Published online May 27, 2005

Nonstructural Carbohydrate and Digestibility Patterns in Orchardgrass Swards during Daily Defoliation Sequences Initiated in Evening and Morning

Thomas C. Griggs,* Jennifer W. MacAdam, Henry F. Mayland, and Joseph C. Burns

ABSTRACT

Herbage soluble carbohydrate (SC) levels vary diurnally and livestock intake can be higher for herbage harvested or allocated to animals in the evening than in the morning. Few assessments of SC and digestibility patterns have been made during sward depletion in rotationally stocked orchardgrass (*Dactylis glomerata* L.). We tested the hypothesis that simulated evening daily pasture allocation increases 24-h mean herbage SC and digestibility levels relative to morning allocation. Total nonstructural carbohydrate (TNC) and in vitro true dry matter digestibility (IVTDMD) levels were compared during 24-h clipping sequences initiated at 1900 h (PM) and 0700 h (AM). Sward height was progressively reduced from 40 to 8 cm at 6-h intervals in October, June, and August. Successively lower horizons from defoliation sequences and also from control areas that were not under progressive defoliation were analyzed. Digestibility and TNC levels varied diurnally and seasonally, and were often higher for PM sequences, but differences among 24-h means were small. Daily mean TNC levels for defoliation sequences initiated in PM and AM were 138 vs. 132, 93 vs. 88, and 72 vs. 60 g kg^{-1} in October, June, and August, respectively. In all periods, digestibility decreased from approximately 920 to 800 to 890 g kg^{-1} during sward depletion and displayed similar patterns between defoliation sequences. Patterns of TNC and digestibility during sward depletion may not be represented by those in intact swards, and PM allocation of daily herbage may not increase 24-h mean dietary TNC density relative to AM allocation. Daily quantities of ingested TNC could be higher for PM herbage allocation if livestock consume proportionately more herbage in the PM than we simulated.

Management of grazing systems for high animal performance includes facilitation of high intakes of pasture dry matter (DM) by livestock. Constraints to grazing animal performance include sward structural and herbage compositional factors that determine rates and concentrations of dietary energy intake (Orr et al., 1997; Vazquez and Smith, 2000; Barrett et al., 2001). Herbage SC and digestibility concentrations, two indices of dietary energy density, usually vary diurnally according to daily patterns of photosynthesis, respiration, and translocation of SC. In temperate climates, herbage SC concentrations are generally highest in evening and lowest in morning (Holt and Hilst, 1969; Orr et al., 1997; Barrett et al., 2001). Herbage SC and digestibility concentrations also vary seasonally, with generally higher SC levels in spring and lower levels in summer or fall (Dent and Aldrich, 1963; Deinum et al., 1968; Delagarde et al., 2000). In contrast, high fall or winter SC levels are reported by Jung et al. (1974) and Mayland et al. (2000), while Radojevic et al. (1994) reported highest levels in late summer and lowest levels in winter. Herbage digestibility and SC levels also vary among genotypes (Dent and Aldrich, 1963; Wilson and Ford, 1973; Jung et al., 1976), growth stages (Jung et al., 1976; Fulkerson et al., 1998; Delagarde et al., 2000), plant parts (Terry and Tilley, 1964; Lechtenberg et al., 1971), and vertical horizons (Buxton and Marten, 1989; Delagarde et al., 2000) within cool-season grass and legume swards.

Experimental shading treatments and sampling across times of day, genotypes, stages of growth, and environmental conditions have shown positive associations between levels of herbage SC and feed preference (Fisher et al., 1999, 2002; Ciavarella et al., 2000; Mayland et al., 2000) and energy intake and livestock performance (Michell, 1973; Lee et al., 2000; Miller et al., 2001). Increased SC levels may also increase efficiency of rumen microbial protein synthesis and livestock N retention through improved balance or synchronization of energy and protein levels (Fulkerson et al., 1998; Lee et al., 2000; Miller et al., 2001). Timing of daily herbage allocation in rotationally stocked pastures affects diurnal patterns of leaf area reduction and may therefore affect the daily balance of sward photosynthetic gain and respiratory loss and energy intake by livestock. Interpretation of temporal SC patterns has led to suggestions that animal performance may be higher under afternoon or evening allocation of daily pasture area, relative to morning allocation (Lechtenberg et al., 1971; Delagarde et al., 2000; Orr et al., 2001). This increase would be a function of matching higher evening herbage DM (Orr et al., 1997, 2001; Gibb et al., 1998; Delagarde et al., 2000), SC, and digestibility levels with possibly higher evening intake rate or meal size (Orr et al. (1997) and 2001; Gibb et al., 1998; Barrett et al., 2001). In the last 4 wk of a 10-wk grazing trial comparing PM and AM allocation of daily herbage, milk production was 6% higher for dairy cattle in the PM treatment (Orr et al., 2001).

Dietary preferences and intake and performance improvements have been shown for relatively small increases in herbage SC levels associated with genotype, environment, or management (Fisher et al., 1999, 2002;

T.C. Griggs and J.W. MacAdam, Dep. of Plants, Soils, and Biometeorology, Utah State Univ., 4820 Old Main Hill, Logan, UT 84322-4820; H.F. Mayland, USDA-ARS Northwest Irrigation and Soils Research Lab., Kimberly, ID 83341-5076; and J.C Burns, USDA-ARS Plant Science Research Unit, and Depts. of Crop Science and Animal Science, Room 1119, Box 7620, North Carolina State Univ., Raleigh, NC 27695-7620. This research was supported by the Utah Agricultural Experiment Station and USDA-ARS, Kimberly, ID and Raleigh, NC. Approved as journal paper no. 7583. Received 24 Nov. 2003. *Corresponding author (tgriggs@ext.usu.edu).

Published in Crop Sci. 45:1295–1304 (2005).
Forage & Grazing Lands
doi:10.2135/cropsci2003.0613

Abbreviations: DM, dry matter; IVTDMD, in vitro true dry matter digestibility; NIRS, near-infrared reflectance spectroscopy; SC, soluble carbohydrates; TNC, total nonstructural carbohydrates.

Ciavarella et al., 2000; Orr et al., 2001). Diurnal cycling of SC and digestibility is widely reported for mechanically harvested forages and for herbage samples gathered during nongrazing periods or under the relatively steady state conditions of continuous stocking. Patterns have not been as clearly defined under the more dynamic conditions of daily sward depletion in rotationally stocked paddocks. Relationships between SC levels and livestock energy intake and performance have been developed largely with ryegrass (*Lolium*) species and only to a limited extent with orchardgrass. Our objective was to test the hypothesis that simulated evening allocation of daily herbage in a rotationally stocked orchardgrass pasture increases 24-h mean herbage TNC and digestibility levels relative to morning allocation.

