Temporal and Vertical Distribution of Nonstructural Carbohydrate, Fiber, Protein, and Digestibility Levels in Orchardgrass Swards

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ABSTRACT

Herbage nonstructural carbohydrates (NC) contribute to livestock performance and silage fermentation. Knowledge of the distribution patterns of NC and other nutritional constituents in orchardgrass (*Dactylis glomerata* L.) swards could support harvest management decisions. Our objective was to determine diurnal and vertical patterns of total NC (TNC), crude protein (CP), and neutral detergent fiber (NDF) concentrations, and in vitro true dry matter digestibility (IVTDMD) and NDF digestibility (NDFD) in orchardgrass swards in October, June, and August. Herbage was sampled at 6-h intervals between 0100 and 1900 h from horizons positioned 40 to 27, 27 to 18, 18 to 12, and 12 to 8 cm above soil surface. Herbage composition varied among horizons in all months, and diurnally only in June and August. In June and August, only TNC with maxima of 109 to 123 g kg^{-1} at 1900 h exhibited consistent diurnal patterns. Swards harvested to residual heights of 18, 12, or 8 cm exhibited little spatial variation in TNC during June and August, but CP, NDF, and IVTDMD varied with harvest depth on all dates. As swards were harvested to successively greater depths, TNC increased in October, but not in June and August. In contrast, CP and IVTDMD decreased, and NDF increased, for harvests to successively greater depths in all months. For harvests in June and August, manipulation of depth would capture more variation in CP, NDF, and IVTDMD, but manipulation of time of day of harvest would capture more variation in TNC to meet animal performance and silage fermentation requirements.

Nonstructural carbohydrate concentration and digestibility of herbage dry matter (DM) contribute to daily energy intake of ruminant livestock, and NC availability also determines fermentation potential of grass silage. In temperate climates, sward NC concentrations and DM digestibility vary diurnally according to patterns of photosynthesis, respiration, and translocation of NC. Perennial grass NC concentrations typically increase from morning to evening, by ≈20 to 30 g kg^{-1} (Holt and Hilst, 1969; Lechtenburg et al., 1972; Burner and Belesky, 2004; Shewmaker et al., 2006) and as much as 90 g kg^{-1} (Barrett et al., 2001). This variation presents opportunities for matching herbage composition with ruminant nutritional or silage fermentation requirements via timing of pasture allocation or mechanical harvesting. Grass NC concentrations and DM digestibility also vary seasonally, although patterns are less consistent than for daily cycles. Grass digestibility and NC concentration have been greater in spring and smaller in summer in some studies (Deinum et al., 1968; Miller et al., 2001; Shewmaker et al., 2006), and may increase again in fall (Dent and Aldrich, 1963; Jung et al., 1974; Mayland et al., 2000). In contrast, Radojevic et al. (1994) and Delagarde et al. (2000) reported highest grass NC concentrations in summer and smaller concentrations in spring and fall. Radojevic et al. (1994) and Wilman et al. (1996) reported independent seasonal patterns for herbage NC concentration and DM digestibility in perennial grasses; digestibility increased between summer and fall while NC concentration decreased. Digestibility and NC concentration of cool-season grasses also vary among genotypes (Dent and Aldrich, 1963; Wilson and Ford, 1973; Smit et al., 2006); growth stages (Davies, 1976; Jung et al., 1976); plant parts (Davies, 1976; Wilman et al., 1996); and vertical horizons (Sprague and Sullivan, 1950; Wilman and Altimimi, 1982; Delagarde et al., 2000).

Dietary preferences and intake and performance improvements have been shown for relatively small increases of ≈5 to 30 g kg^{-1} in herbage NC associated with genotype and time of day (Lee et al., 2001; Fisher et al., 2002; Burns et al., 2005; Smit et al., 2006). Elevated NC concentrations may also increase efficiency of rumen microbial protein synthesis and livestock N retention through improved synchrony of energy and protein concentrations (Lee et al., 2001; Miller et al., 2001), although this was not confirmed by Tas et al. (2006). While much of our understanding of relationships between NC concentration and livestock energy intake and performance is based on ryegrasses (*Lolium* spp.), NC concentrations in orchardgrass are often smaller than in ryegrasses (Dent and Aldrich, 1963; Michell, 1973; Wilson and Ford, 1973; Jung et al., 1974). Orchardgrass NC concentrations are also sometimes below the threshold of 70 to 160 g kg^{-1} (Dent and Aldrich, 1963; Michell, 1973; Wilson and Ford, 1973; Jung et al., 1974) considered adequate for silage fermentation (Jung et al., 1976; Wilkinson et al., 1983; Leibensperger and Pitt, 1988; Haigh, 1990). Reports of diurnal or vertical distribution patterns of orchardgrass composition are limited (Sprague and Sullivan, 1950; Davies, 1976; Burner and Belesky, 2004), particularly for vegetative herbage. More complete information could support decisions regarding conservation as hay vs. silage, cutting schedules and

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Abbreviations: CP, crude protein; DM, dry matter; IVTDMD, in vitro true dry matter digestibility; NC, nonstructural carbohydrate; NDF, neutral detergent fiber; NDFD, neutral detergent fiber digestibility; NIRS, near-infrared reflectance spectroscopy; TNC, total nonstructural carbohydrates; WSC, water soluble carbohydrates.

heights to meet nutritional value and silage fermentation targets, and timing of pasture allocation. Our objective was to determine diurnal and vertical patterns of herbage TNC, CP, and NDF concentrations, and IVTDMD and NDFD in orchardgrass swards in October, June, and August in northern Utah.

