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Canopy Structure and Neutral Detergent Fiber Differences among Temperate Perennial Grasses

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ABSTRACT

Intake of animals grazing grass pasture is in part influenced by canopy density. Our objective was to determine the vertical distribution of dry matter and neutral detergent fiber (NDF) within temperate perennial grass swards. The study was conducted in 2004 and 2005 on a Plano silt loam (fine-silty, mixed, superactive, mesic Typic Argiudolls). When leaf height of each grass reached 25 cm in spring, summer, and fall, canopy layers were harvested from 20 to 25, 15 to 20, and 10 to 15 cm. Differences in canopy density were usually not significant when precipitation was below normal. With abundant spring precipitation, quackgrass [*Elymus repens* (L.) Gould] had greater upper canopy density (1.9 mg dry matter [DM] cm^{-3}) than any of the other grasses studied. Grasses typically grazed at shorter heights such as bluegrass (*Poa pratensis* L.) and perennial ryegrass (*Lolium perenne* L.) had greater density in the lower canopy layer (1.0–1.3 g DM kg^{-1}). While soft-leaf tall fescue (*Festuca arundinacea* Schreb.), reed canarygrass (*Phalaris arundinacea* L.), and meadow fescue (*Festuca pratensis* Huds.) had lower density in the upper canopy than timothy (*Phleum pratense* L.) and quackgrass in the spring, the reverse was true in the summer. Herbage NDF of grasses generally increased from the upper to lower canopy layer (mean difference of 50 g kg^{-1}); perennial ryegrass and meadow fescue often had the lowest NDF throughout the canopy (range of 392–452 and 418–469 g kg^{-1}, respectively). Pasture intake may benefit from a diverse species composition because animals can graze a mixture having optimum density and NDF throughout the canopy.

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Abbreviations: DM, dry matter; NDF, neutral detergent fiber.

Canopy structure can be defined as the distribution and arrangement of aboveground plant parts within a community, including the weight and percentage contribution of these parts to the sward, and their spatial and angular distribution (Rhodes and Collins, 1993). While canopy structure strongly influences the photosynthetic capacity of a plant community (Monsi et al., 1973; Sheehy and Cooper, 1973), the structure of a pasture canopy can also have a large impact on herbage intake by grazing animals (Barrett et al., 2003). Individual bite weight of a grazing animal is a product of bite volume and canopy density (Casey and Brereton, 1999), which is influenced by canopy height, tiller density, proportion of leaf and stem, and physical characteristics of the leaf such as the angle of attachment to the tiller, dimensions, and rigidity (Rhodes and Collins, 1993; Duru et al., 2004). The canopy structure of grasses also influences the energy required to graze them (Griffiths and Gordon, 2003; Illius et al., 1995).

Due to its productivity, forage quality, and prevalence in major grazed temperate grasslands, the canopy structure of perennial ryegrass (*Lolium perenne* L.) has probably been studied more than any other forage grass species. Rhodes (1971a) found significant differences in vertical distribution of leaf area index within the canopy strata of two contrasting perennial ryegrass cultivars, which he suggested was the reason for a differential response of cultivars to cutting frequency. Selection for contrasting combinations of leaf rigidity and tiller angle demonstrated that ryegrass productivity under

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frequent cutting was greatest in genotypes with greater leaf area index in the basal layers of the canopy (Rhodes, 1971b). Within a ryegrass canopy, dry matter (DM) and chemical composition vary as well. From the upper (>15 cm) to the lower layer (0–5 cm), Delagarde et al. (2000) reported vertical gradients in DM (increase of 80 g kg^{-1} fresh grass), crude protein (decrease of 100 g kg^{-1} organic matter), and neutral detergent fiber (NDF, increase of 250 g kg^{-1} organic matter). Depending on the ploidy (diploid vs. tetraploid) and maturity (early, intermediate, or late), Gilliland et al. (2002) noted significant differences in canopy structure (proportion of lamina, green leaf mass, sward and tiller height, and bulk density) and herbage nutritive value (water-soluble carbohydrate concentration and proportion of linoleic and α-linolenic fatty acids).

The relationship between canopy structure and intake by grazing animals has been established in both cattle and sheep. McGilloway et al. (1999) reported that sward height was the principal determinant of bite weight in lactating dairy cows grazing perennial ryegrass, but that the influence of sward bulk density on intake became greater as sward height declined. Casey and Brereton (1999) reported similar findings when the bulk density of perennial ryegrass was altered by removing tillers; bite weight increased as sward height and density increased and the effect of height was greater than that of density. The effect of sward density, however, increased as sward height decreased. In sheep, pasture intake was related to sward height when tiller density was constant, and to bulk density at similar sward height (Black and Kenney, 1984).