MATERIALS AND METHODS

Progressive utilization of a 24-h herbage allocation was simulated by clipping. Established pastures of irrigated orchardgrass were on an association of Greenson loam (fine-silty, mixed, mesic Aquic Calciustolls) and Nibley silty clay loam (fine, mixed, mesic Aquic Argiustolls) at Logan, UT (41°46′ N, 111°50′ W, 1406 m elevation) with adequate levels of soil water and fertility for high herbage production. Experimental periods were 12 through 13 Oct. 2000, 20 through 22 June 2001, and 16 through 17 Aug. 2001. Vegetative grass sampled in each period had regrown for approximately 3 to 4 wk to a lax sward height of approximately 40 cm following grazing by rotationally stocked cattle. Herbage mass to soil surface averaged approximately 5200, 5350, and 5320 kg DM ha^{-1} at October, June, and August samplings, respectively. Sward height and herbage mass approached maximum levels normally encountered with rotationally stocked orchardgrass, but October sward conditions were representative of late-summer stockpiled forage. For consistency among periods, June and August sampling areas were selected for similarity of sward height and herbage mass with those of October. Cattle were absent during experimental periods. Treatments were a factorial arrangement of (A) sample types representing (i) progressive sward depletion over 24 h, or (ii) instantaneous removal of control samples every 6 h from areas not under progressive defoliation; and (B) 24-h defoliation sequences initiated at (i) 1900 h (PM) and (ii) 0700 h (AM) Mountain Daylight Saving time, in which successive horizons were removed at 6-h intervals (Fig. 1). In each period, plots were located in three 5- by 17-m randomized complete blocks. Portable guide rails were used to define clipping heights within sampling areas of 0.5 by 0.7 m. Different sets of plots were used for PM and AM sampling sequences.

In each 24-h defoliation sequence, 0.33 of current remaining sward height was removed every 6 h from each plot. Successive horizons were 40 to 27, 27 to 18, 18 to 12, and 12 to 8 cm above soil surface (Fig. 1). This proportional height reduction was consistent with observations of cattle bite depth as approximately 0.32 to 0.34 of tiller height under continuous (Barrett et al., 2001) and rotational stocking (Wade et al., 1989). Proportions of total herbage mass above an 8-cm stubble height for 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. Residual herbage mass in 8 cm of stubble averaged 1580 kg DM ha^{-1}. Successive horizons were clipped from nonadjacent paired plots such that a given horizon was sampled at the beginning of a 6-h interval of sward depletion from one plot and at the end of that interval from the other plot. The next horizon was then sampled from each paired plot 6 h later. This allowed estimation of mean herbage composition within each 6-h time interval, representing gradual sward depletion. Since PM and AM defoliation sequences were initiated 12 h apart, the duration of total sampling was 36 h in each period. Sampling began with the AM treatment in October and August, and with the PM treatment in June, according to logistics of labor availability.

Control herbage was clipped from intact sward areas in each block that were not under progressive defoliation, as composites of three-to-four random grab samples to an 8-cm residual height. Control samples were gathered to evaluate whether

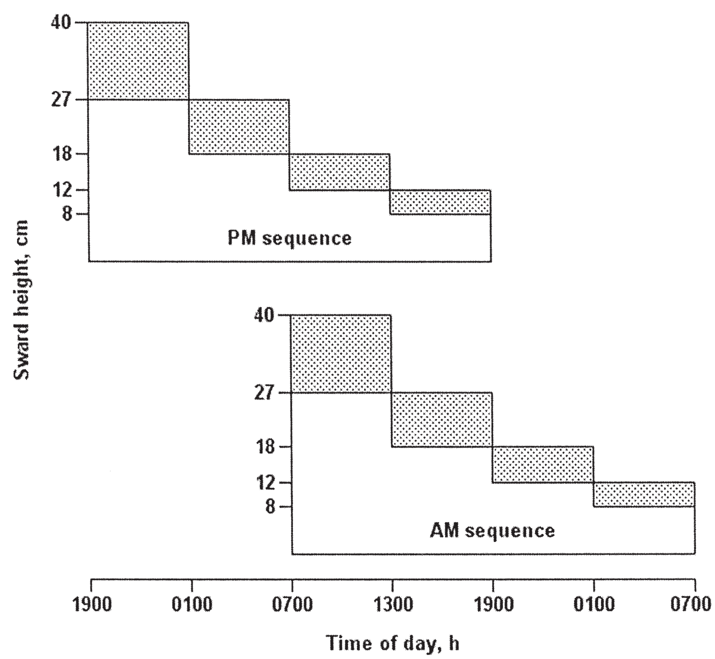

Fig. 1. Removal of 0.33 (shaded horizons) of orchardgrass sward height at the beginnings and ends of 6-h intervals in 24-h defoliation sequences initiated at 1900 (PM) and 0700 (AM) h. Control samples from intact swards were also clipped and sectioned into horizons at each time.

diurnal patterns of herbage composition in horizons of intact swards are representative of those in swards undergoing progressive defoliation. This approach was taken because reports of diurnal patterns of herbage SC and digestibility concentrations are often based on samples from intact swards that are clipped instantaneously to residual stubble height (Holt and Hilst, 1969; Lechtenberg et al., 1971; Miller et al., 2001), rather than on removal of successive horizons as occurs under grazing. Controls were sampled at the same times and sectioned into the same horizons as in defoliation sequences. Individual horizons within control samples were presumed to represent different energy balances among photosynthetic gain and respiratory loss during 24-h sampling periods than in corresponding horizons in defoliation sequences. These presumptions are based on differing leaf masses in intact swards than in those undergoing progressive defoliation.

