RELATIONSHIP OF DEVELOPMENTAL MORPHOLOGY AND CANOPY ARCHITECTURE IN SWITCHGRASS TILLER POPULATIONS TO DRY MATTER YIELD AND FIBER QUALITY

by

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RELATIONSHIP OF DEVELOPMENTAL MORPHOLOGY AND CANOPY ARCHITECTURE IN SWITCHGRASS TILLER POPULATIONS TO DRY MATTER YIELD AND FIBER QUALITY

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The ability to genetically manipulate dry matter (DM) yield and in vitro DM disappearance (IVDMD) has been demonstrated with switchgrass (*Panicum virgatum* L.). The objectives of this research were to determine if phenotypic selection for increased DM yield and IVDMD in six switchgrass populations altered relationships of canopy architecture and developmental morphology with DM yield and fiber quality. The study was conducted on a Sharpsburg silty clay loam (fine, smectitic, mesic, Typic Argiudoll) near Mead, NE and on a Webster silty clay loam (fine-loamy, mixed, mesic, Typic Haplaquoll) near Ames, IA during 1993 in a randomized complete block design with four replications at each location. Tiller populations were harvested on 9 June, 19 July, and 27 August at Ames, IA and on 10 June, 27 July, and 26 August at Mead, NE. Tillers were separated into morphological components and combined by primary growth stage, with DM yield and fiber quality determined on the morphological components and on a derived whole-plant basis. Genotype x environment (G x E) interactions occurred for forage yield and tiller density. Additional collared leaves and stem internodes developed in some populations to explain yield increases when tiller densities were similar; however, dry weight contributions of morphological components and canopy traits were stable across environments. Selection for increased DM yield and IVDMD apparently altered

morphological changes within the sward, but had no effect on whole-plant fiber quality. True digestibility (TD) was relatively stable across environments, although the leaf blades of the highest ranking population based on TD in a vegetative sward were not higher than the other populations in the reproductive swards. Thus, leaf to stem ratio may have no value for predicting TD at later sward maturities. Phenotypic selection for increased DM yield and IVDMD in selected switchgrass populations induced changes in canopy architecture which helped explain observed genotype and G x E interactions for DM yield and TD of individual morphological components.

INTRODUCTION

Warm-season grasses are important components of livestock feeding systems in the Central Great Plains. These grasses are valuable forage resources during the summer months when cool-season grasses are not productive and low in quality. Additionally, switchgrass (*Panicum virgatum* L.) is one of the most promising species for biomass fuel production. The cumulative effects of genetics and environment interact and are expressed in the developmental morphology and phenology of grass plants and thus affect both potential yield and fiber quality. Genotype x environment (G x E) interactions, including location and harvest date, exist for yield and forage quality in switchgrass populations. Because G x E interactions are significant, multiple location studies are necessary to properly evaluate sward growth and development and fiber quality.

As a grass plant matures, canopy architecture, dry matter (DM) partitioning, and fiber composition change. Canopy architecture is a term including, but not limited to, plant and tiller demographics, leaf area index, leaf mean tilt angle, leaf blade length and width, and stem internode length. Canopy architecture changes are due to cellular division in the intercalary meristematic regions that result in lengthening and widening of the leaves. Intercalary meristematic regions located above and below the internodes cause the internodal region to elongate. These changes result in increased leaf area and increased canopy height. Plant maturity is the primary determinant of forage quality within a species. Likewise, DM partitioning is affected similarly by the same changes in plant maturity. Dry matter accumulations of the morphological components comprising each tiller will increase,

but the contributions made by each component will vary due to the different rates of DM accumulation which also affects fiber quality.