Although pasture intake is influenced primarily by DM allowance, NDF of available pasture has relevance in grazing-based dairy systems because it is negatively associated with potential intake (Vazquez and Smith, 2000). The general role of NDF in the diet of dairy cows was described by Mertens (1997): if the forage consumed has excessive NDF, energy density may be low and intake and productivity may be reduced. Thus, the amount of dietary fiber can have an impact on pasture utilization.

Depending on management goals and pasture composition, practitioners of managed intensive rotational grazing typically have a target sward height at which they begin and end grazing. For tall-growing temperate grasses, current recommendations suggest that grazing begin at a 25-cm height and end when a 10-cm stubble is reached (Undersander et al., 2002). Given these criteria, the objective of this study was to determine seasonal differences in canopy density and NDF among temperate grasses common to the Midwest and Northeast USA.

MATERIALS AND METHODS

The study was conducted in 2004 and 2005 at the University of Wisconsin's Arlington Agricultural Research Station (43.30°N, 89.35°W) on a Plano silt loam (fine-silty, mixed, superactive, mesic Typic Argiudolls). Mean and monthly precipitation during the experiment are presented in Fig. 1. Mean daily soil temperature at 5-cm depth is presented in Fig. 2. The site had a pH of 6.5, 52 mg kg^{-1} P, and 117 mg kg^{-1} K (Bray P1). In April 2003, 'Park' Kentucky bluegrass (*Poa pratensis* L., KBG), 'Mara' perennial ryegrass (PRG), 'Bronc' orchardgrass (*Dactylis glomerata* L., OGR), 'Itasca' timothy (*Phleum pratense* L., TIM), 'Johnstone' tall fescue (*Festuca arundinacea* Schreb., TFK), 'Barolex' soft-leaf tall fescue (TFS), 'Bartura' meadow fescue (*Festuca pratensis* Huds., MDF), 'Lincoln' smooth bromegrass (*Bromus inermis* Leyss., SBG), 'Rival' reed canarygrass (*Phalaris arundinacea* L., RCG), and common quackgrass [*Elymus repens* (L.) Gould, QGR] were broadcast seeded in 4.56- by 6.08-m plots on a prepared seedbed. The seeding rate for each species was the following: bluegrass, 16.8 kg ha^{-1}; perennial ryegrass, 28 kg ha^{-1}; orchardgrass, 11.2 kg ha^{-1}; timothy, 9.0 kg ha^{-1}; tall and meadow fescue, 11.2 kg ha^{-1}; smooth bromegrass, 17.9 kg ha^{-1}; reed canarygrass, 6.7 kg ha^{-1}; and quackgrass, 22.4 kg ha^{-1}. Plots were separated by 1-m alleys of 'Phoenix' turf-type tall fescue and were arranged in a randomized complete block design with four replicates. Plots were clipped to a 10-cm stubble and fertilized with 56 kg N ha^{-1} as NH_4NO_3 in June and August 2003.

Before spring grass growth began, plots were mowed to remove residue in early April 2004 and 2005 and fertilized with 56 kg N ha^{-1} as NH_4NO_3. The canopy structure of primary spring growth was sampled in mid-May by a stratified clipping method (Rhodes and Collins, 1993) using a 25- by 100-cm aluminum quadrat supported by four cylindrical legs. Each leg passed through a circular ring welded to the corners of the quadrat. The circumference of each leg was grooved at 5.0-cm

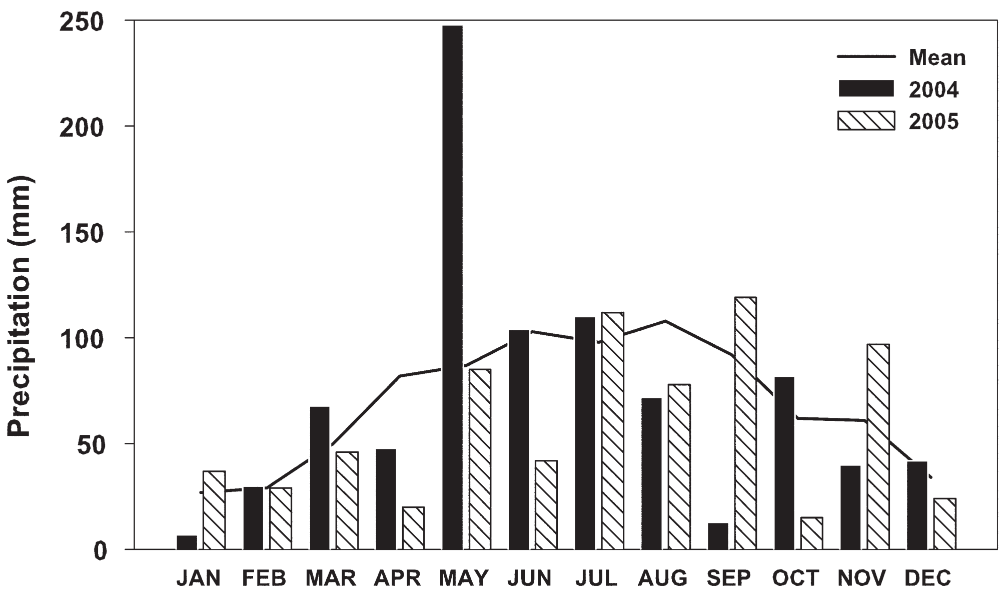

Figure 1. Monthly precipitation during 2004 and 2005, and 30-yr mean at Arlington, WI.

