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Wheat pasture bloat dynamics, in vitro ruminal gas production, and potential bloat mitigation with condensed tannins¹

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ABSTRACT: The aim of this study was to determine the effect of winter wheat (*Triticum aestivum* L.) forage growth stage, forage allowance, time of day, and commercial condensed tannins (CT) on steer bloat dynamics and in vitro ruminal gas production. Twenty-six cross-breed steers (Angus × Hereford × Salers; average initial BW = 194 ± 26 kg) were used. Wheat forage allowances were either 18 kg (high forage allowance) and 6 kg (low forage allowance) of DM/(100 kg BW·d). In each bloat observation period, fresh wheat forage samples were hand-clipped to ground level in all study pastures for nutrient and in vitro ruminal gas production analyses. In vitro ruminal gas accumulation was measured at 0, 1, 2, 3, 4, 5, 6, and 12 h. Commercial CT was added at 0, 10, 15, and 20 mg of CT/g of DM. Bloat was scored once per week on two consecutive days at 0800 and 1500 during the vegetative stage and once every 2 wk during the reproductive stage of wheat development. Mean bloat score was calculated for each steer by time of day, stage of plant growth, and forage allowance. Bloat was detected in 65.8% of the observation periods. Average bloat scores were four and 2.5 times greater

($P < 0.05$) in cattle grazing at a high forage allowance than at a low forage allowance in the vegetative and reproductive growth phases of wheat, respectively. Rate of gas production was greater ($P < 0.001$) in the vegetative stage than in the reproductive stage. Steer bloat score was positively correlated with forage CP ($r = 0.22$; $P < 0.05$) and IVDMD ($r = 0.32$; $P < 0.05$). Rate of ruminal gas production was positively correlated ($P < 0.01$) to forage CP ($r = 0.48$), NPN ($r = 0.40$), soluble protein ($r = 0.32$), and IVDMD ($r = 0.47$). Conversely, negative correlations were found for forage DM ($r = -0.20$; $P < 0.05$), insoluble protein ($r = -0.40$), NDF ($r = -0.69$), and forage height ($r = -0.49$; $P < 0.01$) on the rate of ruminal gas production. Addition of CT at levels greater than 10 mg of CT/g of DM decreased ($P < 0.05$) the rate of in vitro ruminal gas and methane gas production after 5 h of incubation. Wheat pasture bloat is a complex disorder that varies across an array of forage and environmental conditions. Condensed tannins have the potential to decrease bloat by altering ruminal gas production and soluble protein digestibility from wheat forage.

Key Words: Bloat, Condensed Tannins, Forage Allowance, Ruminal Gas, Wheat Forage

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Introduction

Frothy bloat, which is characteristic of wheat pasture bloat, is caused by the capture of ruminal gases in a polysaccharide slime layer (Hungate et al., 1955; Cole and Boda, 1960). Resultant increases in intraruminal pressure and physical distention suppress nerve receptors at the esophagus reticulorumen juncture that regulate eructation, leading to a cessation of eructation (Cole and Boda, 1960). Ruminants experiencing frothy

bloat when grazing wheat pasture frequently die from bloat induced cardiac or pulmonary arrest (Horn et al., 1977).

Frothy bloat results from complex interactions among plant, animal (Clarke and Reid, 1974; Jones and Mangan, 1977), and environmental (Majak et al., 1995) factors. Animal factors include ruminal gas and foam production dynamics, rate of passage, and ruminal microbial populations (Hungate et al., 1955; Cole and Boda, 1960; Bartley and Bassette, 1961). Total and soluble forage proteins have been identified as precursors to bloat on wheat pasture (Bartley et al., 1975). The rapid release of soluble protein into ruminal fluid promotes the formation of the polysaccharide slime (Clarke and Reid, 1974; Howarth et al., 1991).

Legumes containing condensed tannins (CT) decrease ruminal gas formation and microbial deamina-

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tion and prevent bloat because of CT plant protein interactions (Jones and Lyttleton, 1971; Waghorn and Jones, 1989; Min et al., 2003). Commercial CT (Quebracho CT) added to a tannin-free diet decreased protein digestibility in a dose-dependent manner in mule deer (*Odocoileus hemionus hemionus*) and Suffolk sheep (*Ovis aries*; Hagerman et al., 1992). Apparently Quebracho CT decreases ruminal digestibility of dietary compounds in a manner similar to forage CT.

