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Alkali-Labile Cell-Wall Phenolics and Forage Quality in Switchgrasses Selected for Differing Digestibility

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ABSTRACT

Alkali-labile cell-wall phenolics have been implicated in previous research as factors that affect forage digestibility by ruminants. Alkali-labile cell-wall phenolics, in vitro dry matter digestibility (IVDMD), neutral-detergent fiber (NDF), acid-detergent fiber (ADF), lignin (permanganate-oxidation), and crude protein (CP) were determined in three switchgrass (*Panicum virgatum* L.) strains differing genetically for IVDMD to determine relationships between these quality parameters and IVDMD during the grazing season. Grazed (upper 1/3 of grazed plants) and ungrazed (whole plants in caged exclosures) forage was collected weekly from replicated 0.4-ha pastures of 'Trailblazer' (high IVDMD), 'Pathfinder', and a low-IVDMD strain during three grazing seasons from 1983 to 1985. The principal alkali-labile phenolics (g kg^{-1} NDF) detected were *p*-coumaric acid (PCA) and ferulic acid (FA). Increased PCA concentration due to increased maturity averaged >70% during each grazing season and corresponded with increased NDF, ADF, and lignin and decreased IVDMD, CP, and FA/PCA ratio. Ferulic acid concentration either declined slightly or remained unchanged. Averaged across 3 yr, Trailblazer had higher ($P < 0.06$) IVDMD, lower ($P < 0.09$) PCA and higher ($P < 0.10$) FA/PCA ratio than a divergently selected low-IVDMD strain. Differences between strains in detergent-fiber constituents, FA, and CP were either not apparent or inconsistent with strain differences in IVDMD. Results were consistent with both grazed and ungrazed switchgrass and indicate that alkali-labile cell-wall phenolic composition in switchgrass is heritable and genetically correlated to IVDMD.

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LIGNIFICATION is associated with reduced forage digestibility (Moore and Mott, 1973; Cowling, 1975; Jung and Vogel, 1986) and poor animal performance (Duble et al., 1971), although the precise mechanism by which this control is exerted is unclear. Some studies (Van Soest, 1973; Cowling, 1975) suggest that lignin functions to physically prevent accessibility of digestive enzymes. Other evidence (Hartley, 1972; Morrison, 1974; Gaillard and Richards, 1975) indicates that lignin is chemically linked to cell-wall carbohydrates, which also limit digestion.

In grasses, lignin may be partitioned into core and noncore fractions (Hartley, 1972; Gordon, 1975). Core lignin arises from three phenylpropanoid monomers (*p*-coumaryl, coniferyl, and sinapyl alcohols), which are interconnected in varying proportions and random sequences, primarily through C–C bonds and ether linkages (Harkin, 1973). Noncore lignin consists mainly of ester-linked PCA and FA (Hartley, 1972).

Information pertaining to changes in noncore lignin components during forage maturation and their relationship to cell-wall fiber constituents and forage digestibility is limited. Most studies have examined legumes and cool-season grasses (Hartley and Jones, 1977; Burritt et al., 1984; Scalbert et al., 1985); however comparable research involving temperate warm-season forage grasses, such as switchgrass, has not been reported.

Vogel et al. (1981) described the progress achieved in improving switchgrass IVDMD following one cycle of divergent selection. Although the high- and low-IVDMD strains resulting from this work were similar in maturity and forage yield, differences in IVDMD were significant. Subsequent research (Vogel et al.,

1984) indicated that hay quality of the high- and low-IVDMD strains and Pathfinder switchgrass was comparable when using the detergent system of analysis (Goering and Van Soest, 1970). Similar results with these same strains were obtained by Anderson et al. (1988) for herbage collected during grazing trials with yearling cattle (*Bos taurus*). However, superior average daily gains were obtained for animals grazing the high-IVDMD strain (Trailblazer). Ward et al. (1989) showed that there was not any differential selectivity by esophageal-fistulated steers grazing these grasses. These studies indicate that differences among switchgrass strains for IVDMD and animal performance are not adequately explained by the detergent-system forage-quality parameters. It is possible that selection for increased IVDMD in switchgrass breeding programs may alter alkali-labile cell-wall phenolic composition and thereby contribute to improved fiber digestion in ruminants.

The objectives of this study were to (i) determine the effect of maturity on alkali-labile cell-wall phenolics (i.e., noncore lignin), forage fiber constituents, and crude protein in grazed and ungrazed switchgrass and (ii) determine if the genetic differences among the switchgrass strains described previously for IVDMD are associated with differences in alkali-labile lignin phenolics.