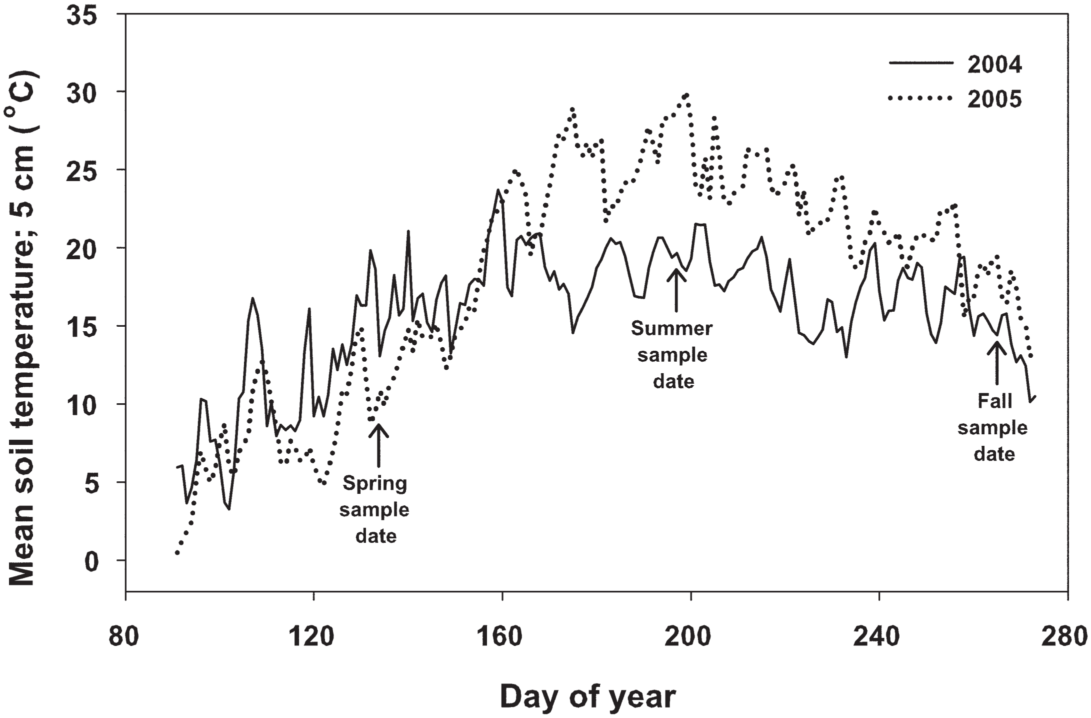

Figure 2. Mean daily soil temperature at 5-cm depth during the experiment at Arlington, WI, and mean sampling date of grasses in 2004 and 2005.

increments and a spring-loaded ball detent was imbedded in each corner ring, allowing the quadrat to slide vertically on the legs between grooves and remain stationary at a specific height. When the mean nonextended leaf height of each grass species reached 25 cm, the frame was placed in two random locations in the plot and the quadrat set at 20-cm height. Herbage within the quadrat above this height was grasped by hand and harvested with hand clippers; at no time did leaves of one canopy stratum extend into a lower stratum. The quadrat was subsequently lowered to 15 cm and then to 10 cm, and the harvesting process repeated. Herbage from the same canopy layer within a plot was placed in a paper bag, dried at 65°C for 48 h, and weighed. After all grasses were sampled in the spring, plots were clipped to a 10-cm stubble and permitted to grow for approximately 21 d, at which time plots were again clipped to a 10-cm stubble and fertilized with 56 kg N ha^{-1} as NH_4NO_3. The canopy structure of the regrowth was sampled in mid-July (summer) as described above. Plots were managed after the summer sampling in a manner similar to that following the spring sampling before canopy structure was measured in late September (fall). Spring, summer, and fall sampling periods will be referred to as *seasons*.

Herbage from each layer was ground to pass a 1-mm screen in a Wiley mill. Samples were analyzed for NDF concentration by calibrated near-infrared reflectance spectroscopy. The NDF of calibration samples was measured by the method of Mertens (2002) using 600-mL beakers. Calibration statistics for NDF were the following: standard error of prediction corrected for bias [SEP(C)] = 1.1, R^2 = 0.98.