MATERIALS AND METHODS

Herbage samples were clipped from irrigated orchardgrass monocultures that had been established for $\geq$5 yr on an association of Greenson loam (fine-silty, mixed, mesic Aquic Calciustolls) and Nibley silty clay loam (fine, mixed, mesic Aquic Argiustolls) soils at Logan, UT (41°46′ N, 111°49′ W, 1406 m elevation). Soil test concentrations to a 0.3-m depth were pH 7.8 and $\geq$36, 400, and 8 mg kg^{-1} P, K, and SO_4–S, respectively. Nitrogen was applied at 2- to 9-wk intervals to annual totals of $\approx$110 kg N ha^{-1}. Sets of sampling dates, hereafter also referred to as months, were 12 to 13 Oct. 2000; 20 to 22 June 2001; and 16 to 17 Aug. 2001. Vegetative orchardgrass sampled at each date had regrown for 3 to 4 wk to a lax sward height of $\approx$40 cm following grazing by rotationally stocked beef cattle. Herbage masses were determined by clipping multiple 0.1-m^2 quadrats to 1 cm above soil surface and oven drying to constant weight at 60°C. Sward height and herbage masses of 5200 to 5350 kg DM ha^{-1} were representative of late-summer stockpiled pasture or a canopy suitable for mechanical harvesting. Herbage mass in 8 cm of residual stubble averaged 1580 kg DM ha^{-1}. Daily environmental conditions during sampling times are summarized in Table 1.

Within each set of dates, swards were sampled at duplicate times of 0100, 0700, 1300, and 1900 h Mountain Daylight Time during a 36-h period, except for single sampling at 0100 h in October and August and 1300 h in June. Samples from each time were sectioned into horizons positioned 40 to 27, 27 to 18, 18 to 12, and 12 to 8 cm above soil surface. These horizons correspond to treatments in a companion study (Griggs et al., 2005) in which one-third of current remaining sward height was removed every 6 h to represent herbage consumption under rotational stocking. These horizons are described in Fig. 1 to 5 according to their mean heights of 34, 22, 15, and 10 cm above soil surface. Proportions of oven-dry sward mass in successively lower horizons averaged 0.31, 0.27, 0.23, and 0.19, respectively, in October, and 0.27, 0.25, 0.25, and 0.23, respectively, in June and August.

For each sampling date, plots were located in each of three 5- by 17-m randomized complete blocks. At each sampling time, three to four random 40-cm-tall grab samples were clipped to an 8-cm residual height and composited within each block, then banded at the base to maintain vertical organization of the sample. Clipped samples were cooled over ice in the field for $\leq$2 h, sectioned into horizons at a laboratory bench, frozen and stored at $^{-}9$°C, lyophilized, and ground to pass a 1-mm screen of an impact mill. Herbage composition was analyzed with near-infrared reflectance spectroscopy (NIRS) via a scanning monochromator (Model 5000, FOSS NIRSystems, Inc., Silver Spring, MD) and chemometrics software (Infrasoft International, State College, PA). Calibration samples (140–143) selected to represent the spectral distribution of the experimental material were analyzed by reference wet chemistry procedures. Dry matter was determined by overnight drying at 105°C. Total nitrogen was determined (AOAC, 1990) by autoanalyzer (Technicon AutoAnalyzer II, Bran+Luebbe, Inc., Buffalo Grove, IL) and multiplied by 6.25 to estimate CP. Neutral detergent fiber (Van Soest et al., 1991) and IVTDMD (Goering and Van Soest, 1970) were determined with filter bags in batch refluxing or fermentation vessels (Ankom Technology Corp., Fairport, NY). Neutral detergent fiber was determined without amylase and sodium sulfite. Digestibility samples were incubated for 48 h at 38 to 39°C in rumen fluid and artificial saliva with addition of urea (Schmid et al., 1969), followed by refluxing of indigestible residues in neutral detergent solution. Digestibility of NDF was calculated from sample NDF and IVTDMD concentrations, and is expressed as a proportion of NDF. Total nonstructural carbohydrates were analyzed according to Smith (1969) using amyloglucosidase, sulfuric acid, and titration. Glucose was determined (AOAC, 1990) by autoanalyzer (Technicon AutoAnalyzer, Bran+Luebbe, Inc., Buffalo Grove, IL) in samples with and without amyloglucosidase for calculation of starch by difference. Standard errors of cross-validation for NIRS prediction equations from modified partial least squares regression for CP, IVTDMD, NDF, TNC, and starch were 4, 13, 13, 8, and 2 g kg^{-1} DM, respectively. These errors were comparable with those of Fisher et al. (2002) and Burns et al. (2005). Subsequent references to TNC and water soluble carbohydrates (WSC) assume inclusion and absence of starch, respectively.

Within each set of sampling dates, duplicate compositional values were averaged for each time point. In the following sections, herbage composition is compared in two ways: among (i) individual sward horizons (Fig. 1–5); and (ii) weighted means of horizons combined to represent increasing depths of harvest to residual heights of 18, 12, and 8 cm (Table 2). Weighted means are sums of concentrations in two, three, or four individual horizons multiplied by their respective proportions of harvested mass for increasing harvest depths. Herbage constituents were evaluated as a factorial arrangement of sampling times and horizon positions or depths of harvest by analysis of variance with the GLM procedure of SYSTAT, v. 11 (SYSTAT Software, Inc., Richmond, CA). Sampling dates were analyzed as three subplots in a split plot in time (Steel and Torrie, 1980, p. 390–392). All experimental treatments including sampling dates were analyzed as fixed effects. Date effects were tested with an error term of blocks × sampling dates, and interactions of dates × treatments were tested with residual error. References to treatment and interaction effects assume significance at $P \leq 0.05$ unless otherwise indicated.