Clipped samples were sealed in polyethylene bags, stored in a cooler with dry ice for up to 2 h, frozen (−9°C) and stored, lyophilized, and ground through an impact mill to pass a 1-mm screen. Spectra were obtained via near-infrared reflectance spectroscopy (NIRS) with a scanning monochromator (Mod. 5000, FOSS NIRSystems, Inc., Silver Spring, MD) from ground samples for prediction of chemical composition. Calibration samples were selected according to guidelines of Shenk and Westerhaus (1991) to represent the range and spectral distribution of the experimental material and were analyzed by reference wet chemistry procedures. Dry matter concentration was determined by overnight drying at 105°C. In vitro true DM digestibility (Goering and Van Soest, 1970) was determined in batch fermentation vessels (Ankom Technology Corp., Fairport, NY) by incubating samples in filter bags for 48 h at 38 to 39°C in rumen fluid and artificial saliva with addition of urea (Schmid et al., 1969). Rumen fluid was obtained from a cannulated mature Hereford steer fed alfalfa (*Medicago sativa* L.) hay. In the second stage of the IVTDMD procedure, indigestible residues were refluxed in neutral detergent solution (Van Soest and Robertson, 1980) in a batch processor (Ankom Technology Corp., Fairport, NY). Neutral detergent solution was prepared with 2-ethoxyethanol and without decalin, amylase, and sodium sulfite. Total nonstructural carbohydrates were analyzed according to Smith (1969) using amyloglucosidase to digest starch to glucose, sulfuric acid to hydrolyze soluble sugars to reducing sugars, and titration to determine concentration. Sample composition was predicted via NIRS equations developed with modified partial least squares regression according to guidelines of Shenk and Westerhaus (1991). Summary statistics for NIRS calibration and cross-validation (Table 1) are comparable with those of Fisher et al. (1999, 2002) and Welle et al. (2003) for SC concentration and DM digestibility.

Weighted means for combined control horizons, i.e., reconstituted swards, were plotted at each sampling time (Fig. 2). Weighted means were sums of individual horizon compositional levels multiplied by their respective proportions of sward mass. Means for sequentially lower horizons in defoliation sequences and controls are plotted in Fig. 3 and 4 at midpoints (0400, 1000, 1600, and 2200 h) between sampling times to represent gradual depletion by grazing. Plotted values therefore represent a combination of responses to time of day, horizon position, and defoliation schedule. Levels of TNC and IVTDMD in the initial and final 6 h of each 24-h sequence, and as 24-h means weighted for proportional mass of each horizon, were compared among sample types (defoliation sequences vs. controls) and defoliation schedules (PM vs. AM initiation) by analysis of variance with the GLM procedure of SYSTAT, ver. 10 (SPSS, 2000). Sampling periods were treated as repeated measures. The significance of effects of sampling periods and their interactions with treatments was tested with residual error (12 df) after partitioning sums of squares among periods and interactions of periods with blocks and treatments. Because of limited power of testing within each period (6 error df), effects were considered significant at $P \leq 0.15$. Subsequent references to significant effects assume this level unless otherwise indicated. Daily environmental conditions during the 24 h before, and within, each sampling period are summarized in Table 2.

RESULTS AND DISCUSSION

Environmental conditions varied from near freezing and overcast with little diurnal temperature variation in October to high irradiance, temperatures, and daily temperature variation in June and August (Table 2). Midday photosynthetic photon flux densities in October, June, and August were 264 to 333, 1892 to 1943, and 1355 to 1372 μmol m^{-2} s^{-1}, respectively. Treatments were confounded with possible differences in environmental conditions for PM and AM treatments within a period, but these variations were small.

Seasonal Variation and Patterns in Intact Swards

Herbage TNC and digestibility levels (initial, final, and 24-h mean) differed among periods ($P < 0.01$). Interactions of period by sample type (defoliation sequence vs. control) occurred for all variables ($P < 0.03$) except final and 24-h mean TNC levels. Interaction of period by defoliation sequence (PM vs. AM) occurred for initial and final TNC and initial digestibility levels ($P < 0.05$). Interaction of period by sample type by defoliation sequence occurred only for final digestibility level ($P = 0.14$). Results are therefore presented by period in tables and figures. Weighted herbage TNC and digestibility concentrations in combined control horizons varied diurnally and seasonally (Fig. 2a and 2b), with highest diurnal levels in PM and highest seasonal levels in

Table 1. Calibration and cross-validation results for NIRS analysis of TNC and IVTDMD concentrations in orchardgrass herbage.

				Calibration		Cross-validation	
Variable	*n*	Range	Math transformation	SEC‡	R^2	SECV§	1-VR¶
		g kg DM^{-1}		g kg DM^{-1}		g kg DM^{-1}	
TNC	143	13–212	2,4,4†	6.2	0.98	7.8	0.97
IVTDMD	142	739–954	1,4,4	9.2	0.96	12.7	0.93

† Order of the derivative of log 1/*R*, number of 2-nm data points over which the derivative is calculated, and number of data points used in a running smooth, respectively.
‡ Standard error of calibration.
§ Standard error of cross-validation.
¶ Proportion of variation in laboratory values accounted for in cross-validation.

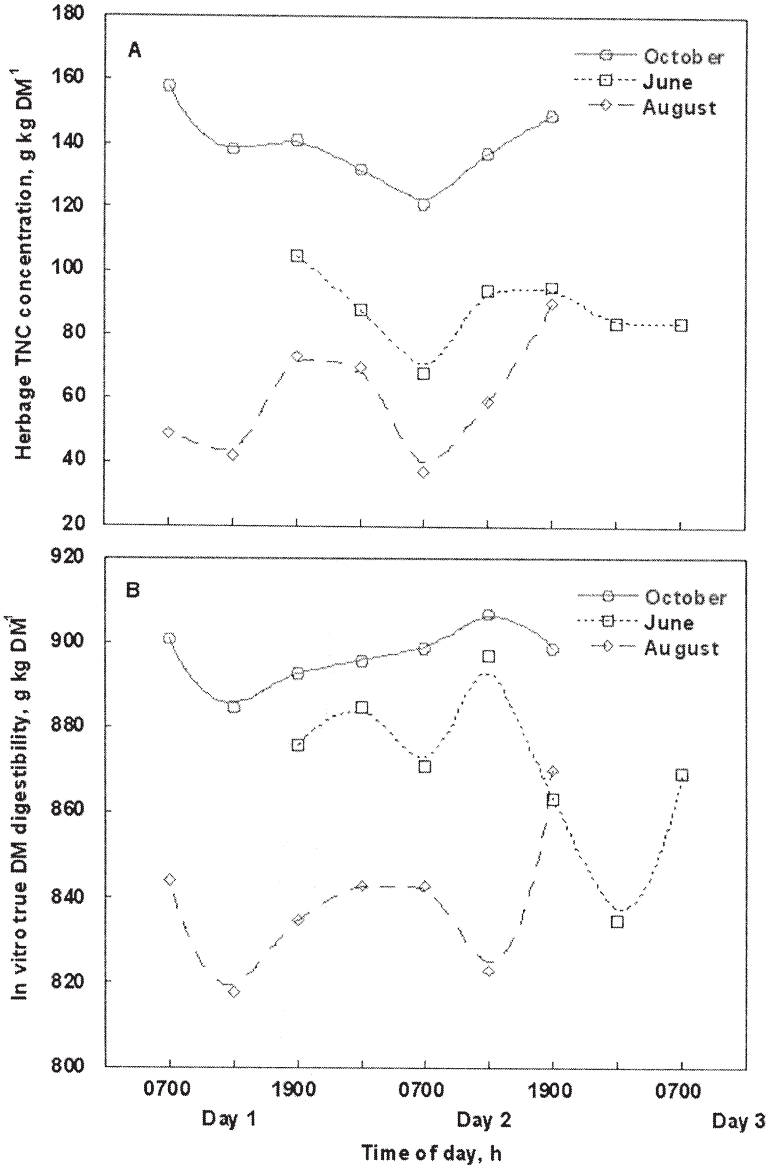

Fig. 2. Herbage a) TNC; and b) IVTDMD concentration in combined orchardgrass control horizons (reconstituted swards) at 6-h intervals during October, June, and August.