Canopy structure was expressed as canopy layer density (mg DM cm^{-3}). Density and NDF were analyzed by analysis of variance using a split-plot-in-time model (Steel et al., 1997). Block and year were assumed to be random effects, while species and season were assumed to be fixed effects. Means for each grass were compared using Fisher's LSD ($P \leq 0.05$).

RESULTS AND DISCUSSION

Canopy layer density and NDF were analyzed by year and by season (spring, summer, fall) due to significant ($P \leq 0.05$) year × grass and season × grass interactions. Not all grasses were present during each season of each year; precipitation, temperature, and apparent winter injury in two cases had marked effects on grass growth and persistence. Due to below-normal precipitation in August and September of 2004 (Fig. 1), Kentucky bluegrass, perennial ryegrass, timothy, and smooth bromegrass produced insufficient growth in the fall. Perennial ryegrass and smooth bromegrass also suffered apparent injury during the 2004–2005 winter. Although smooth bromegrass stands were inadequate for sampling in 2005, perennial ryegrass plots were uniformly recovered by the fall of 2005. Timothy produced inadequate growth for sampling in the summer of 2005, and as others (Riesterer et al., 2000) observed for the Midwest region, quackgrass produced little growth during the late summer and fall, and was not sampled either year.

Canopy Layer Density

Quackgrass is regarded as a noxious weed in cropping systems, but it is considered a valuable early season forage in temperate grazing systems (Asay and Jensen, 1996). Its potential value in pasture settings was observed here as well; quackgrass had greater density (1.89 mg DM cm^{-3}) in the upper canopy layer (20–25 cm) than any other grass in the spring of 2004 (Fig. 3). When sampled at 25-cm height, the leaf blades of quackgrass appeared to droop, whereas the leaf blades of the other grasses were more rigid in either the horizontal or vertical position. Quackgrass canopy density was also greater than all grasses except Kentucky bluegrass, smooth bromegrass, and timothy in the middle canopy layer (15–20 cm). Because of the influence of canopy density on bite weight of a grazing animal (Casey and Brereton, 1999), this density advantage over other grasses would have a significant, positive effect on intake. In the lower canopy layer (10–15 cm), however, grasses commonly exhibiting a more prostrate growth habit (Kentucky bluegrass and perennial ryegrass) had greater density in the spring of 2004 than all grasses except quackgrass (Fig. 3). Kentucky bluegrass and perennial ryegrass are often grazed at a shorter initial height and more closely than the other grasses. Because the influence of canopy density on intake becomes greater as sward height declines (McGilloway et al., 1999; Casey and Brereton, 1999), intake of these more prostrate grasses may differ little from that of other grasses if livestock are forced to graze to a 10-cm stubble.

Orchardgrass is one of the most widely adapted perennial temperate grasses (van Santen and Sleper, 1996) and is found in managed pastures across the Midwest and Northeast. In the spring of 2004, the upper layer canopy density of orchardgrass (0.80 mg DM cm^{-3}) was similar to that of all other grasses except quackgrass, bluegrass, and timothy (Fig. 3). The ranking of orchardgrass density relative to the other grasses, however, became lower in successively lower portions of the canopy. At the lower canopy layer (10–15 cm), orchardgrass had lower density than all grasses except meadow fescue.

Precipitation during the early spring of 2005 (Fig. 1) was below normal and mean daily soil temperature (Fig. 2) was generally lower than that in 2004. These conditions probably explain why few differences in canopy layer density were measured among grasses in the spring of 2005, although the general ranking of grasses within a canopy layer tended to be similar to that within the same layer in 2004. Kentucky bluegrass had the greatest density in the 20- to 25-cm layer, but no significant differences were found among the other grasses in this layer, or among a majority of grasses in the 15- to 20- or 10- to 15-cm layers (Fig. 3). As might be expected, canopy density appears to have the same sensitivity to the effects of environment as total herbage yield.

Ranking of grasses for the upper canopy layer density in the summer of 2004 differed considerably from the spring. While soft-leaf tall fescue, reed canarygrass, and meadow fescue had lower density in the upper canopy layer (20–25 cm) than timothy and quackgrass in the spring (Fig. 3), the reverse was true in the summer (Fig. 4). With the exception of reed canarygrass, which consisted primarily of pseudostem tissue in the middle and lower canopy layers, soft-leaf tall fescue and meadow fescue also had greater density from 15 to 20 and 10 to 15 cm than all grasses except Kentucky bluegrass and perennial ryegrass. Despite favorable precipitation (Fig. 1) and temperature (Fig. 2) conditions during the summer of 2004, the canopy density of orchardgrass in all layers was significantly lower than that of any other grass (Fig. 4).