The objectives of this study were to determine the effect of stage of growth, forage allowance, and time of day on wheat forage chemical composition and steer bloat. The effect of plant chemical composition and exogenous plant CT on in vitro ruminal gas production also was measured.

Materials and Methods

Experiment 1: Effect of Time of Day and Forage Allowance on Bloat, Wheat Nutrient Status, and In Vitro Gas Production Dynamics

A combination of field and laboratory in vitro fermentation research was used to determine the effect of forage allowance (low and high forage allowance), stage of growth (vegetative vs. reproductive stage), and time of day (morning vs. afternoon) on the occurrence of bloat and in vitro ruminal gas production. Daily weather data were recorded (21X [L] Micro logger Weather Station, Campbell Sci., Inc., Logan, UT) to quantify relationships of air temperature (<-1 vs. >10°C) and solar radiation (<20 vs. >20 W/m²) to bloat dynamics.

Research was conducted on four, 4.5-ha paddocks in Wilbarger County, TX (long 33°57'N, lat 99°26'W). The experimental paddocks were cultivated and fertilized with 56 kg of N/ha and 17.8 kg of S/ha on August 30, 2002. On September 26, 2002, paddocks were cultivated and sown to a dual-purpose winter wheat (*Triticum aestivum* L. var. Lockett) at a seeding rate of 67 kg/ha. To suppress weeds, paddocks were sprayed on October 25, 2002 with a mixture of 0.28 kg of active ingredient/ha sulfosulfuron, 0.01 kg of active ingredient/ha chlor-sulfuron, and 0.002 kg of active ingredient/ha metsulfuron-methyl herbicides in water carrier with 0.25% (vol/vol) nonionic surfactant.

The grazing period was from January 29 to April 4, 2003. Paddocks were continuously grazed over the grazing period. High-forage allowance paddocks were stocked with four steers (average initial BW = 196 ± 22 kg) per paddock to establish a forage allowance of 18 kg of DM/(100 kg BW·d). Low-forage allowance paddocks were stocked with nine steers (average initial BW = 192 ± 30 kg) per paddock to establish a forage allowance of 6 kg of DM/(100 kg BW·d). Each forage allowance treatment was replicated twice. Stocking rate was increased in March to maintain forage allowance by decreasing the size of each paddock 37%.

Animals

Twenty-six crossbreed steers (Angus × Hereford × Salers; average initial BW = 194 ± 26 kg) were fed free-choice Bermuda grass and sorghum hays while grazing native range pastures for 30 d before grazing wheat pasture. Steers were preconditioned for 45 d before arrival. There was no morbidity or death loss in the cattle during the experimental period. Cattle had free choice access to water and a mineral supplement containing 150 mg of lasalocid/113.4 g of mineral during the wheat pasture grazing experiment. Mineral composition on an as-fed basis was 13% Ca, 3.0% P, 16% salt, 7% Mg, 400 ppm copper, 20 ppm selenium, 3,000 ppm zinc, and 34,050 IU of vitamin A/kg (ACCO Wheat Advantage Medicated Mineral, Minneapolis, MN). At 14- to 30-d intervals, cattle were individually weighed without shrink adjustment in the early morning within a 30-min period.

Bloat Scoring

From January 29 to April 4, 2003, steers were monitored for bloat on two consecutive days at 0800 (morning) and 1500 (afternoon) at 1-wk intervals during the vegetative (January 29 to February 28) and 2-wk intervals during the reproductive (March 1 to April 4) growth stages of wheat. Bloat scoring followed Paisley and Horn (1998): 0 = normal, no visible signs of bloat; 1 = slight distention of left side of animal; 2 = marked distention of left side of animal, rumen distended upward toward top of back, animal has asymmetrical (egg shape) appearance when walking away; and 3 = severe distension, distention is above the top of the back and is visible from right side of animal. Mean bloat score was calculated for each steer by time of day, stage of plant growth, and forage allowance.

Forage Measurements

Herbage mass and forage allowance were measured at 14- and 35-d intervals. Forage allowance was estimated by hand-clipping wheat standing crop from five, 1 m² quadrats/paddock to ground level. Samples were dried in a forced-air oven at 60°C for 48 h. Forage allowance was calculated as the kg forage DM/(100 kg BW·d) in each paddock.

