casler and Vogel, 2001). Based on 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 USA 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 has higher IVDMD than the parent cultivar but has equivalent yields. Shawnee was developed primarily for use in the Midwest states, USA and similar ecoregions. Trailblazer and Shawnee are the only switchgrass cultivars developed with improved forage quality.

Selection for high IVDMD has continued in the EY × FF population from which Trailblazer was selected. Three cycles of breeding for high IVDMD resulted in a linear increase in IVDMD and a linear decrease in lignin concentration (Casler et al., 2002). It also has resulted in a significant decrease in winter survival. Some families in the high IVDMD populations continue to have high winter survival rates indicating that additional breeding progress may still be feasible (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 multi-year evaluation of breeding nurseries in the environments in which the plant materials will be used (Casler et al., 2002; Vogel et al., 2002b)

Molecular breeding work on switchgrass was initiated in 1992 by Dr. Bob Conger at the University of Tennessee. Since that time, 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, 1996b) including the recent development of a method for regenerating switchgrass plants from cells in suspension culture (Dutta and Conger, 1999). Conger and associates transformed switchgrass by bombarding cells with tungsten particles coated with a dual marker plasmid with the reporter gene *gfp* (green fluorescent protein) and the bialaphos [sodium phosphinothricylalanylalanine] resistance bar gene that codes for resistance to the herbicide Basta [monoammonium 2-amino-4(hydroxymethylphosphinyl)butanoate] and obtained expression of both genes in transgenic plants (Richards et al., 2001). Conger's laboratory also transformed switchgrass with bar and *gus* (β-glucuronidase) genes using *Agrobacterium*-mediated procedures (Somleva et al., 2002). Controlled crosses between transgenic and non-transformed plants resulted in the expected expression of both genes in T₁ plants. Although further improvements in technology will undoubtedly be made, Conger and his associates have developed the basic technology to employ transformation as a breeding procedure in switchgrass.

Conger (1998) and others have pointed out that release of transgenic forage plants could have environmental effects since many forage plants have wild relatives. Traditionally most of the traits in plants modified by plant breeders including dwarfing, absence of dormancy, nonshattering seed, and uniform maturity have an adaptive disadvantage in the wild. Transformed plants could have an adaptive advantage in the wild including resistance to biotic and abiotic stresses. It is possible that these genes could be transferred to wild relatives via natural hybridization. Presence of such genes in wild relatives could have undesirable economic and environmental consequences.

The U.S. Department of Energy's (DOE) Biofuels Feedstock Development Program (BFDP) supported a significant research effort during the 1990s to develop switchgrass into a model herbaceous biomass crop. The DOE-supported breeding and genetics research was conducted in the USA at Lincoln, NE; Stillwater, OK; Athens, GA; Knoxville, TN; Oak Ridge, TN; Madison, WI; and Brookings, SD (Taliaferro et al., 1999). The first cultivar developed from this research program was Shawnee. Other cultivars and germplasm will likely be released in the first decade of the 21st century.

IMPORTANCE

Characteristics that Make the Species Important

Switchgrass has an array of desirable attributes that make it valuable for use in conservation, livestock production, and biomass energy production. It is a broadly adapted, long-lived perennial that can produce high forage and biomass yields on marginal lands (Vogel, 1996). It is a C₄ species that can be grown at northern and equivalent southern latitudes where semi-tropical C₄ species such as bermudagrass [*Cynodon dactylon* (L.) Pers.] often winter kill. Use of switchgrass as a cultivated pasture grass will probably increase in the next 20 yr primarily in the area east of 100° W long where smooth brome grass (*Bromus inermis* Leyss.) and tall fescue (*Festuca arundinacea* Schreb.) are the principal cool-season grasses. Switchgrass has the yield potential to fully use the precipitation in this region and its productivity during the hot months of summer corresponds to a period of low productivity of these cool-season grasses. Its primary advantage over other warm-season grasses is that it can be easily seeded and established if herbicides are used to control weeds. Because of its high biomass yields and its other desirable attributes, it has been identified as a primary species for use in herbaceous biomass energy crop production systems (McLaughlin, S.B., et al., 1999). If biomass energy becomes a reality, switchgrass could be grown on millions of acres in North America as an energy crop (Vogel, 1996; McLaughlin et al., 2002b). It is being evaluated as a biomass energy crop in Europe (Christian et al., 2002; Monti et al., 2001).

Uses

Switchgrass has been seeded in pastures and rangeland in pure stands and mixtures in the Great Plains for more than 60 yr and in the past 20 yr, it has become increasingly important as a pasture grass in the central and eastern USA. Switch-

grass pastures are used primarily to support beef cattle herds in the summer months. In pastures, it is best managed as a monoculture since it tends to be early maturing and competitive. If it is to be planted in a mixture, no more than 20% of the mixture by seed count should be switchgrass. Switchgrass produces good hay if cut when seedheads are beginning to emerge. It also is being used extensively for conservation plantings such as waterways, highway and railway rights-of-way, buffer strips, and for wildlife plantings (Sanderson et al., 2004, this publication).

Switchgrass has potential for use as a biomass energy crop (McLaughlin et al., 1999). The cell walls of grasses such as switchgrass are comprised primarily of cellulose and hemicellulose. These macro-molecules are comprised of simple sugars that can be fermented to produce ethanol. Molecular genetics research has made ethanol production from biomass increasingly feasible (Vogel, 1996). In the Midwest, switchgrass yields of 14 Mg ha⁻¹ have been obtained with existing cultivars (Hopkins et al., 1995a). Annual yields as high as 20 Mg ha⁻¹ have been reported in the southeastern USA (McLaughlin et al., 1999). Assuming a 75% extraction efficiency (Turhollow et al., 1988; Dobbins et al., 1990) ethanol yield would be 330 L Mg⁻¹ biomass which at biomass yields of 15 Mg ha⁻¹ would result in ethanol production of about 5000 L ha⁻¹. Switchgrass can be used in combustion processes to produce heat, steam, or electricity or it can be gasified to produce a syn-gas than can be used in a variety of end point processes (McLaughlin et al., 1999). Conversion processes are still under development and at present switchgrass can be best described as a potential energy crop.

PRODUCTIVITY AND PERSISTENCE

Abiotic Factors

The primary controls of macroclimate are latitude, continental position, and altitude (Bailey, 1995, 1997, 1998). These controls determine thermal and moisture zones which can be further subdivided into subzones based on the seasonality of precipitation. Thermal and moisture zones and subzones characterize conditions for plant growth in a geographical area known as an ecoregion. Latitude affects day length, length of the growing season, and temperature during both the growing and nongrowing or dormant seasons. Populations of a species such as switchgrass from different latitudinal zones within an ecoregion can be differentiated by growing the populations in common nurseries or gardens located at latitudes within the ecoregion (Cornelius and Johnston, 1941; McMillian, 1959, 1965; McMillian and Weiler, 1959). Because of its broad geographic distribution, switchgrass populations or ecotypes and cultivars derived from those populations are available that are adapted to USDA Plant Hardiness Zones and ecoregions east of the Rocky Mountains of North America. Although it only recently has begun to be evaluated in other continents, research experience with other crops would indicate that ecotypes and cultivars will be adapted to other regions of the world with similar ecoregions and plant hardiness zones (Wilsie, 1962). Switchgrass tolerates soil with pH values ranging from 3.9 to 7.6 (Duke, 1978; Hopkins and Taliaferro, 1977).