Before the summer sampling occurred in July 2005, precipitation was below normal (Fig. 1). All grasses

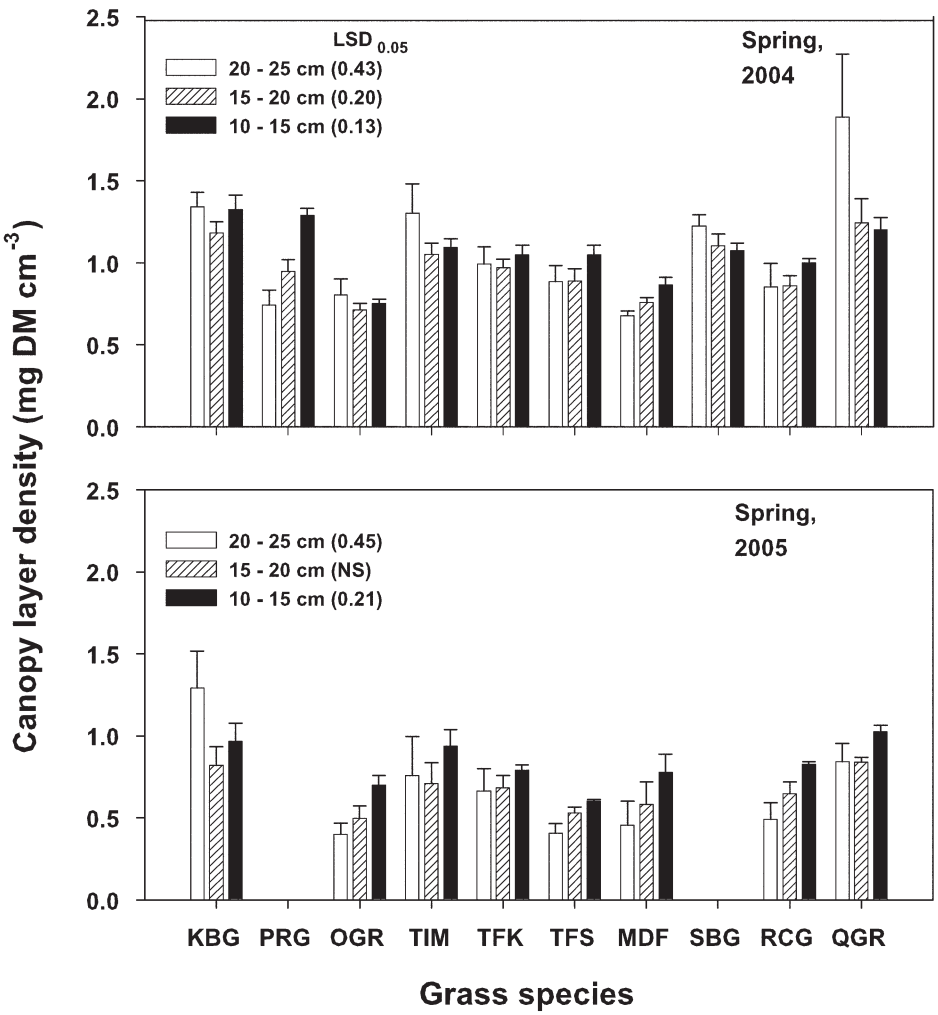

Figure 3. Dry matter density of vertical canopy layers within temperate perennial grasses (KBG, Kentucky bluegrass; PRG, perennial ryegrass; OGR, orchardgrass; TIM, timothy; TFK, Kentucky 31-type tall fescue; TFS, soft-leaf tall fescue; MDF, meadow fescue; SBG, smooth bromegrass; RCG, reed canarygrass; QGR, quackgrass) in the spring of 2 yr. Error bars indicate one standard error.