October. Seasonal differences in TNC were consistent with patterns reported for orchardgrass (Dent and Aldrich, 1963; Jung et al., 1974) and other cool-season grasses (Delagarde et al., 2000; Mayland et al., 2000; Miller et al., 2001). Digestibility levels in control samples followed the same general seasonal trend as TNC levels. Seasonal differences between TNC and digestibility levels may have been in response to temperature regimes, as shown by Deinum et al. (1968) and Wilson and Ford (1973). Digestibility and TNC levels of individual control horizons were not strongly associated within periods (r^2 = 0.13, 0.06, and 0.24 during October, June, and August, respectively; n = 84 each). This is consistent with other reports of similar patterns between herbage digestibility and SC levels on a diurnal scale, but weaker associations across growth stages and environmental conditions that vary among seasons (Dent and Aldrich, 1963; Michell, 1973; Humphreys, 1989).

Herbage TNC Levels in Defoliation Sequences

Herbage TNC levels fluctuated diurnally and seasonally during sward depletion (Fig. 3a–3c). Treatment patterns in October varied from those in June and August, however. In the AM sequence in all periods, TNC concentration for successively lower horizons increased during daylight, even under low irradiance, then leveled or decreased at night. In the PM sequence, TNC levels increased continuously throughout sward depletion in October, whereas in June and August they decreased in the dark as expected, then continued to decrease or increased only slightly in the light. Absence of TNC accumulation during the light in the PM defoliation sequence in June and August may have been a reflection of lower photosynthetic capacity of older leaves in the lower sward horizons, although few sampled leaves were chlorotic or visibly senescing. Increasing TNC concentration

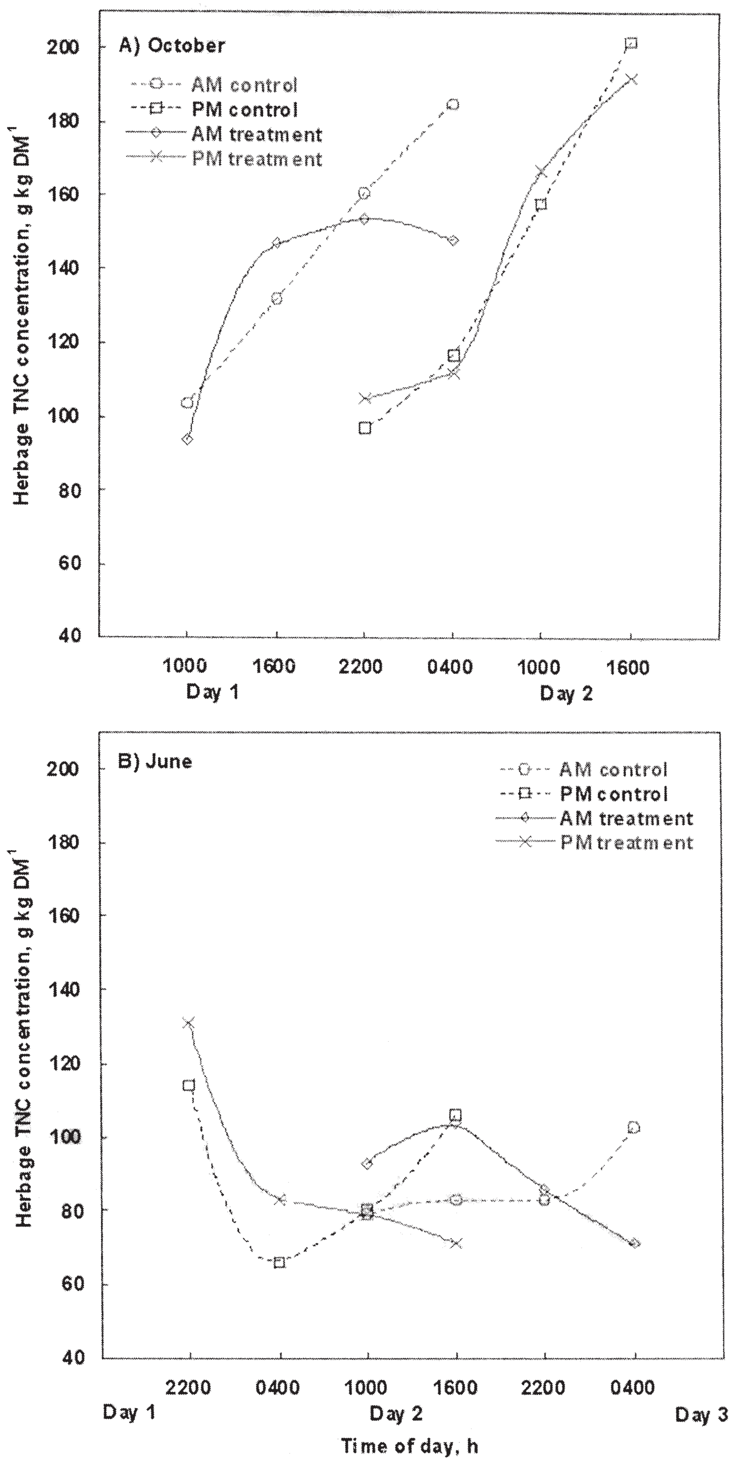

Fig. 3. Continued on next page.

throughout sward depletion in the October PM sequence may have been a reflection of a vertical TNC gradient, low respiratory losses during the dark, or daytime carbohydrate translocation to lower horizons or daughter tillers. Higher herbage SC concentration in lower horizons has been shown for orchardgrass by Davies (1976) and Buxton and Marten (1989), while McGilloway et al. (1999) observed no vertical gradient of SC level and Delagarde et al. (2000) observed decreasing concentrations of SC in lower horizons of ryegrass except in October. Patterns of TNC in control horizons were often unrepresentative of those in the defoliation treatments, particularly in lowest horizons during the last 6 h of sampling sequences. This may be a reflection of differing diurnal profiles of TNC synthesis and metabolism in response to differing leaf masses.