Table 1. Environmental conditions during orchardgrass sampling at North Logan, UT. For each set of sampling dates, means for air temperature, relative humidity, solar radiation, and cloud cover are of hourly values, and total precipitation is cumulative.

			Air temperature†							Cloud cover	
Sampling date	Sunrise	Sunset	Min.	Max.	Mean	Soil temp.‡	Relative humidity	Total precip.	Solar radiation§	Daylight	Dark
	h		°C				%	mm	W m^{-2}	%	
12–13 Oct. 2000	0737	1848	−0.3	10.9	5.4	8.2	84.1	14.4	133	80.4	99.3
20–22 June 2001	0553	2106	11.8	31.5	22.0	17.6	37.8	0.0	547	0.0	0.0
16–17 Aug. 2001	0637	2024	12.5	34.6	23.5	21.6	38.9	0.0	527	7.8	3.9

† 2 m above soil surface.

‡ 10 cm below soil surface, recorded daily at 0800 h.

§ Global radiation (400–1100 nm) between sunrise and sunset from LI-200X silicon pyranometer, LI-COR Biosciences, Lincoln, NE.

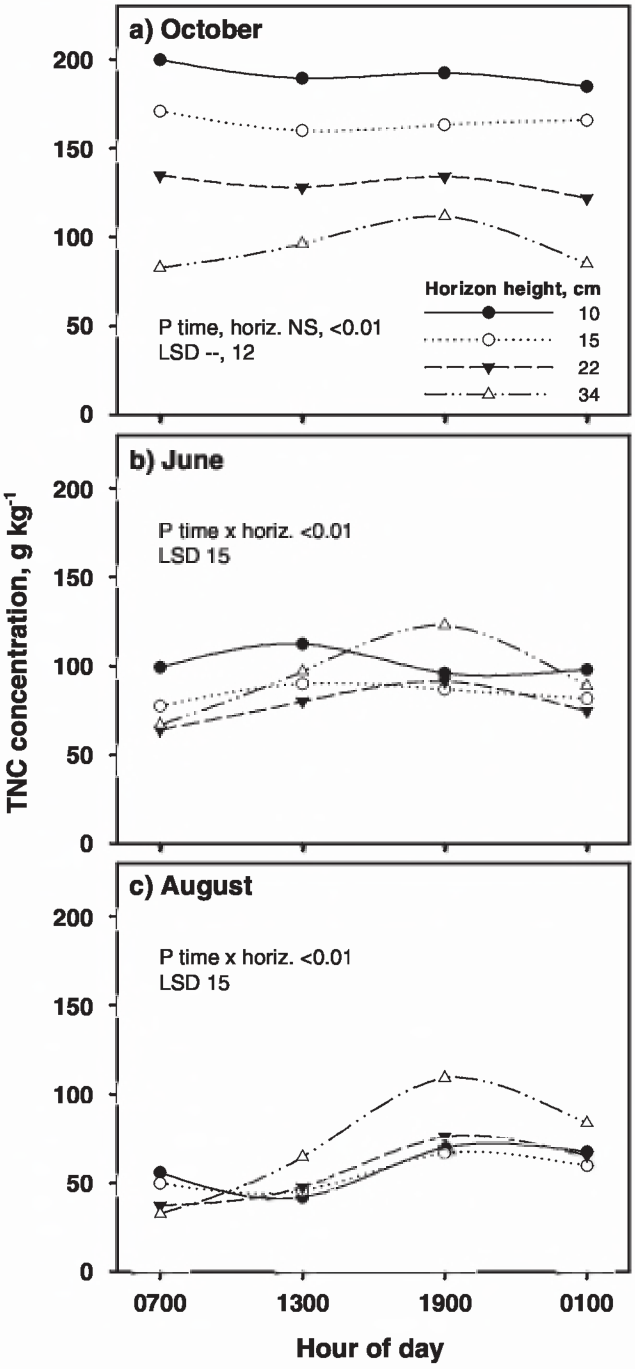

Fig. 1. Orchardgrass TNC concentrations in sward horizons at 6-h intervals in (a) October 2000, (b) June 2001, and (c) August 2001. Mean height of each horizon layer is shown in the legend. Significance and LSD are shown for main or interactive effects of sampling time and horizon height.