Biotic Factors

Herbage feeding insects such as grasshoppers (family Acrididae) are the primary insect pests affecting the biomass productivity of switchgrass. Individual switchgrass plants can be susceptible to an array of diseases (Sprague, 1950) but a range of resistance is found in most populations or cultivars. Principal diseases and causal agent (in parenthesis) include rusts (*Puccinia emaculata* Schwein., *Puccinia graminis* Pers., and *Uromyces graminicola* Burrill), smuts [*Tilletia maclaganii* (Berk.) G.P. Clinton], anthracnose [*Colletotrichum graminicola* (CES) G.W. Wils]; Elsinoë leaf spot (*Elsinoë panici* Tiffany and Mathra), Helminthosporium spot blotch [*Bipolaris sorokiniana* (Sacc. ex Sorok.) Shoem = *Helminthosporium sativum* Pam., King, & Brakke], Phoma leaf spot (*Phoma* sp.), Fusarium root rot (*Fusarium* spp.) (Sprague, 1950; Ray, 1954; Tiffany and Mathre, 1961; Zieders, 1984; Farr et al., 1989; Gravert et al., 2000; Gravert and Munkvold, 2002; Munkvold, 2002). Color photographs of these diseases on switchgrass are available online (Munkvold, 2002). Severe outbreaks of rusts are not common if adapted germplasm is used but rusts can reduce seed yields in seed production fields. Smuts can have a significant impact on both seed yields and biomass production and are a significant problem in Iowa (Gravert et al., 2000; Gravert and Munkvold, 2002; Munkvold, 2002). In Iowa, fields with seed smut incidence more than 50% yielded less than half of the expected biomass (Gravert and Munkvold, 2002). Some infested seed fields had no seed production in Iowa in a number of years. 'Cave-in-Rock' has been the main susceptible cultivar susceptible to seed smut. In Iowa, other nonviral diseases infested plants of populations to varying degrees but usually did not appear to have a significant impact on plant growth and development (Munkvold, 2002). Helminthosporium spot blotch can be a serious pathogen of switchgrass in Pennsylvania and other eastern states (Zeiders, 1984). Genetic variability exists among and within cultivars and populations for resistance to Helminthosporium (Zeiders, 1984) and other pathogens. All foliage diseases reduce forage quality and the subsequent performance by grazing animals.

Panicum mosaic virus (PMV) infestation can cause death of tillers and plants of switchgrass (Sill and Pickett, 1957; Niblett and Paulsen, 1975; McLaughlin et al., 2002a). Symptoms include light green to yellow spots or streaks followed by blotchy light green to yellow mottle and mosaic. Older leaves of infected plants may turn yellow and die from the tip. The virus can be mechanically transmitted (Sill and Pickett, 1957). In space-transplanted switchgrass breeding nurseries in eastern Nebraska, Panicum mosaic infected plants usually are only a small percentage (<5%) of some populations but they usually die within 1 or 2 yr after symptoms appear. One experimental strain became heavily infected and was not released. All cultivars that have been evaluated have some susceptible plants but most plants appear to be resistant or do not exhibit symptoms.

Mycorrhizae

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 all 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).

MANAGEMENT

Establishment

Recommended seeding rates are 200 to 400 pure live seeds (PLS) 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 yr to achieve full production yields. Stands of <10 plants m^{-2} may need to be overseeded or reseeded. Minimum germination temperature for switchgrass is $10^{\circ}C$ (Hsu et al., 1985a). Temperature gradient table studies with several switchgrass cultivars and seedlots demonstrated that near maximum germination was obtained from 19 to $36^{\circ}C$ and optimal germination was between 27 and $30^{\circ}C$ (Dierberger, 1991). Optimum germination temperatures for switchgrass may be lower than those for seedling development (Panciera and Jung, 1984). Seedling growth of switchgrass at $20^{\circ}C$ is much slower than at 25 or $30^{\circ}C$ (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 northeastern USA, a planting window of 3 wk before and 3 wk 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 will overwinter and the cool moist spring conditions results in a natural cold stratification and they will germinate as the weather warms. Switchgrass should not be planted in late summer because it does not have time to develop sufficiently before winter and it can winterkill.

Planting seed too deeply often leads to seeding failures with switchgrass and other small seeded warm-season grasses (Masters et al., 2004, this publication). Switchgrass seed should be planted about 1 to 2 cm deep so the seedbed needs to be firm to prevent a drill from placing the seed too deeply. No-till seeding into crop residues or chemically killed sods is often very effective (Samson and Moser, 1982). Corrective applications of phosphorus (P) or potassium (K) should be made before seeding but nitrogen (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 (AOSA) procedures (AOSA, 1988) includes a period of cold stratification where seed are allowed to imbibe water and are chilled at 4°C for 2 to 4 wk 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 yr at room temperatures. Seed stored for three or more years at room temperature may result in poor stands due to decreased vigor (Vogel, 2002). Switchgrass seed can be stratified by wet chilling to break dormancy but drying the seed can cause some of the seed to revert to a dormant condition (Zhang-Xing et al., 2001). Extended stratification (>42 d) 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 yr 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 to 10 wk 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 the same time that annual weeds develop. Most dicot weeds can be controlled with 2,4-D (2,4-dichlorophenoxyacetic acid) (Anonymous, 2002). 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 C₃ 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 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 active ingredient (a.i.) ha⁻¹ before the grass seedlings emerged, provided excellent weed control and enabled excellent stands of switchgrass to be obtained within 1 yr of planting (Masters et al., 1996). Recent research conducted in the central and northern Great Plains of the USA (K.P. Vogel, unpublished data, 2002) demonstrated that switchgrass establishment was improved following application of atrazine at 1.12 kg a.i. ha⁻¹ and quinclorac (3,7, dicholo-8-quinolinecarboxylic acid) at 1.1 kg a.i. ha⁻¹. This herbicide treatment controlled broad leaf 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. 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] 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-triazin-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 pastures (Anonymous, 2002).

Fertility Management

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, recommended annual rates of N vary from 90 to 110 kg ha⁻¹ when switchgrass is managed for hay or pasture while further west where there is less precipitation, rates of 45 to 70 kg ha⁻¹ are used. When switchgrass is managed for optimal biomass production in the Midwest, approximately 10 to 12 kg ha⁻¹ N needs to be applied for each Mg ha⁻¹ of biomass yield (Vogel et al., 2002a). At fertility rates above this level, nitrates accumulated in the soil profile. Switchgrass may respond to P fertilization if the availability of P in the soil is low (Rehm, 1984; Rehm et al., 1976). Switchgrass and other C₄ grasses should be fertilized in late spring when they are initiating growth. Early spring fertilization will stimulate invasion by C₃ grasses and forbs (Rehm et al., 1976). Nitrogen fertilization increases the forage protein concentration (Perry and Baltensperger, 1979; Rehm, 1984; Rehm et al., 1977; Vogel et al., 2002a) and IVDMD of switchgrass (Perry and Baltensperger, 1979; George et al., 1990).

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⁻¹, switchgrass yields declined 12% compared to C₃ 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

Table 16–2. Summary of switchgrass grazing studies.

Source	Location and year	Average daily gain kg d ⁻¹	Liveweight gain kg ha ⁻¹ yr ⁻¹
Dwyer and Elder (1964)	Oklahoma, 1963	0.6	192
Krueger and Curtis (1979)	South Dakota, 1973–1975	0.9	146
Anderson et al. (1988)	Nebraska, 1982, 1983, 1985	0.65	311
Burns et al. (1984)	Georgia, 1978–1980		
	Spring	1.1	322
	Summer	0.9	550
Barnhardt and Wedin (1984)	Iowa, 1978–1980	0.65	225

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 use it because switchgrass is not active. The stimulated C₃ invaders will increase rapidly and use 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 C₃ plants which can result in the conversion of a switchgrass pasture into a mixed species cool-season pasture.