During sward depletion, herbage TNC concentrations differed in a number of cases between defoliation se-

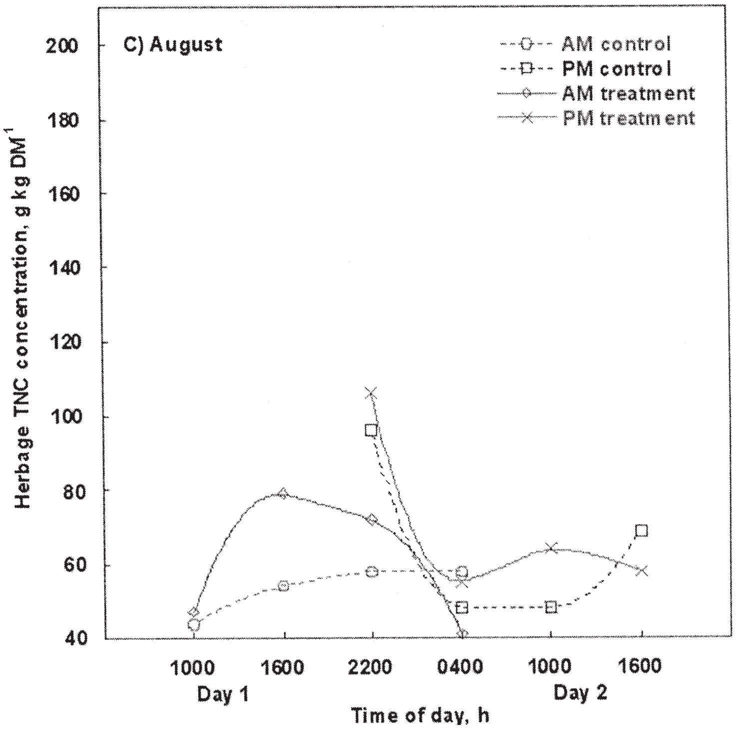

Fig. 3. Herbage TNC concentrations during a) October; b) June; and c) August in successively lower horizons of orchardgrass from control and treatment areas during defoliation sequences initiated at 1900 (PM) and 0700 (AM) h.

quences and from corresponding controls in initial, final, and 24-h mean levels (Table 3). Levels in the initial or final 6 h of sampling, or both, were higher for PM than for AM sequences in some periods, but 24-h mean TNC levels differed only in August, when PM level exceeded AM level by 12 g kg^{-1}. Sample types (defoliation sequences vs. controls) also differed with respect to initial, final, or both TNC levels in each period, but differences were not consistently associated with PM or AM sampling. Differences in initial TNC levels for PM and AM sampling sequences were opposite between defoliation sequences and controls (Table 3). These findings reinforce the dissimilarity of diurnal TNC patterns among samples from defoliation sequences and corresponding horizons in intact swards as shown in Fig. 3.

Bulk density of control sample horizons increased with sward depth, as shown by others (McGilloway et al., 1999; Delagarde et al., 2000; Barrett et al., 2001). Bulk densities were 0.9, 1.1, 1.4, and 1.7 mg DM cm^{-3}, respectively, for successively lower horizons in October, and 0.8, 1.0, 1.6, and 2.2 mg DM cm^{-3} for these horizons in June and August. In spite of increasing bulk density in lower horizons, intake rate of grazing animals would tend to be limited by sward height toward the ends of defoliation sequences (McGilloway et al., 1999; Barrett et al., 2001). Differences among TNC levels in PM and AM sequences in depleted swards would therefore probably have less impact on animal performance than differences in initial TNC level, which were higher in the PM sequence by 38 and 59 g kg^{-1} in June and August, respectively. If defoliation sequences had been terminated at taller residual heights, or livestock consume evening forage at higher rates than simulated in our study, 24-h mean TNC intake could differ more among defoliation sequences than we observed. While our simulation assumes a constant proportional rate of sward height reduction, intake rates and meal sizes for cattle or sheep can be greater in afternoon or evening than in morning (Orr et al., 1997, 2001; Gibb et al., 1998; Barrett et al., 2001). Barrett et al. (2001) observed no difference in dairy cattle intake rates across daily grazing time, but the evening post-milking meal was longer than the morning post-milking meal and comprised 0.34 of total daily grazing time. Similarly, Orr et al. (2001) observed a longer evening meal for dairy cattle on PM daily herbage allocation than on AM allocation, and found that although total daily DM intake was similar under PM and AM herbage allocation, intake between 1645 and 0745 h comprised 0.88 of daily total for cattle receiving PM allocations and only 0.32 for cattle on AM allocation.

Herbage Digestibility in Defoliation Sequences and Relationships with TNC

Herbage digestibility patterns varied seasonally in defoliation sequences and control samples (Fig. 4a–4c). In contrast with TNC patterns, digestibility displayed only minor diurnal variation and decreased rather steadily with sward depletion in PM and AM sequences. As with TNC levels, digestibility patterns in June and August differed from those in October, in that October levels dropped less steeply and extensively. Divergence in diurnal patterns among samples from defoliation sequences and control horizons was not as great as for TNC. Digestibility patterns were not parallel, nor strongly associ-