MATERIALS AND METHODS

The study was conducted during three grazing seasons from 1983 through 1985 at the University of Nebraska Agricultural Research and Development Center near Mead, NE. In 1981, three switchgrass strains, Trailblazer, Pathfinder and a low-IVDMD type (Vogel et al., 1981), were established in 12 0.4-ha pastures in a randomized complete-block arrangement with four replicates per strain. Soil type, planting procedures, stocking rates, and grazing periods were as previously described (Anderson et al., 1988). In 1984, a forage selectivity trial was conducted that utilized beef yearlings and mature, crossbred, esophageal-fistulated steers (Ward et al., 1989). In that study, grazing was initiated on 1 June and terminated 6 August; however, animal performance data were not compiled.

Throughout these grazing trials (Anderson et al., 1988; Ward et al., 1989), the animals selectively grazed the top one-third of the canopy. Therefore, forage samples designated as grazed were randomly clipped at ~ 1-wk intervals from the upper one-third of the grazed plants within each pasture. Sampling periods were initiated and terminated each year to coincide with the first and last day of grazing, respectively. In 1984 and 1985, ungrazed forage samples also were collected using caged exclosures following the same clipping schedule as above. Four exclosures, measuring 1.2 by 1.5 by 1.5 m, were randomly placed within each pasture. On each sampling date, a forage subsample within the exclosures was clipped to a 7.5-cm stubble height and composited. Clipped plants within an exclosure were not resampled. The cages were relocated within the pastures each year. Forage samples were collected from four replicates during 1983; however, in 1984 and 1985, only two pasture replicates of each forage strain were used, due to a limited number of available exclosures. Samples were dried in paper bags at 55 °C in a forced-draft oven, ground to pass a 1-mm screen in a Wiley[1] mill, and stored in plastic vials at room temperature until analyzed.

Estimates of forage digestibility (IVDMD) used the two-stage method of Tilley and Terry (1963) with minor modifications ($HgCl_2$ and Na_2Co_3 were not added after the first step). The rumen fluid was a mixture taken from two fistulated steers maintained on separate diets of alfalfa (*Medicago sativa* L.)–smooth bromegrass (*Bromus inermis* Leyss.) hay or ground corn (*Zea mays* L.) cobs. Crude protein (N × 6.25) was determined following the Kjeldahl procedure (AOAC, 1975). Neutral-detergent fiber, ADF, and lignin (permanganate-oxidation) concentration were sequentially determined as described by Van Soest and Robertson (1980).

Alkali-labile phenolics were extracted from air-dried NDF residues (0.5 g) in 1 *M* NaOH (20 mL) (Hartley, 1972). The residue was agitated in a water bath at 20 °C for ~ 20 h, filtered through a coarse-porosity sintered glass crucible, and washed thoroughly with distilled water. The filtrate was immediately acidified to pH 2.5 using 6 *M* HCl and diluted to 100 mL with distilled water. A Sep-Pak (Waters Associates, Milford, MA) C_{18}–bonded cartridge[1] was used to prepare each sample extract for analysis. The cartridge was pre-wetted by passing 5 mL of methanol through the column followed by 10 mL of distilled water. The cartridge was loaded with a 2-mL aliquot of the acidified sample extract and washed with 10 mL of distilled water to remove aqueous contaminants. Phenolics were eluted from the cartridge in 2 mL methanol and diluted to 6 mL with a 0.87-*M* acetic acid solution. Phenolic compounds were separated by high-performance liquid chromatography (HPLC) using a Bio-Rad Gradient Module system equipped with a Model 1305 ultraviolet (UV) monitor (Bio-Rad Laboratories, Richmond, CA). Separation of the phenolics was accomplished isocratically using a Bio-Rad C_{18} ODS-5S reversed-phase column with a water/glacial acetic acid/methanol (67:3:30) solvent phase. The flow rate was 1 mL min^{-1} and UV detection was at 280 nm. Isolated phenolics were quantified against known standards using a Hewlett-Packard Model 3392A integrator (Hewlett-Packard Co., Sunnyvale, CA).

Switchgrass is a strongly determinate plant in which maturation occurs primarily in response to changing photoperiod but can be modified by temperature (Vogel et al., 1985). Therefore, days of the year were used to quantify maturity. Sampling began when the forage was in an early vegetative growth stage and continued until panicle emergence (plants in caged exlosures). Regression analysis (combined strains) was used to quantify relationships between individual forage quality parameters and maturity (days of the year). Since sampling dates were different each year, the linear regression coefficients relating each quality parameter to maturity were used to compare responses across years. Finally, IVDMD values were separately regressed on cell-wall constituent values, using linear and quadratic models to quantify these relationships.