At the time bloat scores were measured, three hand-clipped forage samples (approximately 500 g fresh basis) for nutritive value analyses were collected from random locations in each paddock. These samples were subsequently pooled, thoroughly mixed, and analyzed for protein fractions. Subsequent forage samples were stored at -20°C for in vitro ruminal gas production analyses or oven dried at 60°C for 48 h and ground (Cyclone sample mill, Udy Co., Fort Collins, CO) to pass a 1-mm sieve for NDF and IVDMD analyses. Fresh frozen forage was minced in a blender (model DS-7, Waring Products Co., Winsted, CT) for use for in vitro experiments. Minced fresh forage is better correlated

with chewed boli for particle distribution than other sample preparation (freeze dried and ground or chopped) methods (Min et al., 2000).

In Vitro Ruminant Incubation and Gas Production

Duplicated in vitro ruminal gas production was measured as plunger displacement (mL) at incubation periods of 0, 1, 2, 3, 4, 5, 6, and 12 h (Alyea, 1992; Paisley and Horn, 1998). Each in vitro run consisted of 16 incubations. The in vitro ruminal incubation procedure consisted of placing 5 g of minced fresh wheat forage in 250-mL volumetric flasks containing 20 mL of ruminal fluid, 30 mL of artificial saliva, buffered to pH 6.8, saturated with CO₂ gas and maintained at 39°C (Min et al., 2000). Total in vitro gas produced was corrected to blank incubations (i.e., no ruminal fluid). Ruminal fluid was collected from a single cannulated steer fed Bermuda grass hay, mixed and strained through four layers of cheesecloth and flushed with CO₂ gas. Flask stoppers were equipped with rubber tubing connected to 60-mL syringes (Tyco Health Care Ltd., Mansfield, MA). All syringes were lubricated with dose syringe oil (Jupiter Vet Products, Harrisburg, PA) to ensure consistent plunger resistance and movement.

Experiment 2: Effect of Condensed Tannins on In Vitro Ruminant Gas Production

In vitro analysis was conducted to determine the effect of CT on ruminal gas production when wheat forage was incubated with ruminal fluid. In vitro incubations were conducted as in Exp. 1. The forage allowance treatments and sampling procedures were also the same as used in Exp. 1. All in vitro analyses were conducted in duplicate.

Commercial CT (a crude extract of the bark of *Shi-nopsis* spp.) was added at 0, 10, 15, and 20 mg CT/g of DM. Gas production was monitored as in the previous experiment. After 12 h of incubation, syringes were removed from in vitro ruminal incubators and capped with a rubber stopper for subsequent measurement of methane gas production.

Laboratory Measurements

Total CP, soluble protein N, insoluble protein N, and NPN from fresh forage samples were determined by the Kjeldahl digestion procedure (AOAC, 1990). Forage samples were prepared as described by Bartley et al. (1975). One gram (fresh sample) of the chopped (0.5 cm) plant material from each sample was analyzed for Kjeldahl N (total N). Wheat forage was fractionated into soluble protein and NPN by blending 5 g of sample with 100 mL of distilled water, and chopping (approximately 500 rpm) for two 15-s intervals in a blender (Waring model DS-7). Homogenate was vacuum-filtered through Whatman No. 4 filter paper (Whatman Ltd., Maidstone, U.K.). The residue was transferred to Kjeldahl flasks to determine insoluble protein. Eighty

milliliters of the measured filtrate was acidified by the addition of 10 mL of 15% (vol/vol) trichloroacetic acid to precipitate soluble proteins (Waghorn and Jones, 1989) and refrigerated (4°C) overnight. The mixture was vacuum filtered through Whatman No. 2 filter paper, and the filtrate was transferred to Kjeldahl flasks to determine NPN. Soluble protein N was calculated as soluble protein N = CP - (NPN + insoluble protein N). The NDF and IVDMD of dried forage samples were determined using the filter bag technique (Ankom Technology Corp., Fairport, NY). Methane gas was determined from 12 h in vitro incubation gas samples in an open-circuit respiration calorimetric system (Puchala et al., 2005; Sable Systems, Henderson, NV). The gas analyzer was calibrated against certified methane gas with known methane gas concentration at the beginning of each analysis.