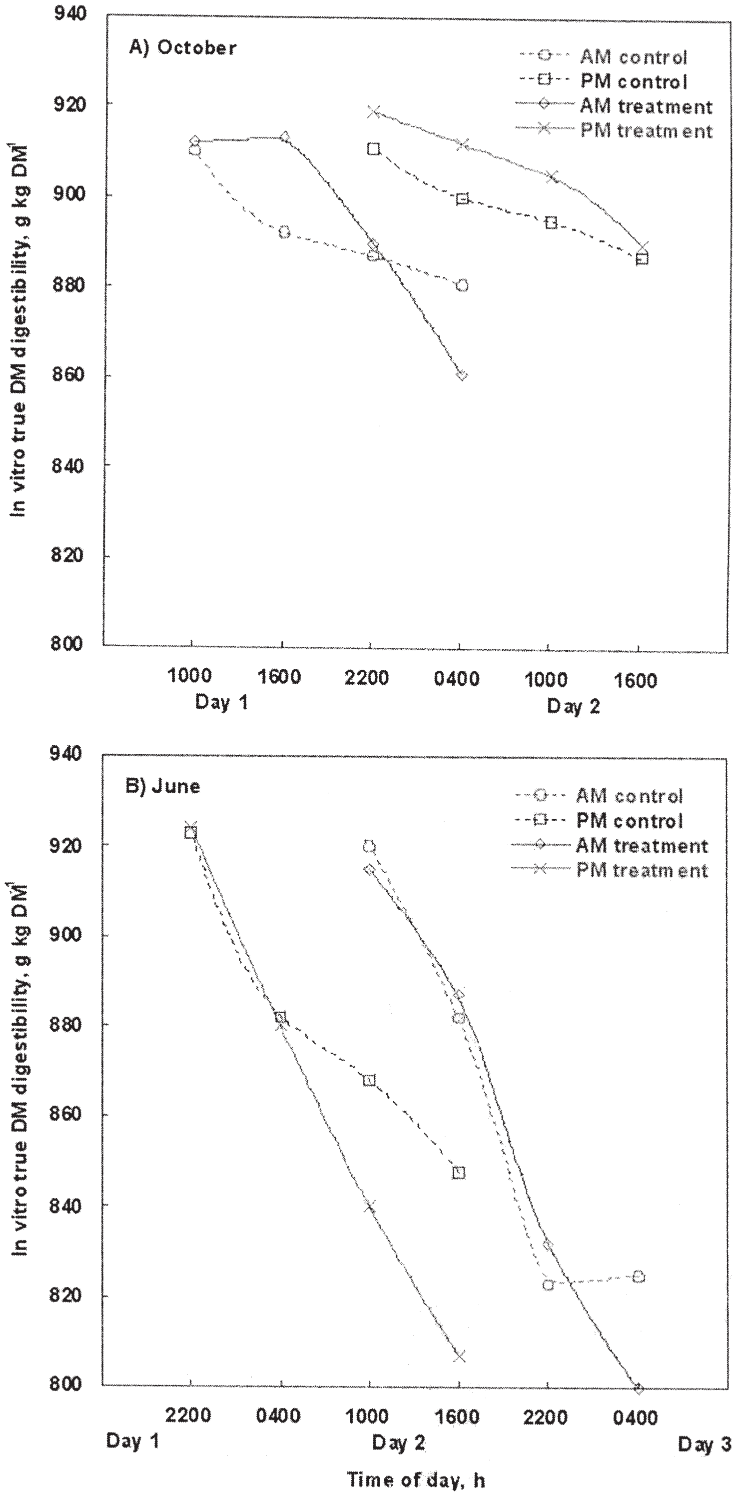

Fig. 4. Continued on next page.

ated, with TNC levels in defoliation sequences (r^2 = 0.07, 0.38, and 0.32 during October, June, and August, respectively; n = 48 each) or corresponding control horizons (r^2 = 0.07, 0.04, and 0.18 during October, June, and August, respectively; n = 48 each), as was also observed with reconstituted swards of combined control horizons (r^2 = 0.01, 0.20, and 0.30 during October, June, and August, respectively; n = 21 each). Initial, final, or both digestibility levels over 24 h were higher for PM than for AM sequences (Table 3), but 24-h mean digestibility differences between treatments were only 11 and 4 g kg^{-1} in October and June, respectively, and treatments did not vary in August. At least one measure of digestibility also varied among samples from defoliation sequences and control horizons in each period, but differences associated with PM or AM sampling were in-

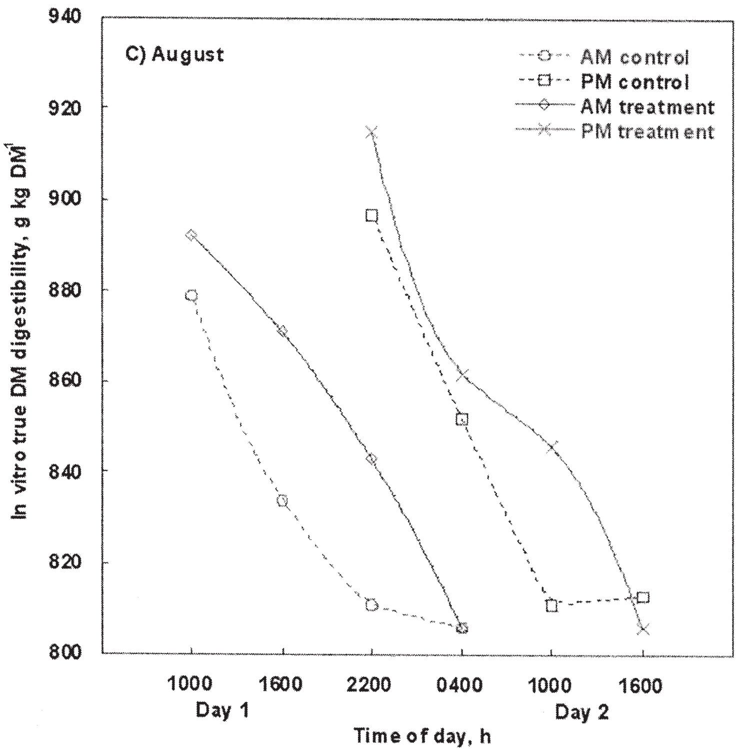

Fig. 4. Herbage IVTDMD concentrations during a) October; b) June; and c) August in successively lower horizons of orchardgrass from control and treatment areas during defoliation sequences initiated at 1900 (PM) and 0700 (AM) h.

consistent. Decreasing herbage digestibility throughout defoliation sequences is consistent with other observations of reduced digestibility in lower horizons (Davies, 1976; Delagarde et al., 2000).

Implications

Small or insignificant differences between mean TNC and digestibility levels during 24-h defoliation sequences do not directly support our hypothesis of higher daily energy intake for PM than for AM herbage allocation. Possible diurnal differences in intake rate and meal size reported by others offer an alternative explanation for a livestock performance advantage for PM herbage allocation. This could result from higher initial TNC and digestibility levels for PM than for AM daily herbage allocation, in conjunction with higher intake rate, longer grazing periods, or larger evening meal size for sheep and cattle than we simulated.

Levels of TNC in control samples from intact swards displayed diurnal patterns similar to those reported by others for samples from mechanical harvesting or gathered during non-grazing periods or under continuous stocking. They were often not representative, however, of patterns during 24-h sward depletion. Additional work with pasture species and defoliation schedules will be required for clearer definition of management impacts on the temporal dynamics of energy intake by grazing animals. Caution should be used in predicting diurnal

Table 2. Environmental conditions during 24 h (i) preceding and (ii) within each orchardgrass defoliation sequence at N. Logan, UT. Daily means for air temperature, relative humidity, solar radiation, and cloud cover are of hourly values.