An analysis of variance (ANOVA) using sampling dates as treatments was conducted each year to test for differences among quality parameter means at the different sampling dates. Values used in the ANOVA for each parameter at each sampling date were the means of the three switchgrass strains for each pasture replicate.

An ANOVA was performed on individual quality parameters to compare switchgrass strains within each sample date each year. Quality parameters also were analyzed on an annual basis using a split-plot design in which switchgrass strains served as mainplots and sample dates served as subplots. Similarly, a combined ANOVA, with strains as mainplots and years as subplots, was used to compare responses across the 3-yr study.

RESULTS AND DISCUSSION

Maturity Effect

Alkali-labile phenolics detected in the switchgrass forage consisted of (i) protocatechuic acid, (ii) *p*-hy-

[1] Names of products are included for the benefit of the reader and do not imply endorsement by the USDA or the University of Nebraska.

droxybenzoic acid, (iii) *p*-hydroxybenzaldehyde, (iv) vanillin, (v) *p*-coumaric acid (PCA), and (vi) ferulic acid (FA). However, the first four were detected only in trace amounts relative to PCA and FA and varied little throughout the grazing season. Therefore, only the results for PCA and FA are reported. As expected, forage quality was higher in the grazed forage (Table 1) than in the ungrazed forage (Table 2) throughout each season, presumably due to a relatively higher proportion of leaves in these samples. As the switchgrass matured and leafiness declined, differences in forage composition between the grazed and ungrazed forage were less pronounced. The effect of maturity on all quality parameters was significant ($P < 0.01$) in both forage treatments each year except for FA concentration, which exhibited an inconsistent response (Fig. 1). Increases in PCA were substantial, particularly during 1983 and 1984, and corresponded to declines in the FA/PCA ratio. The phenolic values at the later stages of maturity are similar to those reported

Table 1. Forage quality constituents and lignin phenolic acids of grazed† switchgrass during three grazing seasons at Mead, NE.

Year	Day of the year	Means‡							
		IVDMD	CP	NDF	ADF	Lignin	FA	PCA	FA/PCA
		g kg^{-1} dry matter					g kg^{-1} NDF		
1983	160	728	184	620	281	27	3.3	2.1	1.62
	171	676	144	680	346	37	3.6	3.4	1.05
	181	699	140	647	332	33	3.3	3.4	0.99
	195	651	114	667	344	41	3.3	3.5	0.94
	203	616	102	666	345	42	3.2	4.0	0.81
	210	576	86	696	369	52	3.1	5.2	0.62
	216	576	98	687	369	60	3.6	5.8	0.62
LSD (0.01)		31	12	34	33	20	NS	1.2	0.18
1984	152	734	191	666	289	31	4.2	2.8	1.53
	159	714	171	703	323	37	3.6	3.4	1.12
	169	677	153	693	344	35	3.9	4.0	0.97
	177	664	137	708	365	35	3.6	4.5	0.83
	183	634	123	719	369	36	3.5	4.5	0.78
	190	626	112	742	385	47	4.1	6.2	0.67
	197	613	88	778	402	52	3.7	6.8	0.54
	204	562	71	770	409	56	3.4	6.4	0.54
	211	535	69	772	411	55	3.6	6.8	0.53
	218	485	63	778	429	60	3.0	6.6	0.45
LSD (0.01		37	6	35	22	20	NS	1.2	0.30
1985	151	636	151	698	320	32	6.6	6.2	1.08
	157	626	141	692	332	31	7.1	6.7	1.06
	164	618	109	694	651	37	6.8	7.1	0.97
	170	574	104	726	383	48	4.4	7.4	0.60
	178	582	96	734	379	45	5.6	7.7	0.73
	184	546	81	719	385	45	5.1	7.9	0.65
	191	481	69	760	399	53	4.4	8.3	0.54
	198	518	77	792	432	57	5.0	9.1	0.56
LSD (0.01)		40	18	32	21	9	0.7	1.8	0.17

† Forage clipped from the upper one-third of grazed plants.
‡ Values represent the mean of three switchgrass strains. IVDMD = in vitro dry matter digestibility, CP = crude protein, NDF = neutral detergent fiber, ADF = acid detergent fiber, FA = ferulic acid, PCA = *p*-coumaric acid, and FA/PCA = ratio of ferulic acid to *p*-coumaric acid.

Table 2. Forage quality constituents and lignin phenolic acids of ungrazed† switchgrass during two grazing seasons at Mead, NE.