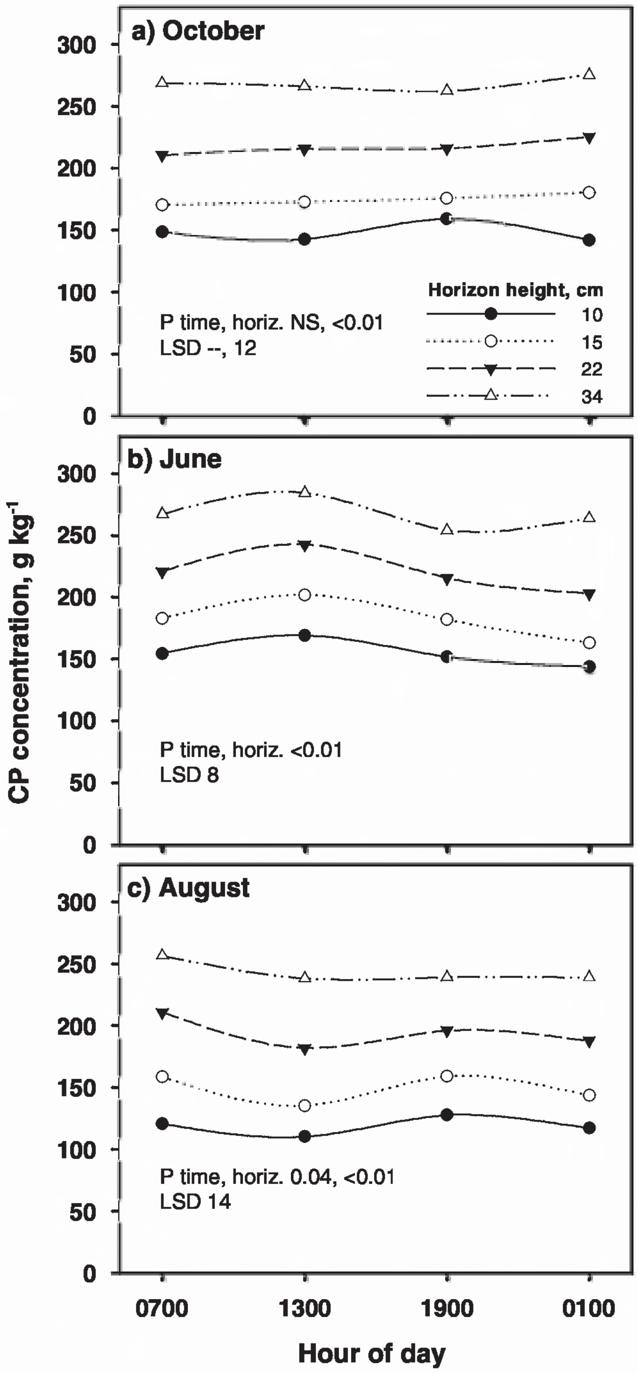

Fig. 2. Orchardgrass CP concentrations in sward horizons at 6-h intervals in (a) October 2000, (b) June 2001, and (c) August 2001. Mean height of each horizon layer is shown in the legend. Significance and LSD are shown for main effects of sampling time and horizon height.

Mean separation was by Fisher's protected LSD. Standard errors of means in Fig. 1 to 5 are similar to those shown in Table 2 for depths of harvest, and those for NDFD were 6.7 to 7.6 g kg^{-1}.

RESULTS AND DISCUSSION

Environmental conditions varied from near freezing, wet, and overcast with little diurnal temperature variation in October to high irradiance, temperatures, and diurnal temperature variation in June and August (Table 1). Midday photosynthetic photon flux densities during sampling in October, June, and August were 264 to 333, 1892 to 1943, and 1355 to 1372 μmol m^{-2} s^{-1}, respectively. Concentrations of constituents in individual (Fig. 1–5) and combined (Table 2) sward horizons varied among dates, except for CP. Concentrations in the uppermost horizon (40–27 cm) in Fig. 1–5 are not re-

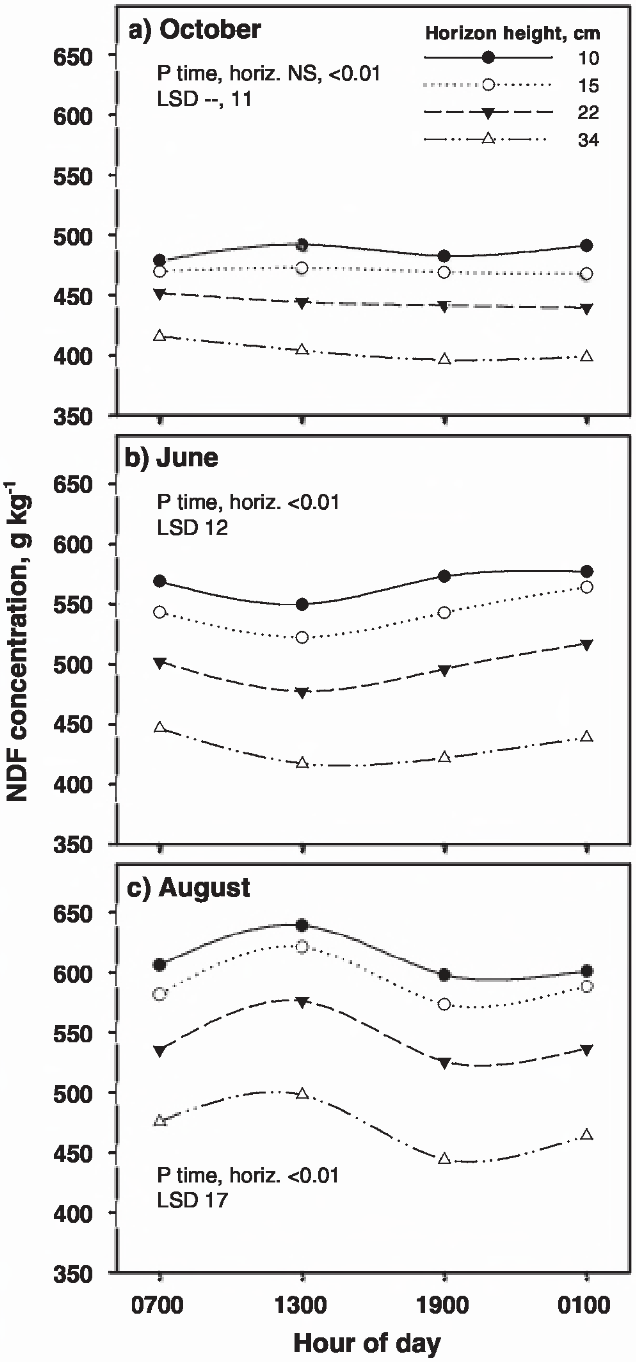

Fig. 3. Orchardgrass NDF concentrations in sward horizons at 6-h intervals in (a) October 2000, (b) June 2001, and (c) August 2001. Mean height of each horizon layer is shown in the legend. Significance and LSD are shown for main effects of sampling time and horizon height.