				Air temperature†							
Initial date	24-h period	Sunrise	Sunset	Max.	Min.	Mean	Soil temp.‡	Relative humidity	Total precip.	Solar radiation§	Cloud cover
		h (MDT)		°C				%	mm	W m^{-2}	%
11 Oct. 2000	AM prior	0735	1851	8.0	−0.3	3.8	10.8	91.9	5.8	78	99
11 Oct. 2000	PM prior			10.9	−0.3	3.9		87.7	3.6	73	85
12 Oct. 2000	AM treatment	0737	1850	10.9	0.9	6.2	8.6	81.3	5.8	73	85
12 Oct. 2000	PM treatment			9.1	4.2	6.1		83.5	10.8	49	97
19 June 2001	PM prior	0552	2105	29.6	9.0	19.6	16.9	36.7	0.0	362	0
20 June 2001	AM prior			29.6	11.8	20.8		36.7	0.0	361	0
20 June 2001	PM treatment			31.5	11.8	21.9		37.6	0.0	362	0
21 June 2001	AM treatment	0553	2106	31.5	11.8	22.8	17.5	37.9	0.0	359	0
15 Aug. 2001	AM prior	0636	2027	28.0	12.5	20.7	22.8	49.3	0.7	173	21
15 Aug. 2001	PM prior			33.0	12.5	22.2		46.0	0.0	289	6
16 Aug. 2001	AM treatment	0637	2025	33.0	13.5	23.0	21.4	39.1	0.0	289	7
16 Aug. 2001	PM treatment			34.6	13.5	23.9		35.0	0.0	285	5

† 2 m above soil surface.
‡ 10 cm below soil surface, recorded daily at 0800 h.
§ Incoming sun plus sky, 400–1100 nm.

Table 3. Herbage TNC and IVTDMD concentrations in orchardgrass swards during 24-h defoliation sequences initiated at 1900 (PM) and 0700 h (AM) and in corresponding control horizons. Weighted means are of sequentially lower horizons throughout 24 h, while initial and final levels are for the top horizon (40–27 cm) during the first 6 h and bottom horizon (12–8 cm) during the last 6 h of each defoliation sequence.

	TNC			IVTDMD		
Period and treatment	**24-h mean**	**Initial**	**Final**	**24-h mean**	**Initial**	**Final**
	g kg DM^{-1}					
12–13 October						
PM defoliation sequence	138	105	192	909	919	890
AM defoliation sequence	132	94	148	898	912	861
PM control sequence	137	97	202	900	912	887
AM control sequence	140	104	185	894	910	881
Mean (SE)	137 (4.3)	100 (3.7)	182 (11.1)	900 (3.4)	913 (2.3)	880 (9.5)
P†, sample type‡	0.49	0.73	*0.08*	*0.12*	*0.06*	0.39
P, defoliation sequence	0.79	0.62	*0.03*	*0.05*	*0.11*	*0.12*
P, type × sequence	0.33	*0.05*	0.26	0.49	0.35	0.26
20–22 June						
PM defoliation sequence	93	131	71	865	924	807
AM defoliation sequence	88	93	71	861	915	800
PM control sequence	92	114	105	882	923	848
AM control sequence	86	79	103	864	920	825
Mean (SE)	90 (4.2)	104 (4.5)	88 (7.6)	868 (4.7)	921 (4.1)	820 (8.6)
P, sample type	0.73	*0.02*	*<0.01*	*0.08*	0.61	*0.01*
P, defoliation sequence	0.29	*<0.01*	0.89	*0.07*	0.18	*0.12*
P, type × sequence	0.91	0.77	0.91	0.21	0.50	0.36
16–17 August						
PM defoliation sequence	72	106	57	859	915	806
AM defoliation sequence	60	47	41	855	892	806
PM control sequence	66	96	69	845	897	813
AM control sequence	53	44	58	834	879	806
Mean (SE)	63 (4.5)	74 (3.4)	56 (3.8)	848 (5.4)	896 (4.8)	808 (4.9)
P, sample type	0.20	*0.10*	*0.01*	*0.02*	*0.02*	0.50
P, defoliation sequence	*0.04*	*<0.01*	*0.01*	0.20	*0.01*	0.50
P, type × sequence	0.92	0.35	0.51	0.56	0.63	0.47

† Significance level of test. Values in italic are significant at $P \leq 0.15$.
‡ Samples are horizons from defoliation sequences or intact swards.

TNC patterns under rotational stocking on the basis of those in intact swards.

ACKNOWLEDGMENTS

Contributions of Ellen Leonard, Susan Buffler, Lisa Mace, and Mary Shepherd are gratefully acknowledged.

REFERENCES

Barrett, P.D., A.S. Laidlaw, C.S. Mayne, and H. Christie. 2001. Pattern of herbage intake rate and bite dimensions of rotationally grazed dairy cows as sward height declines. Grass Forage Sci. 56:362–373.

Buxton, D.R., and G.C. Marten. 1989. Forage quality of plant parts of perennial grasses and relationship to phenology. Crop Sci. 29:429–435.

Ciavarella, T.A., H. Dove, B.J. Leury, and R.J. Simpson. 2000. Diet selection by sheep grazing *Phalaris aquatica* L. pastures of differing water-soluble carbohydrate content. Aust. J. Agric. Res. 51:757–764.

Davies, I. 1976. Developmental characteristics of grass varieties in relation to their herbage production. 1. An analysis of high-digestibility varieties of *Dactylis glomerata* at three stages of development. J. Agric. Sci. 87:25–32.

Deinum, B., A.J.H. Van Es, and P.J. Van Soest. 1968. Climate, nitrogen and grass. II. The influence of light intensity, temperature and nitrogen on in vivo digestibility of grass and the prediction of these effects from some chemical procedures. Neth. J. Agric. Sci. 16:217–223.

Delagarde, R., J.L. Peyraud, L. Delaby, and P. Faverdin. 2000. Vertical distribution of biomass, chemical composition and pepsin-cellulase digestibility in a perennial ryegrass sward: Interaction with month of year, regrowth age and time of day. Anim. Feed Sci. Technol. 84:49–68.

Dent, J.W., and D.T.A. Aldrich. 1963. The inter-relationships between heading date, yield, chemical composition and digestibility in varieties of perennial ryegrass, timothy, cocksfoot, and meadow fescue. J. Nat. Inst. Agric. Bot. 9:261–281.