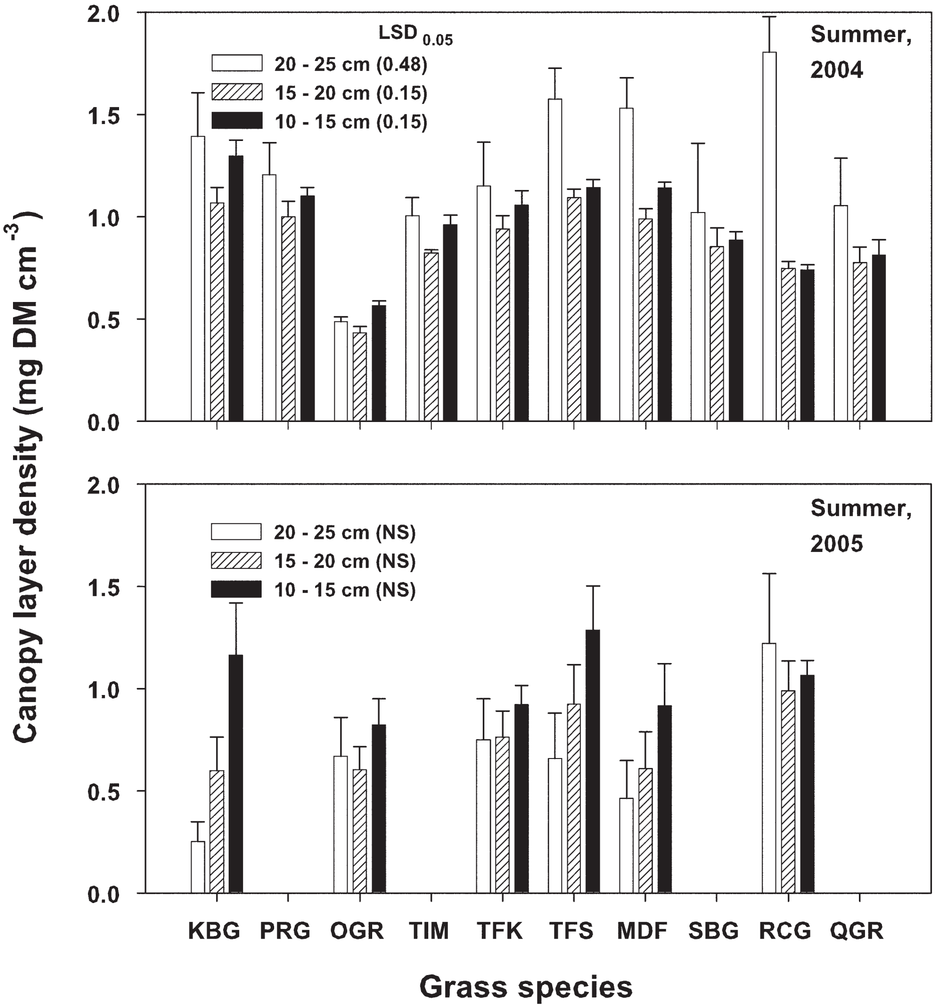

Figure 4. Dry matter density of vertical canopy layers within temperate perennial grasses (KBG, Kentucky bluegrass; PRG, perennial ryegrass; OGR, orchardgrass; TIM, timothy; TFK, Kentucky 31-type tall fescue; TFS, soft-leaf tall fescue; MDF, meadow fescue; SBG, smooth bromegrass; RCG, reed canarygrass; QGR, quackgrass) in the summer of 2 yr. Error bars indicate one standard error.

appeared drought stressed and growth across the plot was variable, which probably explains the lack of density differences among grasses within a particular canopy layer (Fig. 4). Reduced temperate grass productivity during the summer, referred to as the "summer slump" (Balasko and Nelson, 2003), is common in much of the Midwest and Northeast USA, and is more typical than conditions observed in 2004.

Unlike the spring and summer, the pattern of vertical DM distribution in the fall generally increased from the top to the bottom of the canopy in both years, probably due to decreased day length that increased tillering (Leopold, 1949). Tall fescue is noted for its fall growth and suitability as a stockpiled grass (Riesterer et al., 2000). Superior fall growth relative to the other grasses was reflected in the density of soft-leaf tall fescue in 2004 and Kentucky 31-type tall fescue in 2005, particularly in the middle and lower canopy layers (Fig. 5). When precipitation was more abundant before sampling in 2005 than in 2004 (Fig. 1), however, several grasses produced sufficient growth for sampling that were not sampled the previous year. For example, the upper layer density of orchardgrass was greater than that of any grass except soft-leaf tall fescue, and the middle and lower layer density of perennial ryegrass was equivalent to or greater than any grass (Fig. 5).

Canopy Layer Neutral Detergent Fiber

Within each season and year, the ranking of all grasses for NDF and the relative difference between any two grasses were generally similar within all three layers of the canopy. The general pattern was an increase in NDF from the upper to the lower canopy layer, the same pattern Sanderson et al. (2006) observed in both simple and complex grass–legume mixtures. Our results suggest that, unlike canopy density, an analysis of the total herbage or of any portion of the canopy would be suitable for comparing NDF differences among these grasses when grown in monoculture.

In the spring of both years, Kentucky bluegrass had greater NDF throughout the canopy than any other grass (Table 1). In a pasture environment, Kentucky bluegrass is typically grazed at a lower initial height than the height at which it was harvested in this experiment (25 cm), and the herbage would consist primarily of leaves. When harvested at 25-cm height, stems were present in each canopy layer of bluegrass in the spring, which increased total NDF (Karn et al., 2006). In contrast, perennial ryegrass, the other grass typically grazed at a lower initial height, had the lowest NDF throughout the canopy in 2004 due to its inherently high forage quality relative to other temperate grasses (Jung et al., 1996). Among the remaining, more erect grasses, smooth bromegrass had greater NDF in the upper and middle layers than all grasses except quackgrass, while meadow fescue had lower NDF throughout the canopy than any grass except reed canarygrass in the spring of 2004 (Table 1). The lower NDF of meadow fescue may explain why Casler et al. (1998) found that apparent intake of meadow fescue grass and tall fescue was similar despite a significant advantage in available forage by endophyte-free tall fescue. With the exception of Kentucky bluegrass, however, these results were not repeated in the spring of

2005, when few differences in NDF existed among the grasses.