Leaf and stem characteristics may not be correlated well enough with forage quality to be useful in genotypic selection. However, quantification of plant growth and development may be useful for prediction of yield and TD. Mean stage weight accounted for virtually all of the variation for both fiber concentration and in vitro DM disappearance (IVDMD) in alfalfa (*Medicago sativa* L.). However, maturity indices did not predict forage quality adequately in all plant components of red clover (*Trifolium pratense* L.), timothy (*Phleum pratense* L.), and smooth bromegrass (*Bromus inermis* Leyss.). For native, perennial, warm-season grasses, stage of morphological development has been used to predict crude protein (CP) concentration and IVDMD in both switchgrass and big bluestem (*Andropogon gerardii* Vitman cv. Pawnee); however, fiber concentration was more variable.

The ability to manipulate yield and forage quality through phenotypic selection in switchgrass has been demonstrated. Populations have been derived for low- and high-IVDMD from the same base population as 'Trailblazer'. However, the effects of breeding for increased yield and digestibility on canopy architecture, DM partitioning, and fiber composition and digestibility have not been examined because they are indirectly associated with the overall phenotypic evaluation. In summary, many factors interact to define forage quality. The effects of genetics and environment control plant growth and development and subsequent forage quality.

Because switchgrass populations respond differently across locations and environments, selection of specific genotypes for a given management scheme is

essential to ensure maximum productivity. Determination of the developmental morphology effects on canopy architecture and resulting partitioning of DM yield and fiber quality of switchgrass populations is needed for effective management. This study was structured as an indepth investigation of the genotype and G x E study previously reported by Hopkins et al. (1995) using 20 switchgrass strains. More specifically, six subset strains were used to represent the extent of variation that existed for forage yield and forage quality and also strains that showed significant G x E responses.

The objectives of this research were to determine the effects of canopy architecture and developmental morphology of tiller populations from six switchgrass populations known to differ in DM yield or IVDMD, to evaluate canopy architecture as a potential selection criterion in a forage breeding program, and to investigate the effects on fiber quality of morphological components within tillers of primary growth stages and study the relationship with fiber quality of six switchgrass populations selected for increased DM yield and digestibility.

Chapters 1 and 2 are written to conform to the style and guidelines set by the Agronomy Journal. Chapter 3 is written to conform to the style set by Crop Science.

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CHAPTER 1

LITERATURE REVIEW

CULTIVAR DEVELOPMENT

Vogel and Sleper (1994) indicated that forage digestibility of genotypes adapted to their region of use should behave similarly in terms of digestibility over the life of the stand. Forage quality for ruminants can be improved by breeding plants for increased in vitro dry matter (DM) disappearance (IVDMD). Higher digestibility can be accomplished by selection for increased concentrations of cell solubles and/or digestible fiber. If selections are based solely on cell soluble concentration or digestible fiber, the indigestible fiber fraction must not increase or progress will be negated. In switchgrass (*Panicum virgatum* L.), low digestibility has been a primary concern. Improving forage quality has become a major focus for forage breeding projects. Vogel et al. (1981) showed that it was possible to select for increased or decreased IVDMD without any decrease in DM yield. In a subsequent 3-year grazing evaluation, Anderson et al. (1988) found that the genotype selected for increased IVDMD led to a 24% improvement in animal gain and seasonal gains of 311 kg ha^{-1}. The high-IVDMD selection was released subsequently as 'Trailblazer' (Vogel et al., 1991) which was similar in maturity and adaptation to 'Pathfinder' (Newell, 1968), but with increased IVDMD. In other switchgrass germplasm, Godshalk at al. (1988a) demonstrated sufficient variation in fiber concentration within a switchgrass population with high enough heritability to make breeding progress. Godshalk et al. (1988b) also reported that fiber concentration decreased in a

switchgrass population selected for high-IVDMD using N concentration and DM yield as covariates.

The increase in IVDMD observed in the development of Trailblazer has been attributed to changes in cell wall composition. Gabrielson et al. (1990) found that Trailblazer had lower *p*-coumaric acid and a higher ferulic / *p*-coumaric acid ratio than the low-IVDMD strain. Differences in fiber constituents and ferulic acid were not apparent or were inconsistent with the observed strain differences in IVDMD. They concluded that alkali-labile cell-wall phenolic composition was heritable and genetically correlated with IVDMD. Fritz et al. (1991) hypothesized that genotypic selection for higher IVDMD decreased ammonia-labile bonds. They found that ammoniation increased both the rate and extent of fiber digestion, but concluded that genetic improvement in switchgrass was not due to decreasing the number of ammonia-labile bonds.