Fisher, D.S., H.F. Mayland, and J.C. Burns. 2002. Variation in ruminant preference for alfalfa hays cut at sunup and sundown. Crop Sci. 42:231–237.

Fisher, D.S., H.F. Mayland, and J.C. Burns. 1999. Variation in ruminants' preference for tall fescue hays cut either at sundown or at sunup. J. Anim. Sci. 77:762–768.

Fulkerson, W.J., K. Slack, D.W. Hennessy, and G.M. Hough. 1998. Nutrients in ryegrass (*Lolium* spp.), white clover (*Trifolium repens*) and kikuyu (*Pennisetum clandestinum*) pastures in relation to season and stage of regrowth in a subtropical environment. Aust. J. Exp. Agric. 38:227–240.

Gibb, M.J., C.A. Huckle, and R. Nuthall. 1998. Effect of time of day on grazing behaviour by lactating dairy cows. Grass Forage Sci. 53:41–46.

Goering, H.K., and P.J. Van Soest. 1970. Forage fiber analyses. Agric. Handbook No. 379. Agricultural Research Service, US Dep. of Agriculture, Washington, DC.

Holt, D.A., and A.R. Hilst. 1969. Daily variation in carbohydrate content of selected forage crops. Agron. J. 61:239–242.

Humphreys, M.O. 1989. Water-soluble carbohydrates in perennial ryegrass breeding. III. Relationships with herbage production, digestibility and crude protein content. Grass Forage Sci. 44:423–430.

Jung, G.A., R.E. Kocher, C.F. Gross, C.C. Berg, and O.L. Bennett. 1976. Nonstructural carbohydrate in the spring herbage of temperate grasses. Crop Sci. 16:353–359.

Jung, G.A., R.E. Kocher, C.F. Gross, C.C. Berg, and O.L. Bennett. 1974. Seasonal fluctuations of nonstructural carbohydrate concentration in the forage of cool-season grasses. p. 285–293, Grassland Utilization, Part I, Proc. XII Internat. Grassl. Congr., Moscow.

Lechtenberg, V.L., D.A. Holt, and H.W. Youngberg. 1971. Diurnal variation in nonstructural carbohydrates, *in vitro* digestibility, and leaf to stem ratio of alfalfa. Agron. J. 63:719–724.

Lee, M.R.F., E.L. Jones, J.M. Moorby, M.O. Humphreys, M.K. Theodorou, J.C. MacRae, and N.D. Scollan. 2000. Production responses from lambs grazing on *Lolium perenne* selected for high water soluble carbohydrate. p. 45–50. *In* A.J. Rook and P.D. Penning (ed.) Grazing management. Occ. Symp. No. 34, British Grassl. Soc., Reading, Berks, UK.

Mayland, H.F., G.E. Shewmaker, P.A. Harrison, and N.J. Chatterton.

2000. Nonstructural carbohydrates in tall fescue cultivars: Relationship to animal preference. Agron. J. 92:1203–1206.

McGilloway, D.A., A. Cushnahan, A.S. Laidlaw, C.S. Mayne, and D.J. Kilpatrick. 1999. The relationship between level of sward height reduction in a rotationally grazed sward and short-term intake rates of dairy cows. Grass Forage Sci. 54:116–126.

Michell, P.J. 1973. Relations between fibre and water soluble carbohydrate contents of pasture species and their digestibility and voluntary intake by sheep. Aust. J. Exp. Agric. Anim. Husb. 13:165–170.

Miller, L.A., J.M. Moorby, D.R. Davies, M.O. Humphreys, N.D. Scollan, J.C. MacRae, and M.K. Theodorou. 2001. Increased concentration of water-soluble carbohydrate in perennial ryegrass (*Lolium perenne* L.): Milk production from late-lactation dairy cows. Grass Forage Sci. 56:383–394.

Orr, R.J., P.D. Penning, A. Harvey, and R.A. Champion. 1997. Diurnal patterns of intake rate by sheep grazing monocultures of ryegrass or white clover. Grass Forage Sci. 52:65–77.

Orr, R.J., S.M. Rutter, P.D. Penning, and A.J. Rook. 2001. Matching grass supply to grazing patterns for dairy cows. Grass Forage Sci. 56:352–361.

Radojevic, I., R.J. Simpson, J.A. St. John, and M.O. Humphreys. 1994. Chemical composition and *in vitro* digestibility of lines of *Lolium perenne* selected for high concentrations of water-soluble carbohydrate. Aust. J. Agric. Res. 45:901–912.

Schmid, A.R., G.C. Marten, and L.S. Roth. 1969. Effect of N supplementation on *in vitro* digestibility of corn, sorghum, and alfalfa. Agron. J. 61:20–21.

Shenk, J.S., and M.O. Westerhaus. 1991. Population structuring of near infrared spectra and modified partial least squares regression. Crop Sci. 31:1548–1555.

Smith. Dale. 1969. Removing and analyzing total nonstructural carbohydrates from plant tissue. Wisconsin Agric. Exp. Stn. Res. Rep. 41. Univ. of Wisconsin, Madison.

SPSS. 2000. SYSTAT 10 Statistics I. SPSS Inc., Chicago.

Terry, R.A., and J.M.A. Tilley. 1964. The digestibility of the leaves and stems of perennial ryegrass, cocksfoot, timothy, tall fescue, lucerne and sainfoin, as measured by an *in vitro* procedure. J. Br. Grassl. Soc. 19:363–372.

Van Soest, P.J., and J.B. Robertson. 1980. Systems of analysis for evaluating fibrous feed. p. 49–60. *In* W.J. Pigden et al (ed.) Standardization of analytical methodology for feeds. IDRC-134e. Int. Dev. Res. Ctr., Ottawa, Canada.

Vazquez, O.P., and T.R. Smith. 2000. Factors affecting pasture intake and total dry matter intake in grazing dairy cows. J. Dairy Sci. 83: 2301–2309.

Wade, M.H., J.L. Peyraud, G. Lemaire, and E.A. Comeron. 1989. The dynamics of daily area and depth of grazing and herbage intake of cows in a five day paddock system. p. 1111–1112, Proc. XVI Internat. Grassl. Congr., Nice, France.

Welle, R., W. Greten, B. Rietmann, S. Alley, G. Sinnaeve, and P. Dardenne. 2003. Near-infrared spectroscopy on chopper to measure maize forage quality parameters online. Crop Sci. 43:1407–1413.

Wilson, J.R., and C.W. Ford. 1973. Temperature influences on the *in vitro* digestibility and soluble carbohydrate accumulation of tropical and temperate grasses. Aust. J. Agric. Res. 24:187–198.