Grazingland Management

In temperate regions switchgrass pastures will be ready to graze in late spring, about the time the cool-season grasses have completed their spring growth. They are normally grazed when the grass is about 30-cm tall. The date will vary with location. Switchgrass should be grazed heavily to maximize beef production per unit of land (Burns et al. 1984; Barnhardt and Wedin 1984; Anderson et al. 1988). Under continuous stocking, sufficient animals should be kept on a unit of land to keep the switchgrass at about 30-cm tall. Beef cattle graze switchgrass from the top of the canopy giving pastures a clipped appearance. If sufficient animals are not available to maintain this pressure, part of the pasture should be fenced and harvested as hay. After it has headed, its digestibility is low. Under rotational stocking, cattle should be removed and the pastures allowed to regrow when the switchgrass has been grazed to a height of about 20 cm. A short period of grazing to partially defoliate switchgrass in late spring can shift a major portion of the yield to later in the summer and improve summer switchgrass quality (George and Obermann, 1989). Switchgrass stands can be damaged by overgrazing. Switchgrass needs recovery time prior to a frost to replenish stored carbohydrates in perennial tissue. Because of this, plants should be at least 10-cm tall after grazing during the summer and 20-cm tall in the fall after grazing ceases. Beef cattle gains in switchgrass grazing trials ranged from 0.5 to 1.1 kg animal⁻¹ d⁻¹ (Table 16–2). Pure stands of switchgrass should not be grazed by horses (*Equus caballus*) or sheep (*Ovis aries*) due to the toxin it contains (see following section on forage quality).

Hayland Management

Switchgrass should be harvested for hay at about the time panicles are beginning to emerge from the boot to obtain an optimum combination of yield and

quality (Newell and Moline, 1978). Switchgrass forage yields increase with time but forage IVDMD and protein concentration decrease (Perry and Baltensperger, 1979; Anderson and Matches, 1983; Griffin and Jung 1983; Mitchell et al., 2001). Switchgrass harvested when panicles are emerging from the boot will average 500 to 600 g kg⁻¹ IVDMD and 80 to 100 g kg⁻¹ protein (Vogel et al., 1984). Forage yields from 1.5 to more than 20 Mg ha⁻¹ can be obtained depending upon time of harvest, cultivar, fertilization, and location. The earlier switchgrass is grazed or cut for hay, the larger the regrowth yields will be (Vogel et al., 2002a). Close clipping has resulted in stand reduction in the Great Plains but not in Missouri (Anderson and Matches, 1983). Excellent stands have been maintained in the grass breeding nurseries in Nebraska with cutting heights of 8 to 10 cm. Carbohydrate reserves may be severely depleted by excessive harvesting resulting in stand reductions. Under most conditions only one regrowth harvest should be made and this harvest should be made either after a frost or 6 wk before expected frosts to allow carbohydrate reserves to be replenished.

Factors Affecting Utilization by Ruminants

Switchgrass is lower in dry matter digestibility than C₃ grasses when compared at the same stage of development (Griffin et al., 1983). In the genus *Panicum* there are both C₃ and C₄ grasses; differences in the anatomical structure of these two types was reported to be responsible for the higher in vitro digestibilities obtained with C₃ grasses (Akin et al., 1983; Wilson et al., 1983). Switchgrass had higher leaf dry matter digestibility than most of the C₄ *Panicums* evaluated (Wilson et al. 1983). The upper internodes of switchgrass had significantly more of the parenchyma cells digested after 48 h in rumen fluid than the lower internodes and this difference was associated with greater lignification in the lower internodes (Akin et al., 1984).

Rumen microorganisms degrade leaf mesophyll tissue fairly quickly but leaf sheath parenchyma, and cortex, xylem, and bundle sheath cells in the stem are much more resistant to degradation (Twidwell et al., 1990). The bundle sheath cells in the leaf blades of C₄ grasses resist degradation more than those of C₃ species. Stem production is a main factor that reduces forage quality of switchgrass (Twidwell et al., 1988); therefore utilization by cattle should occur before stem elongation. In switchgrass as in other grasses, physiological maturity at harvest has an effect on almost all herbage or biomass characteristics that have been analyzed to date. This includes IVDMD, NDF, hemicellulose, lignin, and other traits (Gabrielsen et al., 1990; Jung and Vogel, 1992; Sanderson and Wolf, 1995b; Madakadze, 1999b). In general, with advancing maturity, lignification increases and forage quality decreases. Because forage quality of switchgrass is largely determined by maturity, plant maturity indices including mean stage count and/or the physiological determinants of maturity, day of the year (DOY) or growing degree day (GDD), can be used to predict forage and biomass quality parameters including IVDMD, CP, and NDF of switchgrass in the central Great Plains (Fig. 16-5) (Mitchell et al., 2001). Similar prediction equations including those for lignocellulose concentration can be developed for cultivars adapted to other regions (Sanderson and Wolf, 1995a; Madakadze, 1999b). Temperature can affect the forage quality of switchgrass

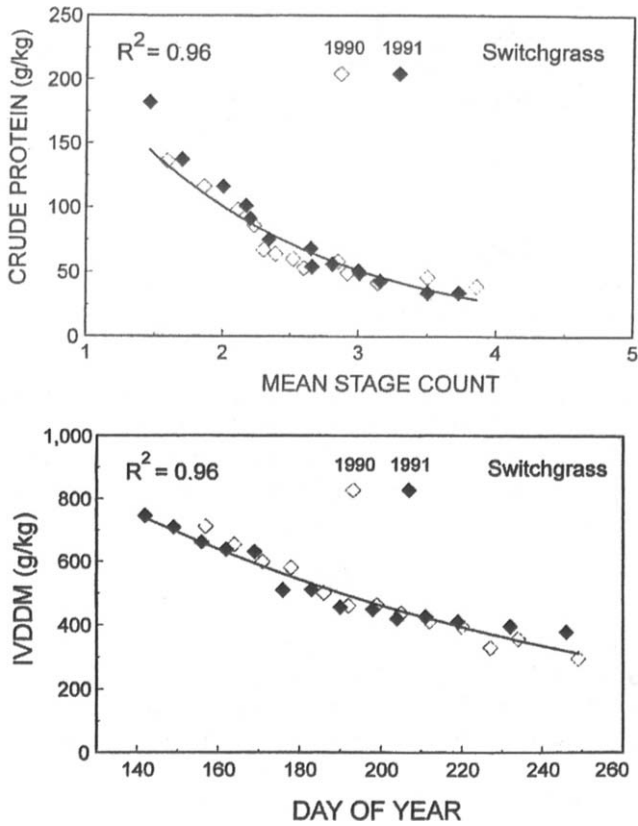


Fig. 16–5. Changes in crude protein (upper) and in vitro dry matter digestibility (IVDDM) (lower) of switchgrass as affected by advancing maturity measured by Mean Stage Count or Day of Year (from Mitchell et al., 2001).

herbage. Switchgrass leaves and stems had higher lignin and lower NDF digestibility when grown at 32°C in comparison to switchgrass grown at 22°C (Wilson et al., 1991).