Statistical Analyses

Data were analyzed as a repeated-measures analysis using the MIXED procedure of SAS (SAS, Inst., Inc., Cary, NC). Data are presented as mean values and the associated SEM. Variables in Exp. 1 included frothy bloat, forage height, protein fractions, NDF, IVDMD, OM, and in vitro ruminal gas production. The model included stage of growth, forage allowance, time of day, replicate, and associated interactions. The relationships between forage chemical composition, ruminal gas production, environmental conditions, forage allowance, and pasture bloat were examined by correlation analysis. Variables in Exp. 2 included those in Exp. 1, except that bloat score was omitted, only morning samples were analyzed, and methane gas production was measured. The model included stage of growth, forage allowance, replicate, CT treatment, and associated interactions.

In vitro gas production rate was calculated using the exponential equation of Ørskov and McDonald (1979):

$$Y = a + b(1 - e^{-ct}) \quad [1]$$

where Y was defined as gas production in time *t*; a, b, and c being constants of the exponential Eq. [1], where a = the gas production at time 0, b = the proportion of gas production during time (*t*), and c = the rate of gas production of the 'b' fraction. The constants b and c for each treatment were calculated with the method described by Min et al. (2000) using the NLIN procedure from SAS. The response of b and c to forage allowance, stage of growth, time of day, CT treatment, and associated interactions was analyzed by repeated-measures analyses, with stage of growth as the repeated measures and replicate as the random effect, using the MIXED procedure of SAS. A protected (*P* < 0.05) LSD mean separation procedure was used in all analyses.

Table 1. The effect of stage of growth (SG; vegetative vs. reproductive), time of day (TD; morning and afternoon), and forage allowance (FA) on in vitro ruminal gas production from wheat forage and bloat characteristics of steers grazing wheat pasture from January 29 to April 4, 2003^a

| Item | Rate of gas production | | Potential gas production | Bloat score (BS) |
|-----------------|------------------------|-------------------|--------------------------|----------------------------|
| | n | c, mL/h | a + b, mL/12 h | Mean BS/steer ^a |
| SG ^b | | | | |
| VS | 16 | 15.9 ^d | 55.7 | 0.26 |
| RS | 16 | 7.2 ^e | 59.3 | 0.19 |
| SEM | | 0.99 | 2.85 | 0.21 |
| TD | | | | |
| Morning | 16 | 12.2 | 58.5 | 0.25 |
| Afternoon | 16 | 10.9 | 56.4 | 0.20 |
| SEM | | 0.99 | 2.86 | 0.05 |
| VS ^b | | | | |
| Morning | 8 | 16.7 | 56.2 | 0.30 |
| Afternoon | 8 | 15.1 | 55.1 | 0.21 |
| RS ^b | | | | |
| Morning | 8 | 7.7 | 60.9 | 0.18 |
| Afternoon | 8 | 6.7 | 57.6 | 0.20 |
| SEM | | 1.41 | 4.05 | 0.07 |
| FA ^c | | | | |
| Low FA | 16 | 11.1 | 62.2 ^d | 0.12 ^e |
| High FA | 16 | 12.0 | 52.7 ^e | 0.34 ^d |
| SEM | | 1.00 | 2.69 | 0.05 |
| VS ^b | | | | |
| Low FA | 8 | 15.2 | 59.2 ^d | 0.13 ^e |
| High FA | 8 | 16.6 | 52.0 ^e | 0.40 ^d |
| RS ^b | | | | |
| Low FA | 8 | 7.0 | 65.2 ^d | 0.10 ^e |
| High FA | 8 | 7.4 | 53.3 ^e | 0.25 ^d |
| SEM | | 1.41 | 3.81 | 0.07 |
| Interaction | | | | |
| SG × FA | | NS | NS | 0.04 |
| SG × TD | | NS | NS | NS |
| SG × TD × FA | | NS | 0.01 | 0.05 |

^aBloat scores (BS) were: 0 = no visible signs of bloat; 1 = slight distention of left side; 2 = marked distention of left side; and 3 = left and right sides distended. The in vitro ruminal gas production (Y) was calculated using the following exponential equation (Ørskov and McDonald, 1979): $Y = a + b(1 - e^{-ct})$, where Y = ruminal gas production in time t, and a, b, and c are constants of the exponential equation, where a = the ruminal gas production at time 0, b = the proportion gas production during time (t), and c = the rate of gas production of the b fraction. Potential ruminal gas production was calculated as a + b.

^bVS = vegetative stage (January to February), RS = reproductive stage (March to April).

^cForage allowance expressed as kg DM/(100 kg BW·d) = high (18 kg) and low (6 kg).

^{d,e}Within a column, means without a common superscript letter differ, $P < 0.05$.