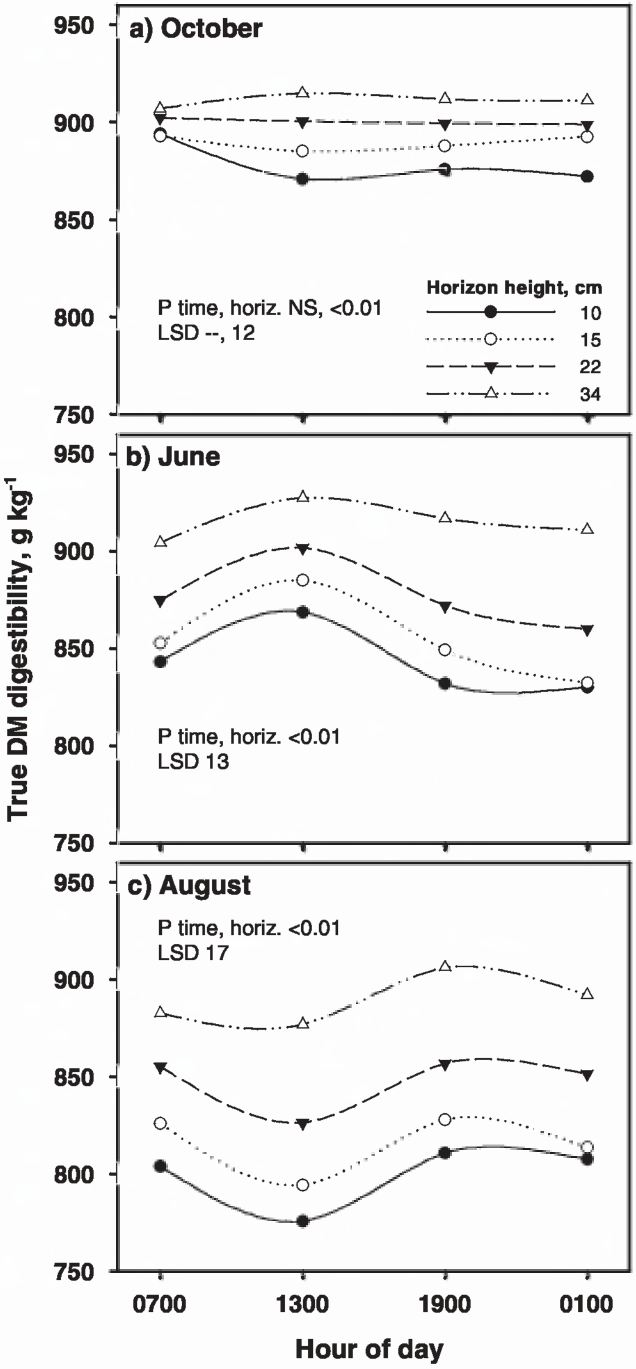

Fig. 4. Orchardgrass IVTDMD in sward horizons at 6-h intervals in (a) October 2000, (b) June 2001, and (c) August 2001. Mean height of each horizon layer is shown in the legend. Significance and LSD are shown for main effects of sampling time and horizon height.

peated, but may be compared with values for other depths of harvest, in Table 2. There were interactions of date × sampling time for all constituents, and date × horizon and date × depth of harvest for all constituents except CP. There were no higher-level interactions for any constituents. Results are therefore presented by sampling date, for which the only interactions were for TNC and were sampling time × horizon in June and August (Fig. 1) and sampling time × depth of harvest in August (Table 2). Starch varied from 3 to 33 g kg^{-1} across dates and treatments, and averaged 14, 19, and 13 g kg^{-1} in October, June, and August, respectively. Starch patterns generally followed those of TNC and will not be reported further.

Patterns in Individual Sward Horizons

Across times of day and horizons, concentrations were greater for TNC and smaller for NDF in October