During a hot, dry summer in West Virginia, 17 lambs out of 104 grazing Cave-in-Rock switchgrass exhibited hepatogenous photosensitization and eight lambs died (Pouli et al., 1992). Hepatotoxicity was confirmed by changes in blood metabolites. Mature ewes were not affected. Photosensitization was not noted in ewes and lambs grazing switchgrass during the previous year which had more nearly normal temperature and rainfall conditions. Symptoms of photosensitization include marked edema of facial tissue, drooping ears, scab formation on the nose, around eyes, and back of the ears, and elevated rectal temperatures. Lambs sought shade and were reluctant to move. Histopathological examinations showed liver damage. During the summer of 2000, five horses grazing a switchgrass pasture in eastern Nebraska developed symptoms of poisoning and one horse died from liver disease (Lee et al., 2001). Subsequent research has demonstrated that switchgrass forage contains the steroidal saponins diosgenin and yamogenin (Fig. 16–6) (Lee et al., 2001). The major

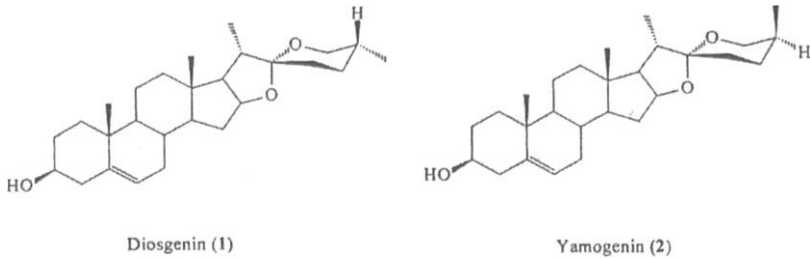


Fig. 16–6. Diosgenin (1) is the major sapogenin in switchgrass. Yamogenin (2) is the major sapogenin in kleingrass (*Panicum coloratum* L.) (from Lee et al., 2001).

sapogenin is diosgenin. These compounds also are found in kleingrass (*Panicum coloratum* L.) (Lee et al., 2001). Research is underway to determine the concentration levels of these compound in switchgrass herbage throughout the growing season. There have not been any reports of toxicity problems with cattle grazing switchgrass.

Conservation Stand Management

Switchgrass was widely used in many regions of the USA including the Midwest and the Great Plains in the Conservation Reserve Program which was designed to take cropland out of production and reduce soil erosion. It is being increasingly used for other conservation practices including buffer strips and herbaceous hedges or barriers (Dewald et al, 1996). Switchgrass buffer strips and hedges are an effective and economical method of reducing soil erosion and improving water quality from agricultural fields (Eghball et al., 2000; Gilley et al., 2000). It is an effective plant for buffer strips and herbaceous barriers because of its dense, strong tillers and culms allowing it to remain erect against water flows and trap silt. Switchgrass is tolerant to herbicides that are often used on adjacent crops, grows in partial shading from cultivated crops, tolerates inundations by sediment, manageable as long narrow strips, nonweedy, tolerant of defoliation if grazed, adapted to local climatic conditions, and long lived if adapted cultivars are used (Dewald et al., 1996). Management practices for switchgrass in conservation plantings are similar to those for hayland management except the forage is not harvested. The accumulated switchgrass biomass on conservation sites should be removed periodically or stands will deteriorate. Prescribed burning is an effective method of removing accumulated biomass.

Biomass Production Management

Cellulosic biomass of herbaceous plants can be used as a feedstock for the production of liquid fuels such as ethanol (Lynd et al., 1991; Sanderson et al., 2004, this publication) and switchgrass has been identified as a promising species for development into a herbaceous biomass fuel crop in the USA (Vogel, 1996). Switchgrass has an array of desirable energy, conservation, environmental, and economic attributes for its use as a bio-energy crop (McLaughlin et al., 2002b). These include

broad adaptation, high yields on marginal and erosive croplands, harvestable with conventional forage equipment, and a very positive energy balance. Several trials have been conducted in the USA and other countries on optimum management practices including time of harvest and N fertilization. In general, a single harvest when switchgrass is fully headed gives the highest yields (Sanderson et al, 1999; Madakadze et al, 1999a, 1999b; Christian et al, 2002; Vogel et al, 2002a). Harvests after a killing frost usually result in decreased biomass yields but may require lower inputs of N fertilizer. Depending on location and cultivar, biomass yields of the best adapted cultivars ranged from 10 to more than 20 Mg ha⁻¹. The conversion technology that will be used to convert cellulosic biomass to liquid fuels including ethanol is still under development. Consequently desirable biomass quality attributes for conversion to energy are unknown.

Seed Production Management

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 USA, and on anecdotal results of seed producers. Cornelius (1950) reported that cultivated seed production fields produce more and higher quality seed 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 to 110 kg ha⁻¹ N after the fields are burned and cultivated to maintain the grass in rows. In Iowa, Cave-in-Rock had higher 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 cv. 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 (Brejda et al., 1994; George et al., 1990). Seed yields in an Iowa study ranged 200 to 1000 kg ha⁻¹ (Kassel et al., 1985). In the Missouri trials, seed yields ranged from 460 to 700 kg ha⁻¹ (Brejda et al, 1994). The difference in cultivar response was due to differences in lodging.

Carbon Sequestration

Switchgrass has the potential to sequester significant amount of carbon (C) in the soil profile because of its extensive root system. Several studies are in progress to measure C sequestration by switchgrass. In an initial report by Garten and Wullschlegel (2000) there was more coarse root C under switchgrass (cv. Alamo) and forest cover than under tall fescue, corn, or pastures with mixed species

composition. Coarse root C in switchgrass fields ranged from 23.8 to 58.7 mg cm⁻² while for corn it ranged from 0.00 to 2.17 mg cm⁻² and for fescue it was 2.5 to 18.5 mg cm⁻². Soil organic carbon (SOC) values were 10-fold larger than those for coarse root carbon. For switchgrass they were 296 to 454 mg cm⁻² SOC while for corn they were 283 to 793 mg cm² SOC and for fallow, the range was 295 to 449 mg cm⁻² SOC (Garten and Wullschleger, 2000).

SUMMARY

The use of switchgrass will increase in both North America and other temperate areas, particularly for conservation purposes including establishment of buffer and barrier strips and herbaceous hedges because its use will allow farmers and land managers to meet environmental rules and regulations. If economical conversion technologies can be developed, it will likely be planted on millions of hectares as biomass energy crop. Switchgrass' use in pure stands and mixtures as a warm-season pasture species will continue to expand in temperate regions where high temperatures inhibit the growth of C₃ species during the summer months.

REFERENCES

- Akin, D.E., R.H. Brown, and L.L. Rigsby. 1984. Digestion of stem tissue in *Panicum* species. *Crop Sci.* 24:769–773.
- Akin, D.E., J.R. Wilson, and W.R. Windham. 1983. Site and rate of tissue digestion in leaves of C₃, C₄, and C₃/C₄ intermediate *Panicum* species. *Crop Sci.* 23:147–155.
- Alderson, J., and W.C. Sharp. 1994. Grass varieties in the United States. *Agric. Handb.* 170. Soil Conserv. Serv., USDA, Washington, DC.
- Alexandrova, K.S., P.D. Denchev, and B.V. Conger. 1996a. In vitro development of inflorescences from switchgrass nodal segments. *Crop Sci.* 36:175–178.
- Alexandrova, K.S., P.D. Denchev and B.V. Conger. 1996b. Micropropagation of switchgrass by node culture. *Crop Sci.* 36:1709–1711.
- Anderson, B.E., and A.G. Matches. 1983. Forage yield, quality, and persistence of switchgrass and caucasian bluestem. *Agron. J.* 75:119–124.
- Anderson, B., J.K. Ward, K.P. Vogel, M.G. Ward, H.J. Gorz, and F.A. Haskins. 1988. Forage quality and performance of yearlings grazing switchgrass strains selected for differing digestibility. *J. Anim. Sci.* 66:2239–2244.
- Anonymous. 2002. Guide for weed management in Nebraska. EC-130-D. Univ. of Nebraska Coop. Ext., Lincoln.
- Association of Official Seed Analysts. 1988. Rules for testing Seeds. *J. Seed Technol.* 12:1–122.
- Bahler, C.C., K.P. Vogel, and L.E. Moser. 1984. Atrazine tolerance in warm-season grass seedlings. *Agron. J.* 76:891–895.
- Bailey, R.G. 1995. Description of the ecoregions of the United States. Misc. Publ. 1391. U.S. For. Serv., Washington, DC.
- Bailey, R.G. 1997. Map: Ecoregions of North America (rev.). USDA Forest Service in cooperation with The Nature Conservancy and the U.S. Geological Survey. U.S. For. Serv., Washington, DC. Available at www.fs.fed.us/institute/ecoregions/na_map.html (verified 24 Mar. 2004)
- Bailey, R.G. 1998. Ecoregions: The ecosystem geography of the oceans and continents. Springer-Verlag, New York.
- Barker, R. E., R.J. Haas, J.D. Berdahl, and E.T. Jacobsen 1990. Registration of 'Dacotah' switchgrass. *Crop Sci.* 30:1158.
- Barnett, F.L., and R.F. Carver. 1967. Meiosis and pollen stainability in switchgrass, *Panicum virgatum* L. *Crop Sci.* 7:301–304.