GROWTH AND DEVELOPMENT

Elementary Morphology

Moore and Moser (1995) defined developmental morphology as the changes occurring during the growth and maturity of an organism. These changes include cellular division, differentiation, and growth. The developmental morphology of perennial grass plants includes distribution of many tillers, which often have different primary growth stages within the sward (Moore and Moser, 1995). Among grass species, similar patterns exist for morphological development. Sward communities

are composed of tillers from individual plants (Briske, 1991), with a phytomer being the basic unit of growth of a tiller (Hyder, 1972; Briske, 1991).

Individual phytomers consist of a leaf blade, leaf sheath, stem internode and node, and the associated axillary bud (Briske, 1991). A tiller is comprised of a series of nodes and internodes, with the leaf sheath attached to the stem at each node and the leaf blade located at the upper end of the sheath. Vegetative shoots produce an infinite number of phytomers, whereas reproductive shoots are determinate (Hyder, 1972; Langer, 1979). Growth proceeds by cellular division in the apical meristem and intercalary meristems located at the nodes and at the base of the leaf blade and leaf sheath. The apical meristem, or growing point, is the region of rapidly dividing cells and is composed of leaf primordia and undifferentiated phytomers. Movement of the leaf blade, leaf sheath, and internode is additive. Consequently, the leaf blades, sheaths, and internodes emerge in a telescopic manner from the growing point of the plant, with the intercalary meristematic tissue at the base of each leaf blade responsible for leaf blade length and width. Likewise, cellular division in the intercalary meristematic region in the base of the leaf sheath causes the sheath to grow upward around the pseudostem. This process occurrs simulataneously with leaf blade and stem elongation. Following differentiation of the reproductive structures, phytomer elongation ceases.

Once the leaf collar has emerged, leaf growth is complete; however, leaves emerging early are usually more narrow than those emerging later (Nelson and Larson, 1984). For an elongating tiller, more energy is required to support cellular

division in the growing point rather than leaf expansion (Brown, 1984). Leaf elongation in vegetative tillers is slower than in reproductive tillers (Parsons and Robson, 1980). Leaf blade length is typically longer if the whorl of leaves through which the leaf blade extended is longer. As the leaf blade and leaf sheath increase in length, the leaf tip emerges through the whorl (Nelson and Larson, 1984). Following culm elongation, additional lengthening of the stems occurs from growth in the intercalary meristems located at the base of the internodes (Briske, 1991).

Canopy Architecture

Canopy architecture is defined by changes that occur in plant and tiller demography (Briske, 1991), leaf area index, leaf mean tilt angle, leaf blade length and width, and canopy height (Welles and Norman, 1991), which typically relates to the distribution of positions, areas and shapes of the leaves, stems, and inflorescences. Leaf area index (LAI), leaf mean tilt angle, foliage density, and estimates of canopy arrangement have often been used to describe canopy architecture. Brougham (1958) suggested that inter- and intra-species variation in LAI would be evident as the growing season progressed. When water and nutrients were not limiting, competition for light was the primary factor determining growth (Donald, 1963). Competition for light occurred as the leaves of one plant cast a shadow on another, or as one leaf shaded another leaf within the same plant.

Perennial ryegrass (*Lolium perenne* L.) cultivars with longer leaves had a higher LAI than other cultivars (Rhodes, 1969) resulting in higher yield potentials

(Rhodes, 1969; 1975). Rhodes (1968; 1971) found that perennial ryegrass cultivars with erect foliage were more productive than cultivars with lax leaves. Light entering a canopy of erect leaves was spread over a larger photosynthetic area than prostrate cultivars resulting in a higher photosynthetic efficiency. Allard et al. (1991) and Kephart et al. (1992) observed that shaded leaves were longer, thinner, and more narrow than those grown in full sunlight.