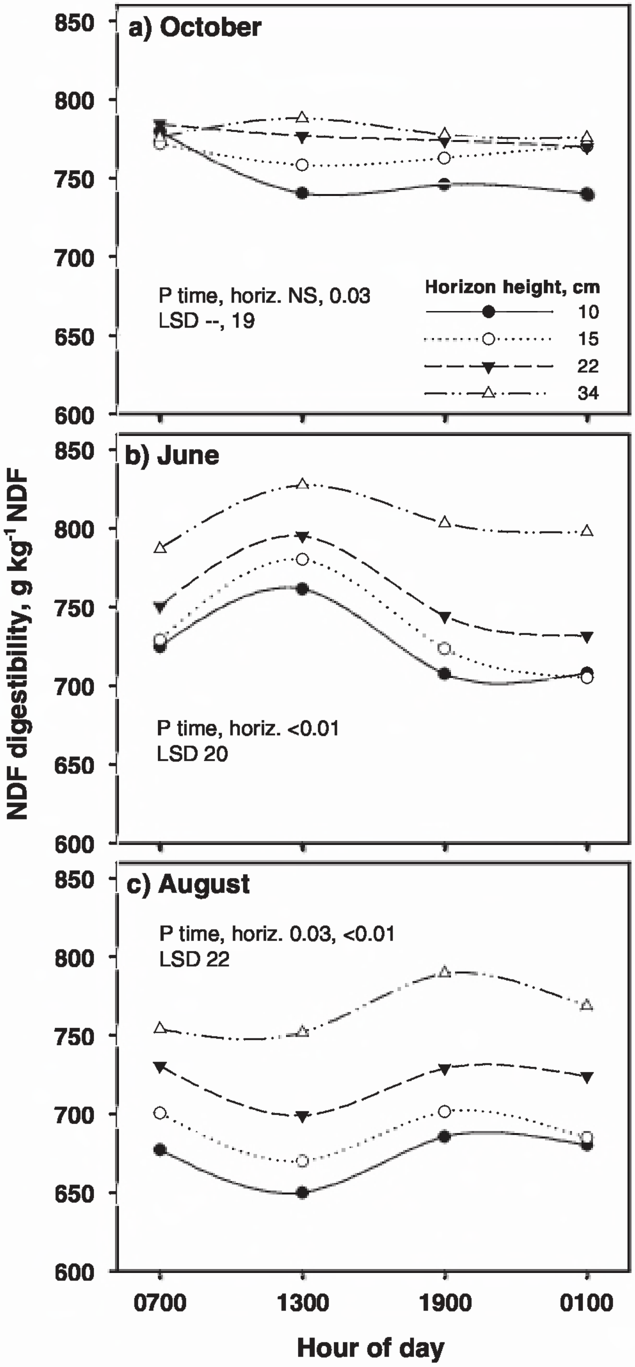

Fig. 5. Orchardgrass NDF digestibility in sward horizons at 6-h intervals in (a) October 2000, (b) June 2001, and (c) August 2001. Mean height of each horizon layer is shown in the legend. Significance and LSD are shown for main effects of sampling time and horizon height.

than in June and August (Fig. 1 and 3). Mean CP did not differ among months, and IVTDMD and NDFD were smaller in August than in October and June (Fig. 2, 4, and 5). All constituents varied diurnally in June and August, but not in October. Diurnal patterns in June and August were similar for TNC (Fig. 1), but dissimilar for other constituents (Fig. 2–5). While TNC increased to maximum concentrations at 1900 h in June and August, CP, IVTDMD, and NDFD peaked at 1300 h in June but at 1900 h in August. Cycles for NDF, which peaked at 1900 to 0100 h in June and at 1300 h in August, were out of phase with those for CP, IVTDMD, and NDFD, which were lowest at these times (Fig. 2–5). For all constituents except TNC, concentrations varied in vertical gradients in each month. Those for CP, IVTDMD, and NDFD decreased from upper to lower sward horizons, whereas those for NDF increased along this dimension. In contrast, TNC increased from upper to lower horizons in October but decreased along this dimension in June and August. Vertical TNC patterns in June and August depended on sampling time, suggesting daytime carbohydrate translocation from upper to lower horizons or daughter tillers.

Although greater NC in lower horizons has also been shown for orchardgrass in early reproductive stage by Davies (1976), Delagarde et al. (2000) observed decreasing NC in lower horizons of vegetative ryegrass, except in October. Peak TNC at 1900 h in June and August are consistent with observations of Lechtenburg et al. (1972), Burner and Belesky (2004), and Shewmaker et al. (2006). Amplitudes of diurnal change in these months were greatest for the upper horizon, consistent with results of Delagarde et al. (2000). Herbage TNC ranged from 33 to 200 g kg^{-1} among dates and treatments (Fig. 1), consistent with reports for orchardgrass by Dent and Aldrich (1963), Michell (1973), Jung et al. (1974), and Burner and Belesky (2004). In addition to being opposite in direction, vertical TNC gradients were less pronounced in June and August than in October, and TNC were often below the range of 92 to 165 g kg^{-1} WSC associated with increased animal performance (Lee et al., 2001; Miller et al., 2001) from ryegrass. Greater NC under cooler temperatures of fall are supported by results of Wilson and Ford (1973), but reduced NC under limited irradiance such as during October in our study have been documented by Auda et al. (1966), Deinum et al. (1968), and Burner and Belesky (2004). Our relatively high fall TNC may have been a function of low respiration rates under cool daytime and nighttime temperatures, in conjunction with higher irradiance due to less cloud cover preceding the sampling period, and are consistent with the weak relationship between daylength or total irradiance and WSC reported by Radojevic et al. (1994) for ryegrass.

The similarity of CP concentrations among months (Fig. 2) is consistent with findings of Dent and Aldrich (1963) and Deinum et al. (1968), but inconsistent with reports of decreasing (Taweel et al., 2005) or increasing (Radojevic et al., 1994; Wilman et al., 1996; Delagarde et al., 2000) concentrations for ryegrasses in fall. Crude protein ranged from 110 to 284 g kg^{-1} among dates and treatments, consistent with other values for vegetative grass (Dent and Aldrich, 1963; Burner and Belesky, 2004). Decreasing CP in lower horizons, as also shown by Davies (1976) and Delagarde et al. (2000), is expected on the basis of distribution of young photosynthetic tissue.

Herbage NDF ranged from 396 to 639 g kg^{-1} among dates and treatments (Fig. 3). Increasing NDF in lower

Table 2. Composition of orchardgrass swards harvested from 40 cm to successively lower residual heights at 6-h intervals throughout a day. Values for harvest depths may be compared with those shown in figures for the top horizon (27-cm residual height).

	Constituent and residual stubble height, cm‡											
	TNC			CP			NDF			IVTDMD		
Date and time of day†	18	12	8	18	12	8	18	12	8	18	12	8
						g kg^{-1} DM						
October												
0100 h	102	121	133	252	231	213	418	433	444	905	901	896
0700 h	106	124	137	242	223	210	432	442	449	905	902	900
1300 h	111	126	138	242	222	207	423	437	448	908	902	896
1900 h	122	134	146	243	224	212	416	430	440	907	902	897
P§ time, depth		*<0.01*			0.17, *<0.01*			*<0.01*			0.92, *<0.01*	
SE time, depth		2.5			3.0			1.9			2.3	
LSD (0.05) time, depth		7			NS, 8			5			NS, 7	
June												
0100 h	82	82	86	234	212	196	478	505	522	885	869	860
0700 h	66	69	76	245	226	209	474	495	512	890	878	870
1300 h	89	89	94	266	247	230	445	468	486	915	906	899
1900 h	107	100	99	235	216	201	459	489	508	895	878	868
P time, depth		*<0.01, 0.03*			*<0.01*			*<0.01*			*<0.01*	
SE time, depth		2.2			2.8			4.0			3.9	
LSD (0.05) time, depth		6			8			12			11	
August												
0100 h	74	69	69	212	190	174	501	530	546	871	852	842
0700 h	35	40	43	235	210	188	504	529	548	870	856	843
1300 h	56	53	50	212	186	170	535	564	580	853	833	821
1900 h	94	85	81	218	200	184	484	512	531	883	866	853
P time, depth		*0.01*¶			*≤0.01*			*<0.01*			*<0.01*	
SE time, depth		4.2¶			4.6			5.6			4.8	
LSD (0.05) time, depth		12¶			13			16			14	