Year	Day of the year	Means‡							
		IVDMD	CP	NDF	ADF	Lignin	FA	PCA	FA/PCA
		g kg^{-1} dry matter					g kg^{-1} NDF		
1984	152	724	185	696	305	34	4.1	3.1	1.36
	159	687	162	704	332	39	4.0	3.9	1.06
	169	644	130	723	369	40	3.5	4.7	0.75
	177	620	107	752	394	49	3.0	5.0	0.61
	183	605	92	756	413	49	3.3	5.9	0.56
	190	574	88	771	426	54	3.3	6.7	0.49
	197	512	68	793	451	63	3.0	7.2	0.43
	204	478	56	777	452	68	2.9	6.8	0.43
	211	503	63	776	441	63	3.0	6.8	0.44
	218	462	54	769	452	65	2.8	6.4	0.44
LSD (0.01)		39	17	43	31	19	0.8	1.5	0.30
1985	151	644	124	725	340	34	6.1	6.4	0.96
	157	617	117	728	352	37	5.6	6.4	0.87
	164	622	123	667	629	34	6.2	6.0	1.04
	170	586	124	693	351	39	6.0	6.7	0.92
	178	544	87	734	396	46	6.1	8.3	0.74
	184	567	95	702	364	42	6.6	8.1	0.82
	191	494	83	749	399	55	6.4	8.5	0.76
	198	531	77	757	431	57	6.8	8.6	0.80
LSD (0.01)		25	30	61	40	8	NS	1.4	0.27

† Whole plants collected from caged exclosures.
‡ Values represent the mean of three switchgrass strains. IVDMD = in vitro dry matter digestibility, CP = crude protein, NDF = neutral detergent fiber, ADF = acid detergent fiber, FA = ferulic acid, PCA = *p*-coumaric acid, and FA/PCA = ratio of ferulic acid to *p*-coumaric acid.