Tillering

Although apical dominance may not directly control tiller development, its effect on canopy architecture must be noted. Apical dominance of older tillers is a process that can control the development of new tillers in a grass plant and it is a hormonal response mechanism. It must be suppressed or moderated in order for new tillers to emerge. Once shoot growth of existing tillers is terminated by removal of the apical meristem, new tiller growth can be generated from tiller buds located in the crown of the plant (Jewiss, 1972).

The generation of new tillers has a dual function in a perennial grass sward. The first role is to maintain the ability of plants in the sward to produce more tillers if a portion of the original plant population declines. Langer et al. (1964) found that a decline in plant numbers of timothy (*Phleum pratense* L.) and meadow fescue (*Festuca pratensis* Huds.) resulted in increased tiller numbers per plant. This increase allows tiller number per unit area to be maintained. Cooper (1948) observed that closely spaced perennial ryegrass plants stopped tillering before more widely-spaced

plants.

The second feature of tiller replacement is the regeneration of growth following removal of growing tillers. Krause and Moser (1977) showed that removal of approximately 67% of the elongated tillers in irrigated smooth bromegrass (*Bromus inermis* Leyss.) increased tillering by suppressing the apparent apical dominance. Lamp (1952) noted two distinguishable tillering episodes in first-growth smooth bromegrass. The first tillering event occurred during stem elongation, with a more active tillering episode following anthesis. These multiple tillering events have not been noted for switchgrass. Thus, sward canopies are comprised of tiller populations that ranged in maturity (Moore et al., 1991).

Developmental Morphology

Several growth staging systems have been developed to describe plant growth. These staging systems were species specific and applicable only to annual grain crops (Large, 1954; Ritchie et al., 1989; Simmons et al., 1985; Vanderlip, 1979). A quantitative system developed by Haun (1973) for wheat (*Triticum aestivum* L.) growth only described vegetative development through culm elongation. One system for classifying perennial growth of temperate grasses was developed by Simon and Park (1983) based on a previous system described by Zadoks et al. (1974) for cereal grasses. The system described by Simon and Park (1983) was modified to account for distinctive growth stages common in perennial grasses.

The ability to accurately quantify stage of morphological development is

necessary for proper forage management. Gillen and Ewing (1992) found that day of the year and accumulated growing degree days equally predicted leaf development including number of leaves per tiller in big bluestem (*Andropogon gerardii* Vitman var. *gerardii* Vitman) and little bluestem [*Schizacharium scoparium* (Michx.) Nash]. These researchers concluded that soil water content, plant competition, genetic composition, and past and present grazing management may exert more influence on plant developmental morphology than growing degree day accumulation. Kalu and Fick (1981) found that it was possible to determine weekly changes in developmental morphology of alfalfa (*Medicago sativa* L.) on either a mean stage by count (MSC) or a mean stage by weight (MSW) basis.

Staging systems have been developed to quantify growth stages of perennial forage grasses (Moore et al., 1991; Sanderson, 1992; West, 1990). Grass growth is comprised of four primary growth stages: (i) vegetative, (ii) elongation, (iii) reproductive, and (iv) seed ripening (Moore et al., 1991). The growth staging system proposed by Moore et al. (1991) may be widely applicable to cool- and warm-season perennial forage grasses. Mitchell et al. (1992), using the system proposed by Moore et al. (1991), found that either growing degree day or day of the year could be used to predict developmental morphology of switchgrass and big bluestem. Hendrickson (1992) found that day of the year and growing degree day accumulation equally predicted plant development in prairie sandreed [*Calamovilfa longifolia* (Hook.) Scribn.] and sand bluestem [*Andropogon gerardii* Vitman var. *paucipilus* (Nash.) Fern]. Sanderson (1992) proposed a maturity index for use with determinate and