† *P*, SE, and LSD values are for main effects of sampling time and sampling depth and pertain to all times and depths within a date. A single value is shown if common to both main effects.

‡ CP, crude protein; DM, dry matter; IVTDMD, in vitro true dry matter digestibility; NDF, neutral detergent fiber; TNC, total nonstructural carbohydrates.

§ Significance level of test. Italicized values are significant at $P \leq 0.05$.

¶ Sampling time × depth interacted ($P = 0.01$) for TNC in August; statistics are for interaction effects and means.

sward horizons would be expected as a function of tissue age, and agrees with observations of Wilman et al. (1996) and Delagarde et al. (2000). Herbage IVTDMD ranged from 776 to 927 g kg^{-1} among dates and treatments (Fig. 4), consistent with reports for fescues (*Festuca* or *Lolium* spp.) and ryegrasses (Deinum and Dirven, 1975; Wilman et al., 1996). Decreasing digestibility in lower horizons agrees with results of Davies (1976), Wilman et al. (1996), and Delagarde et al. (2000). Smaller mean NDFD in August than at other dates (Fig. 5) was also shown by Radojevic et al. (1994). Digestibility of NDF ranged from 650 to 828 g kg^{-1} among dates and treatments, consistent with reports for fescues and ryegrasses (Deinum and Dirven, 1975; Wilman et al., 1996). Vertical gradients of NDF, IVTDMD, and NDFD were less pronounced in October than in June and August. Patterns of NDFD appear to account for those of DM digestibility (Fig. 4–5, Table 3), as also re-

Table 3. Pearson correlation coefficents for relationships of TNC, CP, and IVTDMD with other constituents in orchardgrass sward horizons. Data are combined across sampling dates in October, June, and August, or combined across horizon heights within each sampling date.

		Correlation of‡								
		TNC with				CP with			IVTDMD with	
Horizon height or sampling date†	*n*	CP	NDF	NDFD	IVTDMD	NDF	NDFD	IVTDMD	NDF	NDFD
						r§				
34 cm	63	−0.11NS	−0.59	0.44	0.57	−0.52	0.54	0.61	−0.80	0.92
22 cm	63	0.10NS	−0.80	0.54	0.66	−0.61	0.76	0.74	−0.93	0.97
15 cm	63	0.22NS	−0.90	0.65	0.77	−0.58	0.78	0.74	−0.94	0.98
10 cm	63	0.36*	−0.95	0.71	0.82	−0.54	0.74	0.70	−0.93	0.97
All	252	−0.10NS	−0.47	0.41	0.46	−0.78	0.76	0.79	−0.94	0.97
October	84	−0.80	0.62	−0.18NS	−0.36	−0.93	0.59	0.77	−0.83	0.96
June	84	−0.16NS	−0.14NS	0.30NS	0.25NS	−0.91	0.80	0.86	−0.93	0.98
August	84	0.15NS	−0.52	0.45	0.48	−0.87	0.88	0.90	−0.95	0.98

* $P \leq 0.05$.

† Data are combined across sampling dates (top), all horizon heights and sampling dates, or horizon heights (bottom).

‡ CP, crude protein; IVTDMD, in vitro true dry matter digestibility; NDF, neutral detergent fiber; NDFD, neutral detergent fiber digestibility; TNC, total nonstructural carbohydrates.

§ Coefficients are significant at $P < 0.01$ unless shown as significant (*) or not significant (NS) at $0.01 \leq P \leq 0.05$.

ported by Wilman and Altimimi (1982) and Wilman et al. (1996).

Temporal patterns in Fig. 1–5 suggest possible dilution of other constituents by TNC or CP in June or August, consistent with reports of negative associations between WSC and CP (Humphreys, 1989; Radojevic et al., 1994; Wilman et al., 1996; Delagarde et al., 2000; Taweel et al., 2005) or NDF (Lee et al., 2001; Taweel et al., 2005, Smit et al., 2006). Correlations that might represent dilution of CP and NDF by TNC (Table 3) were inconsistent among months, and nearly all of the association among TNC and CP in October ($r = -0.80$) appears to be due to vertical, rather than temporal, distribution of constituents (Fig. 1–2). Since quantities of NDF would not be expected to vary diurnally from a metabolic standpoint, correlations of $r = -0.59$ to -0.95 between NDF and TNC within sward horizons suggest possible dilution by TNC fluxes, particularly in August (Table 3, Fig. 1 and 3). Reasons for inconsistent relationships of TNC with NDF among June and August (Fig. 1 and 3) are unclear, but the change from a negative to a positive correlation between August and October corresponds with reversal of the vertical gradient of TNC between months. The possibility of NDF dilution by CP ($r = -0.52$ to -0.61 within sward horizons) is consistent across months (Table 3 and Fig. 2–3).