Results

Bloat Dynamics

Across forage allowance treatments and replicates, there were 76 morning and afternoon bloat observation periods conducted from January 29 to March 20, 2003 (data not shown). Bloat occurred in at least one steer

in 65.8% of the observation periods (50 out of 76 observation periods). Over 92% of observed bloat was classified as bloat score 1. Overall group average bloat scores were <1 as a result of low bloat severity rather than low bloat frequency (Table 1).

Mean bloat scores across days and replicates were 0.34 and 0.12 for high and low forage allowances, respectively (Table 1). Across forage allowance, average percentage of bloated animals in the low forage allowance treatment was less ($9.06 \pm 3.04\%$; $P < 0.01$) than in animals grazing the high forage allowance treatment ($41.25 \pm 6.9\%$; data not shown). Cattle grazing wheat in a vegetative stage of development at high forage allowances exhibited four times greater ($P < 0.05$) group average bloat scores than cohorts grazed at low forage allowances (Table 1). Group average bloat scores when grazing in the reproductive stage of development were 2.5 times greater ($P < 0.05$) for cattle at high forage allowance than cattle at low forage allowance. There was a stage of growth × forage allowance interaction ($P < 0.04$) and a stage of growth × forage allowance × time of day interaction ($P < 0.05$) for bloat score. The stage of growth × forage allowance interaction resulted from bloat scores decreasing less (23%) in low forage allowance from the vegetative stage to reproductive stage than corresponding decreases (38%) in high forage allowance treatments. Similarly, the stage of growth × forage allowance × time of day interaction occurred because bloat scores decreased from morning (bloat score = 0.53) to afternoon (bloat score = 0.27) during the vegetative stage of growth at the high forage allowance and not changing from morning (bloat score = 0.27) to afternoon (bloat score = 0.23) in the reproductive stage of growth at the high forage allowance. There was no effect ($P = 0.92$) of forage allowance treatment on individual animal weight gain. Across forage allowance treatments, cattle gained 1.1 ± 0.16 kg/d.

In Vitro Ruminal Gas Production Dynamics

The estimated rate of ruminal gas production, c (mL/h), over 12 h was 55% greater ($P < 0.001$) during the vegetative growth (January to February) than for the reproductive stage of development (Table 1). The rate of gas production did not differ ($P > 0.10$) between morning and afternoon forage samples, or between high and low forage allowances. No interaction for the rate of gas production among forage allowance, time of day, and stage of growth variables was detected.

Potential gas production (a + b) varied primarily as a function of forage allowance (Table 1). Potential gas production was greater ($P < 0.001$) for the low forage allowance than for the high forage allowance. The relationship of potential gas production to forage allowance was more pronounced in the reproductive ($P < 0.01$) than in the vegetative ($P < 0.05$) growth phase.

Table 2. Correlations (*r*) of temperature and solar radiation, time of day (morning vs. afternoon), and forage allowance (FA; low vs. high) to mean bloat score (BS)

| Item | n | Low FA BS ^a | | High FA BS ^b | |
|------------------------------|---|------------------------|------------------------|-------------------------|------------------------|
| | | Morning ^c | Afternoon ^c | Morning ^c | Afternoon ^c |
| 1st measurement ^d | | | | | |
| Low temperature | 8 | -0.24 | -0.07 | -0.31 | 0.21 |
| High temperature | 8 | -0.53 | -0.40 | -0.37 | 0.33 |
| Low radiation | 8 | 0.25 | -0.31 | -0.06 | 0.21 |
| High radiation | 8 | 0.30 | -0.21 | 0.53 ^e | 0.12 |
| 2nd measurement ^d | | | | | |
| Low temperature | 8 | -0.62 ^e | -0.13 | -0.30 | 0.19 |
| High temperature | 8 | 0.31 | -0.17 | 0.06 | -0.42 |
| Low radiation | 8 | 0.31 | -0.06 | 0.21 | 0.19 |
| High radiation | 8 | 0.60 ^e | -0.05 | 0.43 ^e | -0.11 |

^aLow FA BS = low forage allowance (6 kg of DM/[100 kg BW·d]) bloat score.

^bHigh FA BS = high forage allowance (18 kg of DM/[100 kg BW·d]) bloat score.

^cTime of day = morning (0800) and afternoon (1500).

^d1st measurement = January 28 to February 19. 2nd measurement = February 20 to March 7.