- Barnhardt, S.K., and W.F. Wedin. 1984. Management and utilization of switchgrass (*Panicum virgatum*) by yearling steers in western Iowa. p. 181–185. *In* Proc. Am. Forage Grassl. Council., Houston, TX. 23–26 Jan. 1984. Am. Forage Grassl. Council., Lexington, KY.
- Beatty, E.R., J.L. Engel, and J.D. Powell. 1978. Tiller development and growth in switchgrass. *J. Range Manage.* 31:361–365.
- 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.
- Bennett, M.D., and J.B. Smith. 1976. Nuclear DNA amounts in angiosperms. *Philos. Trans. R. Soc. London B* 334:309–345.
- Boe, A., and P.O. Johnson. 1987. Deriving a large-seeded switchgrass population using air-column separation of parent seed. *Crop Sci.* 27:147–148.
- Boe, A., and J.G. Ross. 1998. Registration of ‘Sunburst’ switchgrass. *Crop Sci.* 38:540.
- Brejda, J.J., J.R. Brown, G.W. Wyman, and W.K. Schumacher. 1994. Management of switchgrass for forage and seed production. *J. Range Manage.* 47:22–27.
- Brejda, J.J., L.E. Moser, and K.P. Vogel. 1998. Evaluation of switchgrass rhizosphere microflora for enhancing yield and nutrient uptake. *Agron. J.* 90:753–758.
- Brejda, J.J. 1996. Evaluation of arbuscular mycorrhiza populations for enhancing switchgrass yield and nutrient uptake. Ph.D. diss. Univ. of Nebraska-Lincoln, Lincoln (Diss. Abstr. AAG9715956).
- Brunken, J.N., and J.R. Estes. 1975. Cytological and morphological variation in *Panicum virgatum* L. *Southwest Nat.* 19:379–385.
- Burns, J.C., R.D. Mochrie, and D.H. Timothy. 1984. Steer performance from two perennial Pennisetum species, switchgrass, and a fescue—‘Coastal’ bermudagrass system. *Agron. J.* 76:795–800.
- Burton, G.W. 1974. Recurrent restricted phenotypic selection increases forage yield of Pensacola bahiagrass. *Crop Sci.* 14:831–835.
- 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.
- Casler, M.D., and K.P. Vogel. 2001. Accomplishments and impact from breeding for increased forage nutritional value. *Crop Sci.* 39:12–20.
- Cathey, H.M. 1990. USDA Plant hardiness zone map. USDA Misc. Publ. 1475. U.S. Natl. Arboretum, USDA-ARS, Washington, DC. 1998 U.S. Natl. Arboretum web version is available at www.usna.usda.gov/hardzone/ushzmap.html (verified 29 Mar. 2004).
- Christian, D.G., A.B. Riche, and N.E. Yates. 2002. The yield and composition of switchgrass and coastal panic grass grown as a biofuel in Southern England. *Bioresour. Tech.* 83:115–124.
- Conger, B.V. 1998. Genetic transformation of forage grasses. p.49–58. *In* E.C. Brummer et al. (ed.) Molecular and cellular technologies for forage improvement. CSSA Spec. Publ. 26. CSSA, Madison, WI.
- Cornelius, D.R. 1950. Seed production of native grasses. *Ecol. Mono.* 20:1–27.
- Cornelius, D.R., and C.O. Johnston. 1941. Differences in plant type and reaction to rust among several collections of *Panicum virgatum* L. *J. Am. Soc. Agron.* 33:115–124.
- Denchev, P.D., and B.V. Conger. 1994. Plant regeneration from callus culture of switchgrass. *Crop Sci.* 34:1623–1627.
- Dewald, C.L., J. Henry, S. Bruckerhoff, J. Richtie, S. Dabney, D. Shepard, J. Douglas, and D. Wolf. 1996. Guidelines for establishing warm season grass hedges for erosion control. *J. Soil Water Conserv.* 51:16–20.
- Dierberger. 1991. Switchgrass germination as influenced by temperature, chilling, cultivar, and seed lot. M.S. thesis. Univ. of Nebraska, Lincoln.
- Dobbins, C.L., P. Preckel, A. Mdrafi, J. Lowenburg-DeBoer, and D. Stucky. 1990. Evaluation of potential herbaceous biomass crops on marginal crop lands: 2) Economic potential. Final report. ORNL/Sub/85-27412/5&P2. Oak Ridge Natl. Lab., Oakridge, TN.
- Duke, J.A. 1978. The quest for tolerant germplasm. p.1–61. *In* G.A. Jung (ed.) Crop tolerance to sub-optimal land conditions. ASA Spec. Publ. 32. ASA, Madison, WI.
- Dutta, G.S., and B.V. Conger. 1999 Somatic embryogenesis and plant regeneration from suspension cultures of switchgrass. *Crop Sci.* 39:243–247.
- Dwyer, D.D., and W.C. Elder. 1964. Grazing comparisons of Woodward sand bluestem and Caddo switchgrass in Oklahoma. *Bull. B-628. Okla. Agric. Exp. Stn., Stillwater.*
- Eberhardt, S.A., and L.C. Newell. 1959. Variation in domestic collections of switchgrass, *Panicum virgatum*. *Agron. J.* 51:613–616.
- Eghball, B., J.E. Gilley, L.A. Kramer, and T.B. Moorman. 2000. Narrow grass hedges effects on phosphorus and nitrogen in runoff following manure and fertilizer application. *J. Soil Water Conserv.* 55:172–176.