Similar to the results measured in the spring, Kentucky bluegrass NDF was greater than that of any grass in all canopy layers in the summer of 2004, ranging from 511 g kg^{-1} at the top of the canopy to 596 g kg^{-1} at the bottom (Table 2). Among the other grasses, reed canarygrass NDF was greater than all grasses except orchardgrass in the upper and middle layers of the canopy. As in the spring, the presence of stems or pseudostems in Kentucky bluegrass and reed canarygrass, respectively, contributed to increased NDF relative to the other grasses. With the exception of smooth bromegrass, which had the lowest NDF in the upper layer, few differences in NDF existed among the other grasses in any layer. In the summer of 2005, below-normal precipitation (Fig. 1) had the same effect on NDF as canopy density (Fig. 4): few if any differences in NDF existed among the grasses in any canopy layer (Table 2).

Among the grasses that were sampled in the fall of both years (Kentucky 31-type and soft-leaf tall fescue, orchardgrass, and meadow fescue), meadow fescue had the lowest NDF throughout the canopy (Table 3). When adequate growth was produced the following year, however, the NDF of reed canarygrass, perennial ryegrass, and timothy was similar to or less than that of meadow fescue in all canopy layers.

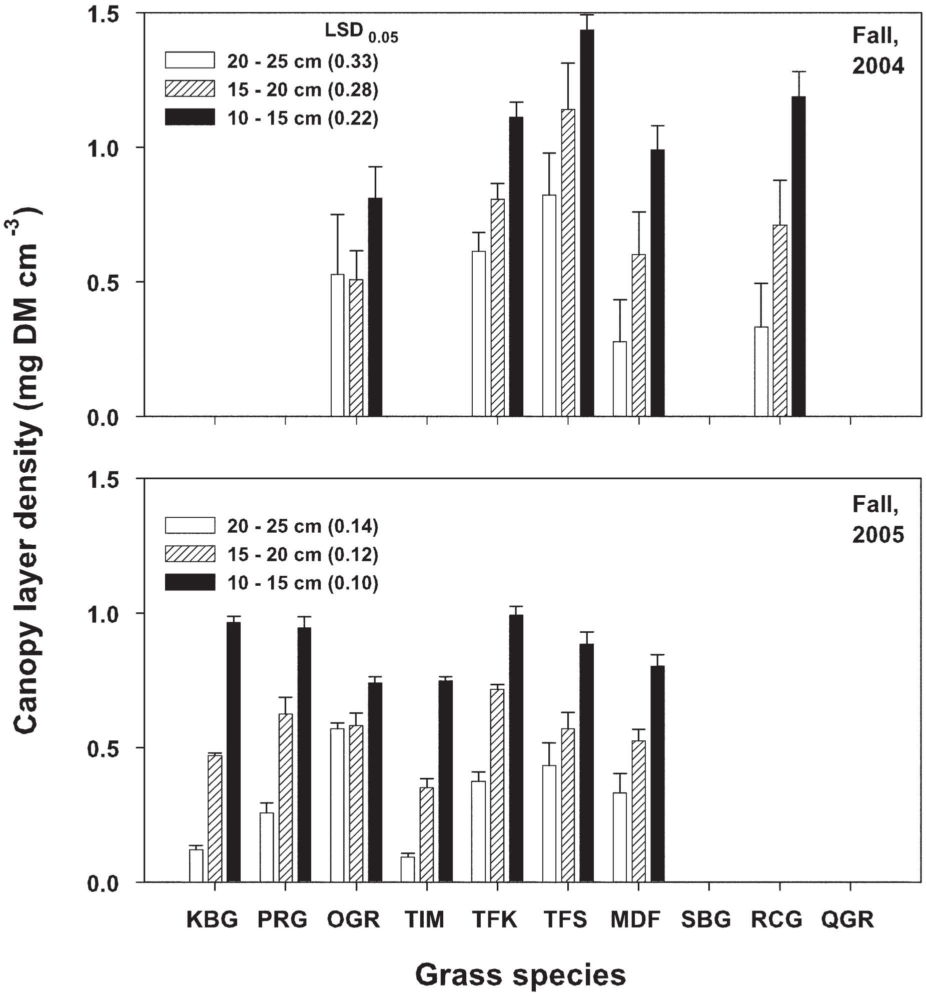

Figure 5. Dry matter density of vertical canopy layers within temperate perennial grasses (KBG, Kentucky bluegrass; PRG, perennial ryegrass; OGR, orchardgrass; TIM, timothy; TFK, Kentucky 31-type tall fescue; TFS, soft-leaf tall fescue; MDF, meadow fescue; SBG, smooth bromegrass; RCG, reed canarygrass; QGR, quackgrass) in the fall of 2 yr. Error bars indicate one standard error.