^eTended to differ within forage allowance between morning and afternoon sampling periods. $P = 0.13$ for the 1st measurement, High-FA-BS, High radiation; $P = 0.07$ for the 2nd measurement, Low FA-BS, Low temperature; $P = 0.09$ for the 2nd measurement, Low FA-BS, High radiation; and $P = 0.15$ for the 2nd measurement, High FA-BS, Low temperature.

Relationships of Forage Characteristics and Environmental Conditions to Bloat and Ruminal Gas Production

Forage CP ($r = 0.22$; $P < 0.05$) and IVDMD ($r = 0.32$; $P < 0.05$) were positively correlated to bloat score (data not shown). Forage NDF was negatively correlated to bloat score ($r = -0.27$; $P < 0.01$). Forage CP content was positively correlated to ($P < 0.001$) soluble protein N ($r = 0.55$) and IVDMD ($r = 0.64$). Forage CP was negatively correlated to forage height ($r = -0.71$; $P < 0.001$) and NDF ($r = -0.65$; $P < 0.01$) content.

Averaged across all temporal variables, CP ($r = 0.48$), NPN ($r = 0.40$), soluble protein N ($r = 0.32$), and IVDMD ($r = 0.47$) were positively ($P < 0.01$) correlated to the rate of gas production. In contrast, forage DM ($r = -0.20$; $P < 0.05$), insoluble protein N ($r = -0.40$), NDF ($r = -0.69$), and forage height ($r = -0.49$; $P < 0.01$) had negative effects on the rate of gas production. The NDF content had a positive ($r = 0.23$; $P < 0.05$) effect on the potential gas production. Forage CP ($r = -0.19$; $P < 0.05$) had a negative effect on potential ruminal gas production. The rate of gas production and potential gas production was not significantly correlated ($P > 0.10$) to degree of bloat.

Overall, forage allowance, temperature, and solar radiation were correlated to bloat (Table 2). Across the grazing season, high solar radiation was positively correlated to bloat score in low ($r = 0.3$ on first measurement and $r = 0.6$ on second measurement; $P = 0.09$) and high forage allowance ($r = 0.53$ on first measurement; $P = 0.13$ and $r = 0.43$ on second measurement; $P = 0.15$). In the morning, low temperature ($< -1^\circ\text{C}$) and low forage allowance were negatively ($r = -0.62$; $P = 0.07$) correlated to bloat score on first measurement. Bloat score was relatively greater for low temperature ($< -1^\circ\text{C}$) and high solar radiation than for high tempera-

ture and low solar radiation in high forage allowance; however, the relationships between bloat and weather were more variable at the low forage allowance.

Forage Standing Crop and Nutritive Value Dynamics

Across the grazing season, herbage mass in wheat pasture was greater ($P < 0.001$) for high forage allowance (2,140 kg of DM/ha) than for low forage allowance (707 kg of DM/ha; data not shown).

Forage IVDMD was greater ($P < 0.05$) under high vs. low forage allowances during the vegetative stage and similar in the reproductive stage of growth (Table 3). Similarly, forage OM was greater ($P < 0.05$) in the vegetative stage and similar in the reproductive phase. Decreased OM content at the low forage allowance in the vegetative phase suggests more soil contamination. Overall, CP ($P < 0.01$) and percentage of IVDMD content in wheat forage decreased ($P < 0.01$) from the vegetative to reproductive growth stage. Conversely, NDF ($P < 0.01$) and DM ($P < 0.09$) percents increased in the reproductive growth stage. Wheat forage in the vegetative growth stage (January to February) had greater ($P < 0.001$) proportions of soluble protein N and NPN than in the reproductive growth stage (March to April; Table 3). There tended to be a stage of growth \times time of day interaction ($P = 0.09$) for soluble protein N and insoluble protein N. Soluble protein N content increased ($P < 0.05$) from morning to afternoon periods in the vegetative stage. In contrast, morning to afternoon soluble protein N levels did not differ ($P > 0.10$) in the reproductive stage. Insoluble protein N tended to decrease from morning to afternoon in the vegetative stage and decrease or remain unchanged in the reproductive stage. Overall, the proportion of insoluble protein N was 23% lower ($P < 0.01$) in the vegetative growth stage than in the reproductive stage. Across growth stages, forage