- Farr, D.F., G.F. Bills, G.P. Chamuris, and A.Y. Rossman. 1989. Fungi on plants and plant products in the United States. Am. Phytopathol. Soc., St. Paul, MN
- Gabrielsen, B.C., K.P. Vogel, B.E. Anderson, and J.K. Ward. 1990. Alkali-labile lignin phenolics and forage quality in three switchgrass strains selected for differing digestibility. *Crop Sci.* 30:1313–1320.
- Garten, C.T. Jr., and S.D. Wullschleger. 2000. Soil carbon dynamics beneath switchgrass as indicated by stable isotope analysis. *J. Environ. Qual.* 29:645–653.
- George, J.R., and D. Obermann. 1989. Spring defoliation to improve summer supply and quality of switchgrass. *Agron. J.* 81:47–52.
- George, J.R., G.S. Reigh, R.E. Millen, and J.J. Junczak. 1990. Switchgrass herbage and seed yield and quality with partial spring defoliation. *Crop Sci.* 30:845–849.
- Gilley, J.E., B. Eghball, L.A. Kramer, T.B. Moorman. 2000. Narrow grass hedge effects on runoff and soil loss. *J. Soil Water Conserv.* 55:190–196.
- Gould, F.W. 1975. The grasses of Texas. Texas A&M Univ. Press, College Station.
- Gravert, C.E., and G.P. Munkvold. 2002. Fungi and diseases associated with cultivated switchgrass in Iowa. *J. Iowa Acad. Sci.* 109:30–34.
- Gravert, C.E., L.H. Tiffany, and G.P. Munkvold. 2000. Outbreak of smut caused by *Tilletia maclaganii* on cultivated switchgrass in Iowa. *Plant Dis.* 84:596.
- Griffin, J.L., and G.A. Jung. 1983. Leaf and stem forage quality of big bluestem and switchgrass. *Agron. J.* 75:951–956.
- Gunter, L.E., G.A. Tuscan, and S.D. Wullschleger. 1996. Diversity of switchgrass based on RAPD markers. *Crop Sci.* 36:1017–1022.
- Hall, K.E., J.R. George, and R.R. Riedel. 1982. Herbage dry matter yields of switchgrass, big bluestem, and indiangrass with N fertilization. *Agron. J.* 74:47–51.
- Heidemann, G.S., and G.E. Van Riper. 1967. Bud activity in the stem, crown, and rhizome tissue of switchgrass. *J. Range Manage.* 20:236–241.
- Hintz, R.L., K.R. Harmony, K.J. Moore, R.J. George, and E.C. Brummer. 1998. Establishment of switchgrass and big bluestem in corn with atrazine. *Agron. J.* 90: 591–596.
- Hitchcock, A.S. 1951. Manual of the grasses of the U.S. USDA Misc. Publ. 200. 2nd ed. U.S. Gov. Print. Office, Washington, DC.
- Hopkins, A.A., and C.M. Taliaferro. 1997. Genetic variation within switchgrass populations for acid soil tolerance. *Crop Sci.* 37:1719–1722.
- Hopkins, A.A., C.M. Taliaferro, C.D. Murphy, and D'Ann Christian. 1996. Chromosome numbers and nuclear DNA content of several switchgrass populations. *Crop. Sci.* 36:1192–1195.
- Hopkins, A.A., K.P. Vogel, and K.J. Moore. 1993. Predicted and realized gains from selection for in vitro dry matter digestibility and forage yield in switchgrass. *Crop Sci.* 33:253–258.
- 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.
- Hopkins, A.A., K.P. Vogel, K.J. Moore, K.D. Johnson, and I.T. Carlson. 1995b. Genetic variability and genotype x environment interactions among switchgrass accessions from the Midwestern USA. *Crop Sci.* 35:565–571.
- Hoshikawa, K. 1969. Underground organs of the seedlings and the systematics of Gramineae. *Bot. Gaz. (Chicago)* 130:192–203.
- Hsu, F.H., C.J. Nelson, and A.G. Matches. 1985a. Temperature effects on germination of perennial warm-season forage grasses. *Crop Sci.* 25:215–220.
- Hsu, F.H., C.J. Nelson, and A.G. Matches. 1985b. Temperature effects on seedling development of perennial warm-season forage grasses. *Crop Sci.* 25:249–255.
- 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.
- Hultquist, S.J., K.P. Vogel, D.E. Lee, K. Arumuganathan, and S. Kaeppler. 1997. DNA content and chloroplast DNA polymorphisms among accessions of switchgrass from remnant Midwestern prairies. *Crop Sci.* 37:595–598.
- Jones, M.D., and J.G. Brown. 1951. Pollination cycles of some grasses in Oklahoma. *Agron. J.* 43:218–222.
- Jones, M.D., and L.C. Newell. 1946. Pollination cycles and pollen dispersal in relation to grass improvement. *Res. Bull.* 148. Nebr. Agric. Exp. Stn., Lincoln.
- Jung, G.A., J.A. Shaffer, and W.L. Stout. 1988. Switchgrass and big bluestem responses to amendments on strongly acid soil. *Agron. J.* 80:669–676.

- Jung, H.G., and K.P. Vogel. 1992. Lignification of switchgrass (*Panicum virgatum*) and big bluestem (*Andropogon gerardii*) plant parts during maturation and its effect on fibre degradability. *J. Sci. Food Agric.* 59:169–176.
- Kassel, P.C., R.E. Mullen, and T.B. Bailey. 1985. Seed yield response of three switchgrass cultivars for different management practices. *Agron. J.* 77:214–218.
- Krueger, C.R., and D.C. Curtis. 1979. Evaluation of big bluestem, indiagrass, side-oats grama, and switchgrass pastures with yearling steers. *Agron. J.* 71:480–482.
- Lee, S.T., B.L. Stegelmeier, D.R. Gardner, and K.P. Vogel. 2001. The isolation and identification of steroidal saponin in switchgrass. *J. Natural Toxins* 10:273–281.
- Lu, Ku, S.M. Kaepler, K.P. Vogel, K. Arumuganathan, and D.J. Lee. 1998. Nuclear DNA content and chromosome numbers in switchgrass. *Great Plains Res.* 8:269–280.
- Lynd, L.L., J.H. Cushman, R.J. Nichols, and C.F. Wyman. 1991. Fuel ethanol from cellulosic biomass. *Science (Washington, DC)* 231:1318–1323.
- Madakadze, I.C., K.A. Stewart, P.R. Peterson, B.E. Coulman, and D.L. Smith. 1999a. Cutting frequency and nitrogen fertilization effects on yield and nitrogen concentration of switchgrass in a short season. *Crop Sci.* 39:552–557.
- Madakadze, I.C., K.A. Stewart, P.R. Peterson, B.E. Coulman, and D.L. Smith. 1999b. Switchgrass biomass and chemical composition for biofuel in eastern Canada. *Agron. J.* 91:696–701.
- Martin, A.R., R.S. Moomaw, and K.P. Vogel. 1982. Warm-season grass establishment with atrazine. *Agron. J.* 74:916–920.
- Martinez-Reyna, J.M., and K.P. Vogel. 1998. Controlled hybridization technique for switchgrass. *Crop Sci.* 38: 876–878.
- Martinez-Reyna, J.M., and K.P. Vogel. 2002. Incompatibility systems in switchgrass. *Crop Sci.* 42:1800–1805.
- Martinez-Reyna, J.M., K.P. Vogel, C. Caha, and D. J. Lee. 2001. Meiotic stability, chloroplast DNA polymorphisms, and morphological traits of upland x lowland switchgrass reciprocal hybrids. *Crop Sci.* 41:1579–1583.
- Masters, R.A., P. Mislevy, L.E. Moser, and F. Rivas-Pantoja. 2004. Stand establishment. p. 145–178. *In* L.E. Moser et al. (ed.) Warm-season (C₄) grasses. *Agron. Monogr.* 45. ASA, CSSA, and SSSA, Madison, WI.
- Masters, R.A., S.J. Nissen, R.E. Gaussoin, D.D. Beran, and R.N. Stougaard. 1996. Imidazolinone herbicides improve restoration of Great Plains grasslands. *Weed Technol.* 10:392–403.
- McLaughlin, M.R., R.C. Larsen, L.E. Trevathan, C.E. Eastman, and A.D. Hewings. 2002a. Virus diseases of American pasture and forage crops. p. 323–361. *In* S. Charkraborty et al. (ed.) Pasture and forage crop pathology. ASA, CSSA, and SSSA, Madison, WI.
- McLaughlin, S.B., J. Bouton, D. Bransby, R. Conger, W. Ocumpaugh, D. Parrish, C. Taliafferro, K. Vogel, and S. Wullschlegler. 1999. Developing switchgrass as a bioenergy crop. p. 282–299. *In* J. Janick (ed.) Perspectives on new crops and new uses. *Proc. 4th Natl. New Crops Symp.*, Phoenix, AZ. 8–11 Nov.1998. Am. Soc. Hortic. Sci. Press, Alexandria, VA.
- McLaughlin, S.B., D.G. De La Torre Ugarte, C.T. Garten Jr., L.R. Lynd, M.A. Sanderson, V.R. Tolbert, and D.D. Wolf. 2002b. High-value renewable energy from prairie grasses. 2002. *Environ. Sci. Technol.* 36:2122–2129.
- McMillian, C. 1959. The role of ecotypic variation in the distribution of the central grassland of North America. *Ecol. Mono.* 29:285–308.
- McMillian, C. 1965. Ecotypic differences with four North American prairie grasses: II. Behavioral variation with transplanted community fractions. *Am. J. Bot.* 52:55–65.
- McMillian, C., and J. Weiler. 1959. Cytogeography of *Panicum virgatum* in central North America. *Am. J. Bot.* 46:590–593.
- McMurphy, W.E., C.E. Demman, and B.B. Tucker. 1975. Fertilization of native grasses and weeping lovegrass. *Agron. J.* 67:233–236.
- Mitchell, R.B., K.J. Moore, L.E. Moser, J.O. Fritz, and D.D. Redfern. 1997. Predicting developmental morphology in switchgrass and big bluestem. *Agron. J.* 89:827–832.
- Mitchell, R.B., J.O. Fritz, K.J. Moore, L.E. Moser, K.P. Vogel, and D.D. Redfern, 2001. Predicting forage quality in switchgrass and big bluestem. *Agron. J.* 93:118–124.
- Monti, A., P. Venturi, and P.W. Elbersen. 2001. Evaluation of the establishment of lowland and upland switchgrass (*Panicum virgatum* L.) varieties under different tillage and seedbed conditions in northern Italy. *Soil Tillage Res.* 63:75–83.
- Moore, K.J., L.E. Moser, K.P. Vogel, S.S. Waller, B.E. Johnson, and J.F. Pedersen. 1991. Describing and quantifying growth stages of perennial forage grasses. *Agron. J.* 83:1073–1077.
- Munkvold, G. 2002. Identifying switchgrass diseases in Iowa. [Online]. Available at <http://www.plant-path.iastate.edu/extension/switchgrass/index.html> (verified 24 Mar. 2004).