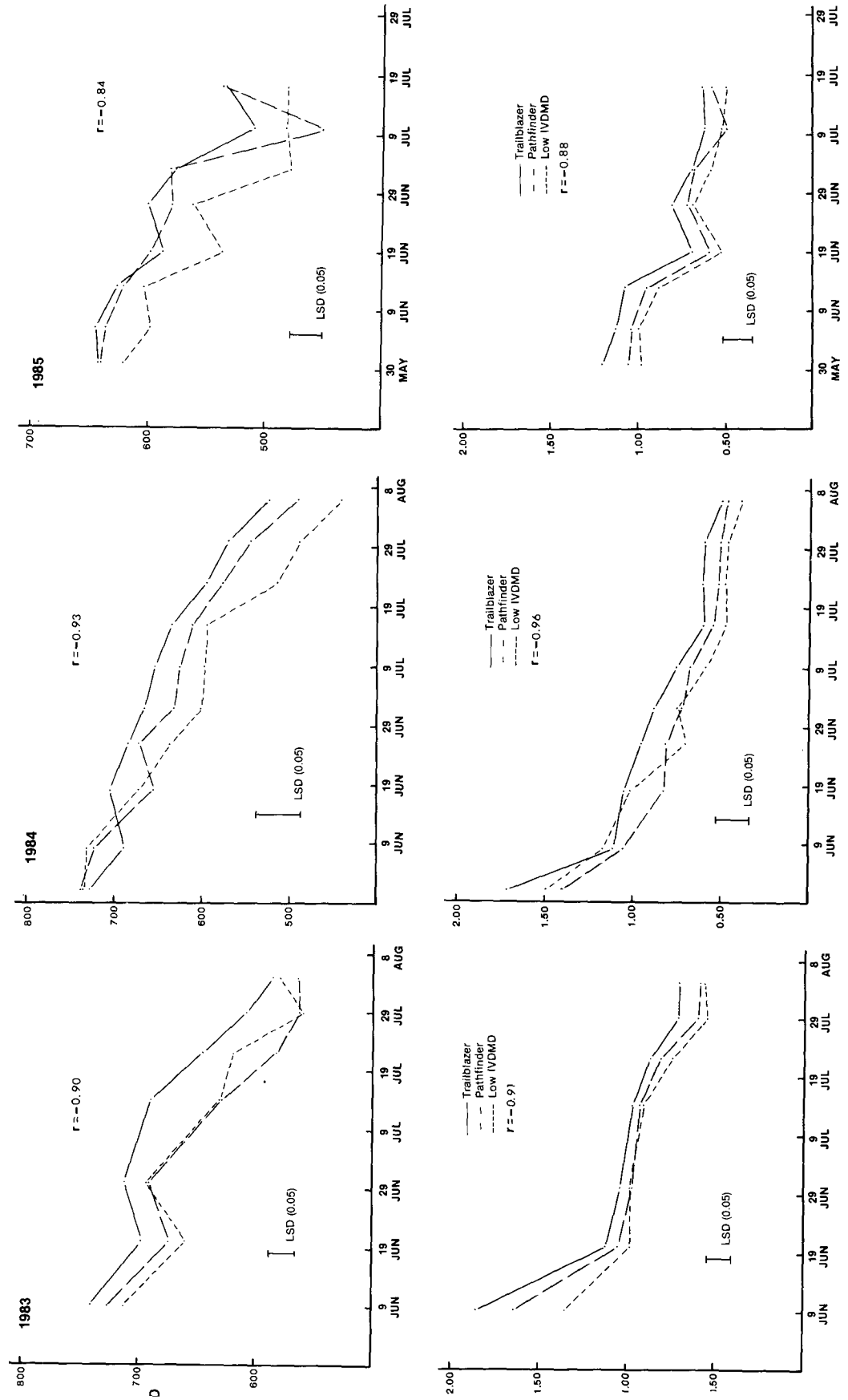

Fig. 1. In vitro dry matter digestibility (IVDMD) and ferulic acid/*p*-coumaric acid (FA/PCA) ratio in grazed switchgrass forage of three different strains during 1983, 1984, and 1985. Correlation coefficients (*r*) are for linear (IVDMD) and quadratic (FA/PCA) regressions with maturity, respectively, analyzed across strains. Note scale differences for IVDMD. The LSD is for comparison of strains within sampling dates.

by Cherney et al. (1988) for switchgrass harvested at a late stage of maturity. As expected, NDF, ADF, and lignin concentration increased with maturity, while IVDMD and CP declined.

Regression analysis of each forage-quality parameter with sampling dates indicated significant linear correlations ($r > 0.80$; $P < 0.001$) between each trait, except for FA, and maturity within both forage treatments each year (data not shown). Linear regression coefficients representing the daily rate of change for each quality parameter with maturity were used to compare responses between years (Table 3). The response of a few quality parameters indicated some variation across years, particularly within the grazed forage. This was especially evident for FA, which was correlated with maturity in some years and not in others. The slower rate of decline in IVDMD in the ungrazed forage during 1985 (Table 3) appears to reflect the relatively lower initial level of forage digestibility that occurred during the early portion of the grazing season in that year (Table 2).

Researchers (Hartley, 1972; Burritt et al., 1984) examining alkali-labile lignin phenolics in various species of maturing cool-season grasses have reported similar results; however, concentrations of PCA and FA appear to be greater in switchgrass. Burritt et al. (1984), observed that grass samples with high lignin concentration also contained high levels of PCA and low ratios of FA/PCA. In addition, increases in PCA concentration during growth were larger and more consistent than for FA. Accordingly, Akin (1982) found that PCA monomers were markedly more toxic than FA monomers to forage-degrading rumen microflora. Our results with switchgrass appear to support these findings, indicating that PCA is an important cell-wall constituent that may influence forage degradation in grasses.

In 1985, the quality of the switchgrass forage generally was lower than in previous years (Tables 1 and 2). This response may have resulted, in part, from the relatively warm temperatures that occurred during growth prior to the grazing period. The average day/night temperature during April and May was 22/10 °C in 1985, compared with an average of 18/5 °C for 1983 and 1984. In a study using controlled environments, Akin et al. (1987) reported that alkali-labile phenolic acids in fall fescue (*Festuca arundinacea* Schreb.) increased under increasing temperature regimens with a concomitant decrease in forage tissue degradation. In the present study, the average PCA and FA concentrations were > 60 and 55% higher, respectively, in the grazed forage during 1985 compared with the previous 2 yr, whereas NDF, ADF, and lignin changed very little. Crude protein and IVDMD values also were lower in 1985. A comparable response was observed in the ungrazed forage.

Linear responses were sufficient to describe relationships between most of the fiber constituents and IVDMD (Table 4). An exception to this was FA, which generally was not well correlated with forage digestibility. In vitro dry matter digestibility and the FA/PCA ratio tended to be quadratically related. This also was apparent for ADF and lignin content, although to a lesser extent. A plot of IVDMD v. FA/PCA (not shown) indicated that forage digestibility declined more rapidly at higher concentrations of PCA.