CONCLUSIONS

The results of this study indicate that temperate grasses commonly used for pasture in the Midwest and Northeast USA differ in canopy layer density and NDF. Like total herbage yield, canopy density and NDF are impacted by both season and the environmental conditions within a season, the most apparent change being a shift in the pattern toward greater density in lower canopy layers during the fall. In addition, apparent differences in canopy layer density among grasses were most evident under good growing conditions (summer, 2004), but were not significant under dry conditions (summer, 2005).

Studies of perennial ryegrass have demonstrated that canopy structure significantly influences herbage utilization by grazing animals. Differences in canopy density translate practically into differences in available forage,

Table 1. Neutral detergent fiber of vertical canopy layers within 10 temperate perennial grasses in the spring of 2 yr.

Grass	Neutral detergent fiber					
	2004			2005		
	20–25 cm	15–20 cm	10–15 cm	20–25 cm	15–20 cm	10–15 cm
	g kg^{-1}					
Kentucky bluegrass	585	603	608	533	522	522
Perennial ryegrass	405	427	444	–†	–†	–†
Orchardgrass	468	492	526	404	417	438
Timothy	460	501	524	447	462	473
Tall fescue	440	486	517	414	436	455
Tall fescue (soft-leaf)	470	507	519	399	420	442
Meadow fescue	425	465	486	399	424	454
Smooth bromegrass	492	535	541	–†	–†	–†
Reed canarygrass	457	480	493	402	436	454
Quackgrass	478	517	539	430	451	462
LSD(0.05)	15	20	16	18	16	21
SEM	2.6	3.5	2.8	3.1	2.6	3.6

†Insufficient stand to permit sampling.

Table 2. Neutral detergent fiber of vertical canopy layers within 10 temperate perennial grasses in the summer of 2 yr.

Grass	Neutral detergent fiber					
	2004			2005		
	20–25 cm	15–20 cm	10–15 cm	20–25 cm	15–20 cm	10–15 cm
	g kg^{-1}					
Kentucky bluegrass	511	572	596	497	483	517
Perennial ryegrass	410	454	487	–†	–†	–†
Orchardgrass	448	498	522	490	481	524
Timothy	424	450	474	–‡	–‡	–‡
Tall fescue	435	482	526	536	525	556
Tall fescue (soft-leaf)	427	486	509	461	468	481
Meadow fescue	410	468	497	478	455	468
Smooth bromegrass	385	436	485	–†	–†	–†
Reed canarygrass	465	521	549	509	508	548
Quackgrass	427	481	520	–‡	–‡	–‡
LSD(0.05)	22	32	27	NS§	32	40
SEM	3.8	5.6	4.7	8.7	5.3	6.6

†Insufficient stand to permit sampling.

‡Insufficient growth to permit sampling.

§NS = no significance in terms of difference among means.

Table 3. Neutral detergent fiber of vertical canopy layers within 10 temperate perennial grasses in the fall of 2 yr.

Grass	Neutral detergent fiber					
	2004			2005		
	20–25 cm	15–20 cm	10–15 cm	20–25 cm	15–20 cm	10–15 cm
	g kg^{-1}					
Kentucky bluegrass	–†	–†	–†	493	494	552
Perennial ryegrass	–†	–†	–†	362	382	426
Orchardgrass	439	479	512	433	473	520
Timothy	–†	–†	–†	419	413	466
Tall fescue	480	486	518	430	446	482
Tall fescue (soft-leaf)	456	450	474	463	474	507
Meadow fescue	408	422	451	390	417	459
Smooth bromegrass	–†	–†	–†	–‡	–‡	–‡
Reed canarygrass	387	405	456	–†	–†	–†
Quackgrass	–†	–†	–†	–†	–†	–†
LSD(0.05)	17	22	23	15	19	16
SEM	2.7	3.6	4.1	2.4	3.2	2.6

†Insufficient growth to permit sampling.

‡Insufficient stand to permit sampling.

which, depending on the extent to which a pasture is utilized, is positively associated with pasture intake (Holden et al., 1994) due to greater DM intake per bite (Casey and Brereton, 1999). Neutral detergent fiber concentration of herbage, however, is also a determinant of dietary intake because cell walls contribute to rumen fill (Jung and Allen, 1995). Depending on the season, differences in canopy layer NDF among grasses often exceeded the 50 g kg^{-1} threshold necessary to produce a tangible effect on an animal's dietary intake (D.R. Mertens, personal communication, 2006). For all grasses, the general pattern of increasing NDF from the upper to the lower canopy layer implies lower intake potential as animals are forced to graze lower in the canopy. Thus, pastures with a diversity of particular species may benefit not only in terms of total herbage production (Sanderson et al., 2005), but also in terms of potential intake because animals may graze a forage mixture having optimum density and NDF throughout the canopy.

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