- Newell, L.C. 1968a. Effects of strain source and management practice on forage yields of two warm-season prairie grasses. *Crop Sci.* 8:205–210.
- Newell, L.C. 1968b. Registration of Pathfinder switchgrass. *Crop Sci.* 8:516.
- Newell, L.C., and S.A. Eberhart. 1961. Clone and progeny evaluation in the improvement of switchgrass, *Panicum virgatum* L. *Crop Sci.* 1:117–121.
- Newell, L.C., and W. J. Moline. 1978. Forage quality evaluations of twelve grasses in relation to season for grazing. *Res. Bull.* 283. Nebr. Agric. Exp. Stn., Lincoln.
- Newman, P.R., and L.E. Moser. 1988. Grass seedling emergence, morphology, and establishment as affected by planting depth. *Agron. J.* 80:383–387.
- Niblett, C.L., and A.Q. Paulsen. 1975. Purification and further characterization of panicum mosaic virus. *Phytopathology* 65:1157–1160.
- Nielsen, E.L. 1944. Analysis of variation in *Panicum virgatum*. *J. Agric. Res.* 69:327–353.
- Nielsen, E.L. 1947. Polyploidy and winter survival in *Panicum virgatum*. *J. Am. Soc. Agron.* 39:822–827.
- Panciera, M.T., and G.A. Jung. 1984. Switchgrass establishment by conservation tillage: Planting date responses of two varieties. *J. Soil Water Conserv.* 39:68–70.
- Perry, L.J., and D.D. Baltensperger. 1979. Leaf and stem yields and forage quality of three N-fertilized warm-season grasses. *Agron. J.* 71:355–358.
- Porter, C.L. 1966. An analysis of variation between upland and lowland switchgrass *Panicum virgatum* L. in central Oklahoma. *Ecology* 47:980–992.
- Pouli, J.R., R.L. Reid, and D.P. Belesky. 1992. Photosensitization in lambs grazing switchgrass. *Agron. J.* 84: 1077–1080.
- Ray, W.W. 1954. Unusual or new occurrences of fungus pathogens on grasses in Nebraska. *Plant Dis. Rep.* 38:583–587.
- Redfearn, D.D., K.J. Moore, K.P. Vogel, S.S. Waller, and R.B. Mitchell. 1997. Canopy architectural and morphological development traits of switchgrass and the relationships to forage yield. *Agron. J.* 89:262–269.
- Rehm, G.W. 1984. Yield and quality of a warm-season grass mixture treated with N, P, and atrazine. *Agron. J.* 76:731–734.
- Rehm, G.W., R.C. Sorensen, and W.J. Moline. 1976. Time and rate of fertilizer application for seeded warm-season and bluegrass pastures. I. Yield and botanical composition. *Agron. J.* 68:759–764.
- Rehm, G.W., R.C. Sorensen, and W.J. Moline. 1977. Time and rate of fertilization on seeded warm-season and bluegrass pastures. II. Quality and nutrient content. *Agron. J.* 69:955–961.
- Richards, H.A., V.A. Rudas, H. Sun, J.K. McDaniel, Z. Tomaszewski, and B.V. Conger. 2001. Construction of a GFP-BAR plasmid and its use for switchgrass transformation. *Plant Cell Rep.* 20:48–54.
- Riley, R.D., and K.P. Vogel. 1982. Chromosome numbers of released cultivars of switchgrass, indian-grass, big bluestem, and sand bluestem. *Crop Sci.* 22:1081–1083.
- Samson, J.F., and L.E. Moser. 1982. Sod-seeding perennial grasses into eastern Nebraska pastures. *Agron. J.* 74:1055–1060.
- Sanderson, M.A., G. Brink, K.F. Higgins, and D.E. Naugle. 2004. Alternative uses of warm-season forage grasses. p. 389–416. *In* L.E. Moser et al. (ed.) *Warm-season (C₄) grasses*. Agron Monogr. 45. ASA, CSSA, and SSSA, Madison, WI.
- Sanderson, M.A., J.C. Read, and R.L. Roderick. 1999. Harvest management of switchgrass for biomass feedstock and forage production. *Agron. J.* 91:5–10.
- Sanderson, M.A., and D.D. Wolf. 1995a. Switchgrass morphological development in diverse environments. *Agron. J.* 87:908–915.
- Sanderson, M.A., and D.D. Wolf. 1995b. Switchgrass biomass composition during morphological development in diverse environments. *Crop Sci.* 35:1432–1438.
- Sill, W.H. Jr., and R.C. Pickett. 1957. A new virus disease of switchgrass, *Panicum virgatum* L. *Plant Dis. Rep.* 41:241–249.
- Sims, P.L., L.A. Ayuko, and D.N. Hyder. 1971. Developmental morphology of switchgrass and side-oats grama. *J. Range Manage.* 24:357–360.
- Smart, A.J., and L.E. Moser. 1997. Morphological development of switchgrass as affected by planting date. *Agron. J.* 89:958–962.
- Smart, A.J., and L.E. Moser. 1999. Switchgrass seedling development as affected by seed size. *Agron. J.* 91:335–338.
- Smart, A.J., L.E. Moser, and K.P. Vogel. 2003a. Establishment and seedling growth of big bluestem and switchgrass populations divergently selected for seedling tiller number. *Crop Sci.* 43:1434–1440.
- Smart, A.J., K.P. Vogel, L.E. Moser, and W.W. Stroup. 2003b. Divergent selection for seedling tiller number in big bluestem and switchgrass. *Crop Sci.* 43:1427–1433.