The apparent lack of relationship between FA concentration and IVDMD may be due, in part, to the chemical association of FA with other cell-wall components. Scalbert et al. (1985) reported that most of the alkali-labile phenolics extracted from isolated wheat (*Triticum aestivum* L.) straw lignin consisted of PCA, whereas ≤ 75% of the FA was ether linked and resistant to alkaline hydrolysis. In work with Italian ryegrass (*Lolium multiflorum* Lam.), Hartley and Jones (1976) suggested that FA exists, in part, as a dimer (i.e., diferulic acid) that is esterified between cell-wall carbohydrates and core lignin but remains intact when extracted with alkali or released by cel-

Table 3. Linear regression coefficients for individual forage quality constituents with sampling dates in grazed and ungrazed switchgrass forage at Mead, NE.

Year	Cell-wall constituent†							
	IVDMD	CP	NDF	ADF	Lignin	FA	PCA	FA/PCA
	g kg^{-1} dry matter d^{-1}					g kg^{-1} NDF d^{-1}		
				Grazed‡				
1983	−2.72	−1.57	0.93	1.19	0.50	0	0.054	−0.015
	(0.30)§	(0.12)	(0.22)	(0.20)	(0.06)	–	(0.006)	(0.002)
1984	−3.52	−2.03	1.75	1.95	0.46	0	0.065	−0.014
	(0.26)	(0.05)	(0.14)	(0.09)	(0.06)	–	(0.006)	(0.001)
1985	−3.09	−1.71	1.91	2.13	0.53	−0.05	0.055	−0.012
	(0.43)	(0.13)	(0.23)	(0.15)	(0.06)	(0.01)	(0.006)	(0.002)
				Ungrazed¶				
1984	−4.03	−1.99	1.32	2.26	0.52	−0.02	0.057	−0.013
	(0.21)	(0.11)	(0.17)	(0.18)	(0.05)	(0.004)	(0.008)	(0.001)
1985	−2.85	−1.10	0.86	1.83	0.49	0	0.060	−0.012
	(0.35)	(0.12)	(0.35)	(0.24)	(0.07)	–	(0.009)	(0.002)

† Regression coefficients were determined using the mean values of three switchgrass strains. Weekly sampling coincided with early vegetative growth stage to panicle emergence each year. IVDMD = in vitro dry matter digestibility, CP = crude protein, NDF = neutral detergent fiber, ADF = acid detergent fiber, FA = ferulic acid, PCA = *p*-coumaric acid and FA/PCA = ratio of ferulic acid to *p*-coumaric acid.

‡ Forage clipped from the upper one-third of grazed plants.

§ Values in parentheses are the standard errors (±) of the regression coefficients.

¶ Whole plants collected from caged exclosures.

lulase digestion. These observations, and the inconsistent relationship between FA concentration and maturity observed in the present study, suggest that extraction methods based on alkaline hydrolysis may not accurately assess the role of FA in fiber degradation processes. However, our results indicate that PCA concentration increases substantially in switchgrass cell walls with maturity and may negatively influence forage digestibility.

Table 4. Coefficients of determination† for cell-wall constituents with in vitro dry matter digestibility in grazed and ungrazed switchgrass during three grazing seasons at Mead, NE.

Cell-wall constituent	1983		1984		1985	
	Linear	Quadratic	Linear	Quadratic	Linear	Quadratic
			Grazed§			
NDF‡	0.64**	NS	0.67**	NS	0.58**	NS
ADF	0.67**	0.74*	0.83**	0.90**	0.69**	NS
Lignin	0.74**	NS	0.70**	NS	0.69**	NS
FA	NS	NS	0.35**	NS	0.64**	NS
PCA	0.81**	NS	0.67**	NS	0.72**	NS
FA/PCA	0.76**	0.88**	0.74**	0.88**	0.76**	0.83**
n	21	21	30	30	24	24
			Ungrazed¶			
NDF			0.69**	NS	0.30**	NS
ADF			0.86**	NS	0.66**	NS
Lignin			0.86**	NS	0.66**	0.86**
FA			0.37**	NS	NS	NS
PCA			0.71**	NS	0.69**	NS
FA/PCA			0.74**	0.85**	0.55**	NS
n			30	30	24	24

, * Significant at the 0.05 and 0.01 probability levels, respectively.
† Correlations were determined using the mean values of three switchgrass strains.
‡ NDF = neutral detergent fiber, ADF = acid detergent fiber, FA = ferulic acid, PCA = *p*-coumaric acid, FA/PCA = ratio of ferulic acid to *p*-coumaric acid, and *n* = sample size.
§ Forage clipped from the upper one-third of grazed plants.
¶ Whole plants collected from caged exclosures.