As with NDF, a diurnal basis for NDF digestibility seems unlikely from a physiological standpoint, unless NDFD is being facilitated by NC (Haddad and Grant, 2000; Miller et al., 2001) or CP (Schmid et al., 1969). Enhancement of fiber digestibility by TNC or CP might be difficult to detect because of possible flows of soluble constituents among filter bags during batch processing of our digestibility samples. Facilitation of IVTDMD and NDFD by CP within sward horizons during June and August (Fig. 2, 4, and 5) is suggested by the similarity of temporal patterns for digestibilities and CP. Although correlations of TNC with IVTDMD and NDFD were stronger in lower horizons, these associations are not consistent across months or times of day (Table 3 and Fig. 1, 4, and 5). Others have reported weak or highly variable relationships of WSC to DM digestibility for vegetative orchardgrass (Dent and Aldrich, 1963; Michell, 1973) and ryegrass (Humphreys, 1989; Radojevic et al., 1994; Taweel et al., 2005), or only a moderate relationship ($r = 0.67$) of WSC with lamb liveweight gain (Lee et al., 2001). Our results are consistent with those of Radojevic et al. (1994) and Taweel et al. (2005), showing no improvement in ryegrass fiber digestion as WSC ranged from ≈100 to 300 g kg^{-1}.

Patterns in Combined Horizons Harvested to Different Depths

Patterns of constituents in herbage harvested to residual heights of 18 to 8 cm (Table 2) reflect those of individual horizons (Fig. 1–5) weighted for different masses. Patterns of NDFD in combined horizons (695–828 g kg^{-1} across harvest times, depths, and months) were very similar to those for IVTDMD and are not shown. Vertical gradients with harvest depth were less pronounced in June and August than in October for TNC, similar among months for CP, and more pronounced in June and August than in October for NDF and IVTDMD. Diurnal variation within combined horizons was more pronounced for all constituents in June and August than in October. Under the conditions of our study in October, more variation in herbage composition would be captured through manipulation of harvest depth than time of day. Whether fall distribution patterns of herbage composition would be similar under higher daytime temperatures and irradiance was not tested. In June and August, manipulation of harvest depth would capture more variation in CP, NDF, and IVTDMD, but manipulation of harvest time of day would capture more variation in TNC. Relative to previously cited TNC thresholds of 70 to 160 g kg^{-1} for effective silage fermentation, concentrations were often inadequate in June and August, but adequate in October for herbage harvested to 12 or 8 cm or at the end of the day.

Sward bulk densities calculated from herbage masses in successively lower horizons were 0.9, 1.1, 1.4, and 1.7 mg DM cm^{-3} in October, and 0.8, 1.0, 1.6, and 2.2 mg DM cm^{-3} in June and August. This vertical gradient, also reported by Delagarde et al. (2000) and Barrett et al. (2001), corresponded with herbage masses of ≈1050, 2000, 2900, and 3710 kg DM ha^{-1} to stubble heights of 27, 18, 12, and 8 cm, respectively. This gradient favors harvesting to low residual heights for acquisition of forage mass, but must be reconciled with ruminant nutritional or silage fermentation requirements that may not be met by harvesting to low heights. Opposing vertical gradients of increasing NDF and decreasing NDFD with harvest depth resulted in a more gradual increase for digestible fiber concentration than for NDF with harvests to lower residual heights. Across months, proportions of digestible NDF in herbage from successively lower harvest depths increased from 341 to 373 g kg^{-1}, while NDF concentrations increased from 435 to 501 g kg^{-1}. Averaged across dates and times of harvest, herbage removed to 8 cm rather than 18 cm of residual height was 37 and 18 g kg^{-1} greater in NDF and digestible NDF concentrations, respectively, and 37 and 20 g kg^{-1} less in CP concentration and IVTDMD, respectively.

Implications

Clear variations in herbage constituents among months, times of day, and sward horizons present opportunities for matching composition of harvested forage with animal performance and silage fermentation requirements. Under the conditions of our study, concentrations of constituents other than TNC are more closely associated with depth than with time of day of harvest. There is therefore at least as much potential to capture variation in herbage composition through manipulation of harvest depth as harvest time of day, within limits of acceptable quantity of harvested forage. In all months, CP and IVTDMD decreased, and NDF increased, consistently with depth of harvest. For TNC, there was a less consistent association with depth of harvest than with time of day, because of the reversal of vertical TNC gradients in October relative to June and August. In all months, TNC concentrations associated with different harvest depths were greatest at 1900 h. Relative to other reports, TNC concentrations at differing harvest depths in our study were probably adequate in fall, but low to inadequate in summer for effective silage fermentation and possible enhancement of animal performance. Manipulation of harvest depth or timing may therefore be more critical to realization of adequate herbage TNC in June and August than in October. Seasonal variation in TNC in conjunction with limiting fall climatic conditions for hay drying suggest advantages of harvesting orchardgrass in October as silage and in June and August as hay. Seasonal patterns also indicate that variations of TNC with harvest depth may be less predictable or important than the consistent gradients for CP, NDF, IVTDMD, and NDFD.

Despite inconsistencies among months and times of day in distribution patterns for herbage constituents, our results suggest some practical strategies for orchardgrass harvest management. These are (i) October silage harvests to 8-cm residual height to maximize harvested forage mass and TNC concentration, or to 12- to 18-cm residual height for greater concentrations of CP and IVTDMD with reduced forage mass; and (ii) June and August hay harvests to 8- to 12-cm residual height for maximum harvested forage mass at moderate CP concentration and IVTDMD, or to 18- to 12-cm residual heights for maximum CP concentration and IVTDMD with reduced forage mass. In most cases, harvesting at 1300 to 1900 h may also enhance herbage NC concentration for ruminant livestock performance or silage fermentation. Additional research addressing the consistency of diurnal and vertical patterns and environmental determinants of herbage composition could refine planning of depth and time of day of orchardgrass harvesting.

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