- Smith, D. 1975. Trends of nonstructural carbohydrates in the stem bases of switchgrass. *J. Range Manage.* 28:389–391.
- Somleva, M.N., Z. Tomaszewski, and B.V. Conger. 2002. Agrobacterium-mediated genetic transformation of switchgrass. *Crop Sci.* 42:2080–2087.
- Sprague, R. 1950. Disease of cereals and grasses in North America. The Ronald Press Co., New York.
- Staley, T.E., W.L. Stout, and G.A. Jung. 1991. Nitrogen use by tall fescue and switchgrass on acidic soils of varying water holding capacity. *Agron. J.* 83:732–738.
- 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.
- Taliaferro, C.M., K.P. Vogel, J.H. Bouton, S.B. McLaughlin, and G.A. Tuscan. 1999. Reproductive characteristics and breeding improvement potential of switchgrass. p. 147–153. *In* R.P. Overend and E. Chornet. (ed.) Biomass—A growth opportunity in green energy and value-added products. Proc. of 4th Biomass Conf. of the Americas, Oakland, CA. 29 Aug.–2 Sept. 1999. Elsevier Sci., Kidlington, Oxford, UK.
- Tiffany, L.H., and J.H. Mathre. 1961. A new species of *Elsinoë* on *Panicum virgatum*. *Mycologia* 53: 600–604.
- Tilley, J.M.A., and R.A. Terry. 1963. A two stage technique for in vivo digestion of forage crops. *J. Br. Grassl. Soc.* 18:104–111.
- Tischler, C.R., and P.W. Voigt. 1993. Characterization of crown node elevation in panicoid grasses. *J. Range Manage.* 46:436–439.
- Turhollow, A.F., J.W. Johnson, and J.H. Cushman. 1988. Linking energy crop production to conversion: The case of herbaceous lignocellulosic crops to ethanol. *RERIC Int. Energy J.* 10:41–49.
- Twidwell, E.K., K.D. Johnson, J.H. Cherney, and J.J. Volenec. 1988. Forage quality and digestion kinetics of switchgrass herbage and morphological components. *Crop Sci.* 28:825–830.
- Twidwell, E.K., K.D. Johnson, J.A. Patterson, J.H. Cherney, and C.E. Bracker. 1990. Degradation of switchgrass anatomical tissue by rumen microorganisms. *Crop Sci.* 30:1321–1328.
- Vassey, T.L., J. R. George, and R. E. Mullen. 1985. Early-, mid-, and late-spring establishment of switchgrass at several seeding rates. *Agron. J.* 77:253–257.
- Vogel, K.P. 1987. Seeding rates for establishing big bluestem and switchgrass with pre-emergence atrazine applications. *Agron. J.* 79:509–512.
- Vogel, K.P. 1996. Energy production from forages (or American agriculture - Back to the future). *J. Soil Water Conserv.* 51:137–139.
- Vogel, K.P. 2000. Improving warm-season grasses using selection, breeding, and biotechnology. p. 83–106. *In* K.J. Moore and B. Anderson (ed.) Native warm-season grasses: Research trends and issues. *Crop Sci. Spec. Publ.* 30. CSSA and ASA, Madison, WI.
- Vogel, K.P. 2002. The challenge: High quality seed of native plants to ensure establishment. *Seed Technol.* 24:9–15.
- Vogel, K.P., J.J. Bredja, D. T. Walters, and D.R. Buxton. 2002a. Switchgrass biomass production in the Midwest USA: Harvest and nitrogen management. *Agron. J.* 94:413–420.
- Vogel, K.P., R. Britton, H.J. Gorz, and F.A. Haskins. 1984. In vitro and in vivo analyses of hays of switchgrass strains selected for high and low in vitro dry matter digestibility. *Crop Sci.* 24:977–980.
- Vogel, K.P., and B.L. Burson. 2004. Breeding and genetics. p. 51–94. *In* L.E. Moser et al. (ed.) Warm-season (C₄) grasses. *Agron. Monogr.* 45. ASA, CSSA, and SSSA, Madison, WI.
- Vogel, K.P., F.A. Haskins, and H.J. Gorz. 1981. Divergent selection for in vitro dry matter digestibility in switchgrass. *Crop Sci.* 21:39–41.
- Vogel, K.P., F.A. Haskins, H.J. Gorz, B.A. Anderson, and J.K. Ward. 1991. Registration of 'Trailblazer' switchgrass. *Crop Sci.* 31:1388.
- Vogel, K.P., A.A. Hopkins, K.J. Moore, K.D. Johnson, and I.T. Carlson. 1996. Registration of 'Shawnee' switchgrass. *Crop Sci.* 36:1713
- Vogel, K.P., A.A. Hopkins, K.J. Moore, K.D. Johnson, and I.T. Carlson. 2002b. Winter survival in switchgrass populations bred for high IVDMD. *Crop Sci.* 42:1857–1862.
- Vogel, K.P., and R.A. Masters. 2001. Frequency grid—A simple tool for measuring grassland establishment. *J. Range Manage.* 54:653–655.
- Vogel, K.P., K.J. Moore, and A.A. Hopkins. 1993. Breeding switchgrass for improved animal performance. p.1734–1735. *Proc. XVII Int. Grassl. Congr.*, 17th, Palmerston North, NZ. Feb. 1993. N.Z. Grassl. Soc., Palmerston North, NZ.
- Vogel, K.P., and J.F. Pedersen. 1993. Breeding systems for cross-pollinated perennial grasses. *Plant Breed. Rev.* 11:251–274.

- 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.
- Ward, M.G., J.K. Ward, B.E. Anderson, and K.P. Vogel. 1989. Grazing selectivity and in vivo digestibility of switchgrass strains selected for differing digestibility. *J. Anim. Sci.* 67:1418–1424.
- Weaver, J.E. 1954. *North American Prairie*. Jensen Publ. Co., Lincoln, NE.
- Weimer, M.R., B.A. Swisher, and K.P. Vogel. 1988. Metabolism as a basis for inter- and intra-specific atrazine tolerance in warm-season grasses. *Weed Sci.* 36:436–440.
- Wheeler, W.A., and D.D. Hill. 1957. *Grassland seeds*. D. Van Norstrand Co., Princeton, NJ.
- Wilsie, C.P. 1962. *Crop adaptation and distribution*. W.H. Freeman and Co., San Francisco.
- Wilson, J.R., B. Deinum, and F.M. Engels. 1991. Temperature effects on anatomy and digestibility of leaf and stem of tropical and temperate forage species. *Neth. J. Agric. Sci.* 39:31–48.
- Wilson, J.R., R.H. Brown, and W.R. Windham. 1983. Influence of leaf anatomy on the dry matter digestibility of C₃, C₄, and C₃/C₄ intermediate types of *Panicum* species. *Crop Sci.* 23:141–146.
- Zeiders, K.E. 1984. Helminthosporium spot blotch of switchgrass (*Panicum virgatum*) in Pennsylvania USA. *Plant Dis.* 68:120–122.
- Zheng-Xing, Shen, D.J. Parrish, D.D. Wolf, and G.E. Welbaum. 2001. Stratification in switchgrass seed is reversed and hastened by drying. *Crop Sci.* 41:1546–1551.