Genetic Effects

Performance of cattle grazing these pastures and the IVDMD of the strains over the grazing season for 1983 and 1985 have been previously reported (Anderson et al., 1988). The objective of this portion of the study was to determine if the previously reported genetic differences among the switchgrass strains for IVDMD is associated with genetic difference in FA and PCA concentration of the forages. The three strains in this study were all developed from the same germplasm source and consistently flower on the same date in eastern Nebraska (Vogel et al., 1981; Vogel et al, 1984). Hence, the three strains are similar in phenological development throughout the growing season, so any differences among strains for quality traits on a sample are not due to maturity differences.

In vitro dry matter digestibility was consistently higher in Trailblazer than in Pathfinder and the low-IVDMD strain as previously reported by Anderson et. al. (1988), (Tables 5 and 6). Lower PCA concentrations and high FA/PCA ratios were associated with high forage digestibility. This was particularly evident in both forage sampling treatments when these parameters were considered across all grazing seasons; however, differences in PCA concentration were less apparent when switchgrass strains were compared within grazing seasons. Some variation in FA concentration also occurred; however, responses among

Table 5. Forage quality constituents in three grazed† switchgrass strains during three grazing seasons at Mead, NE.

Strain	Cell-wall constituents‡							
	IVDMD	CP	NDF	ADF	Lignin	FA	PCA	FA/PCA
	g kg^{-1} dry matter					g kg^{-1} NDF		
				1983				
Trailblazer	669	127	662	338	41	3.5	3.7	1.04
Pathfinder	633	119	672	347	43	3.4	4.0	0.94
Low-IVDMD	636	125	664	338	40	3.2	4.0	0.87
LSD	17	6	–	–	–	0.3	–	0.14
Signif. level§	0.01	0.06	NS	NS	NS	0.01	NS	0.02
				1984				
Trailblazer	649	117	727	368	40	3.8	4.9	0.88
Pathfinder	627	119	738	371	44	3.4	5.0	0.76
Low-IVDMD	602	116	734	378	49	3.8	5.6	0.75
LSD	–	2	–	–	6	–	–	–
Signif. level§	NS	0.10	NS	NS	0.10	NS	NS	NS
				1985				
Trailblazer	591	105	728	370	42	6.0	7.2	0.85
Pathfinder	581	106	725	370	43	5.5	7.5	0.76
Low-IVDMD	546	99	727	377	46	5.4	7.8	0.71
LSD	33	–	–	–	3	–	–	0.11
Signif. level§	0.07	NS	NS	NS	0.05	NS	NS	0.08
				1983-1985				
Trailblazer	635	117	706	359	41	4.4	5.3	0.92
Pathfinder	614	115	712	362	43	4.1	5.5	0.82
Low-IVDMD	595	113	708	364	45	4.1	5.8	0.78
LSD	29	2	3	–	–	0.3	0.4	0.10
Signif. level§	0.06	0.05	0.10	NS	NS	0.04	0.09	0.01

† Forage clipped from the upper one-third of grazed plants.
‡ IVDMD = in vitro dry matter digestibility, CP = crude protein, NDF = neutral detergent fiber, ADF = acid detergent fiber, FA = ferulic acid, PCA = *p*-coumaric acid, and FA/PCA = ratio of ferulic acid to *p*-coumaric acid.
§ Significance level of the *F* test for treatment means.

switchgrass strains were inconsistent between grazed and ungrazed forages.

During 1984 and 1985, the average lignin concentration in the grazed forage was significantly ($P \leq 0.10$) lower in Trailblazer than in the low-IVDMD strain. A similar response was not apparent in the ungrazed forage or when lignin concentration was considered across all grazing seasons. In grazed forage, CP content was highest in Trailblazer when averaged across all grazing seasons. However, CP differences between strains in 1983 and 1984 were inconsistent with differences in IVDMD, and no differences in CP content were observed in the ungrazed forages. Strain differences in detergent-fiber constituents were not apparent or were unrelated to differences in IVDMD.

Previous studies with these same switchgrass strains documented comparable responses in both hay (Vogel et al., 1984) and grazed forage (Anderson et al., 1988) when using the detergent system of analysis. Vogel et al. (1984) observed small differences in NDF between these strains, suggesting that improvement in the IVDMD of Trailblazer switchgrass was due, in part to a decrease in cell-wall concentration. The results reported by Anderson et al. (1988) and those observed in this study (Tables 1 and 2) indicate that detergent-fiber components do not account for the observed differences in IVDMD. Ehlke et al. (1986) reached a similar conclusion following evaluation of NDF and ADF concentrations in divergent populations of smooth bromegrass genotypes selected for increased IVDMD; however, lignin concentration was a major limiting factor to IVDMD. Evidence for a similar effect of lignin concentration on IVDMD among the switchgrass strains in our study was indicated only in the grazed forage (Table 5).

Researchers evaluating alkali-labile phenolics in other forage grasses (Hartley, 1972; Chaves et al., 1982; Burritt et al., 1984) have reported that high levels of PCA and low FA/PCA ratios are associated with low forage digestibility. The responses observed in our study seem to support these findings, although strain differences for these quality parameters were not always detected (Tables 5 and 6). Ferulic acid concentration did not appear to be related to strain differences in IVDMD, suggesting a less important role of this cell-wall constituent in fiber digestion processes. In in vitro digestion studies investigating the effect of phenolic monomers on orchardgrass (*Dactylis glomerata* L.), Akin (1982) found that FA was markedly less toxic than PCA to forage-degrading rumen microflora. Other studies (Azuma et al., 1985; Scalbert et al., 1985) suggest that FA resides in a different structural environment than PCA within the cell wall, indicating a differential susceptibility of these compounds to alkaline hydrolysis.

In general, decreases in strain IVDMD followed a linear trend throughout each grazing season, whereas FA/PCA ratios exhibited a curvilinear response, declining more rapidly early in the season (Figures 1, 2, and 3). A significant ($P < 0.05$) strain × date interaction for IVDMD occurred among the grazed forages during 1983 and 1985; however, this appeared to be attributable to measured responses at only one or two sampling dates. Strain × date interactions were not detected for the FA/PCA ratio. Except for a few dates, the strains ranked similarly (Trailblazer > Pathfinder > low-IVDMD) for IVDMD and the FA/PCA ratio during the grazing season for each of the 3 yr of this study.

During grass growth, increases in both PCA and lignin concentration occur which may result in increased esterified cross-linkages between lignin and cell-wall carbohydrates (Hartley, 1972; Mueller-Harvey et al., 1986). Recent studies (Sawai et al., 1983; Jung and Sahlu, 1986) have demonstrated that cellulose degradation is significantly depressed by esterified cinnamic

Table 6. Forage quality constituents in three ungrazed† switchgrass strains during two grazing seasons at Mead, NE.

Strain	Cell-wall constituents‡							
	IVDMD	CP	NDF	ADF	Lignin	FA	PCA	FA/PCA
	g kg^{-1} dry matter					g kg^{-1} NDF		
				1984				
Trailblazer	594	100	746	398	52	3.3	5.3	0.71
Pathfinder	582	101	759	410	52	2.9	5.2	0.61
Low-IVDMD	567	101	750	402	53	3.7	6.3	0.66
LSD	20	–	9	8	–	0.6	0.9	–
Signif. level§	0.05	NS	0.01	0.10	NS	0.06	0.08	NS
				1985				
Trailblazer	588	106	722	372	40	6.4	7.1	0.92
Pathfinder	577	104	718	367	44	6.2	7.1	0.90
Low-IVDMD	561	101	717	372	44	6.0	7.8	0.77
LSD	19	–	–	–	–	–	–	0.12
Signif. level§	0.10	NS	NS	NS	NS	NS	NS	0.01
				1984-1985				
Trailblazer	591	103	734	385	46	4.9	6.2	0.82
Pathfinder	580	102	739	388	48	4.5	6.2	0.75
Low-IVDMD	564	101	734	387	49	4.9	7.1	0.71
LSD	11	–	–	–	–	0.2	0.6	0.06
Signif. level§	0.01	NS	NS	NS	NS	0.05	0.07	0.10

† Whole plants collected from caged exclosures.
‡ IVDMD = in vitro dry matter digestibility, CP = crude protein, NDF = neutral detergent fiber, ADF = acid detergent fiber, FA = ferulic acid, PCA = *p*-coumaric acid, and FA/PCA = ratio of ferulic acid to *p*-coumaric acid.
§ Significance level of the *F* test for treatment means.

acids. This response is probably due to a physical inhibition that restricts cellulase accessibility into the cell-wall matrix. In addition, free cinnamic acids such as PCA, which are released from the cell wall during digestion, may subsequently exert toxic effects on forage-degrading microorganisms (Akin, 1982; Akin and Rigsby, 1985; Varel and Jung, 1986).

Trailblazer and the low-IVDMD strain were divergently selected from the same population for differences in IVDMD. The results reported here indicate that correlated responses for PCA content and the FA/PCA ratio occurred as a result of this selection, indicating that these traits are heritable in switchgrass and that they are genetically correlated to IVDMD. A possible explanation for this correlated response is that the variation in PCA may have been responsible, in part, for the observed differences in IVDMD among the switchgrass strains.

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