Table 3. Effect of stage of growth (SG), time of day (TD), and forage allowance (FA) on nutrient content, protein fractions, in vitro dry matter digestibility, and forage height (FH) of winter wheat forage January 29 to April 4, 2003

| Item | n | % of protein fraction ^a | | | | | | | | |
|-----------------|----|------------------------------------|-------------------|-------------------|-------------------|-------------------|------------------|-------------------|-------------------|-------------------|
| | | DM | OM | CP | ISP | SP | NPN | NDF | IVDMD | FH, cm |
| | | —— % of DM —— | | | —— % of DM —— | | | | | |
| SG ^b | | | | | | | | | | |
| VS | 16 | 26.6 | 88.2 | 17.9 ^e | 41.1 ^f | 53.1 ^e | 5.8 ^e | 27.5 ^f | 94.6 ^e | 12.0 ^f |
| RS | 16 | 27.3 | 90.2 | 14.5 ^f | 53.3 ^e | 43.1 ^f | 3.6 ^f | 36.6 ^e | 89.7 ^f | 24.1 ^e |
| SEM | | 0.25 | 0.92 | 0.56 | 1.41 | 1.01 | 0.15 | 0.54 | 0.39 | 0.85 |
| TD ^c | | | | | | | | | | |
| AM | 16 | 26.5 ^f | 88.1 | 16.3 | 47.7 | 47.7 | 4.6 | 32.8 | 91.6 ^f | 18.4 |
| PM | 16 | 27.4 ^e | 90.4 | 16.2 | 46.7 | 48.5 | 4.8 | 31.4 | 92.7 ^e | 17.7 |
| SEM | | 0.24 | 0.89 | 0.40 | 0.99 | 1.01 | 0.15 | 0.54 | 0.38 | 1.00 |
| VS ^b | | | | | | | | | | |
| AM | 8 | 26.4 | 86.0 | 17.7 | 42.7 | 51.5 | 5.8 | 28.6 ^e | 94.0 | 12.1 |
| PM | 8 | 26.9 | 90.5 | 18.3 | 39.4 | 54.7 | 5.8 | 26.5 ^f | 95.1 | 11.9 |
| RS ^b | | | | | | | | | | |
| AM | 8 | 26.6 ^f | 90.1 | 14.8 | 52.6 | 43.9 | 3.5 | 36.9 | 89.1 | 24.6 |
| PM | 8 | 27.9 ^e | 90.3 | 14.2 | 54.0 | 42.2 | 3.7 | 36.3 | 90.3 | 23.5 |
| SEM | | 0.34 | 1.85 | 0.56 | 1.40 | 1.41 | 0.21 | 0.77 | 0.54 | 1.42 |
| FA ^b | | | | | | | | | | |
| Low FA | 16 | 26.7 | 87.8 ^f | 16.4 | 47.7 | 47.5 | 4.7 | 32.6 | 91.9 | 14.9 ^f |
| High FA | 16 | 27.2 | 90.7 ^e | 17.9 | 46.7 | 48.6 | 4.6 | 31.5 | 92.4 | 21.2 ^e |
| SEM | | 0.25 | 1.39 | 0.39 | 1.41 | 1.01 | 0.21 | 0.76 | 0.54 | 0.85 |
| VS ^b | | | | | | | | | | |
| Low FA | 8 | 26.4 | 86.1 ^f | 18.0 | 41.5 | 52.6 | 5.9 | 28.8 ^e | 94.0 | 10.8 |
| High FA | 8 | 26.9 | 90.5 ^e | 17.9 | 40.7 | 53.7 | 5.6 | 26.3 ^f | 95.1 | 13.2 |
| RS ^b | | | | | | | | | | |
| Low FA | 8 | 27.0 | 89.5 | 14.7 | 53.9 | 42.5 | 3.5 | 36.5 | 89.8 | 18.9 ^f |
| High FA | 8 | 27.5 | 90.9 | 14.4 | 52.7 | 43.6 | 3.7 | 36.7 | 89.9 | 29.2 ^e |
| SEM | | 0.35 | 1.84 | 0.56 | 1.41 | 0.97 | 0.21 | 0.76 | 0.54 | 1.22 |
| Interaction | | | | | | | | | | |
| SG × FA | | NS | NS | NS | NS | NS | NS | NS | NS | 0.001 |
| SG × TD | | NS | NS | NS | 0.09 | 0.08 | NS | NS | NS | NS |
| SG × TD × FA | | NS | 0.05 | NS | NS | NS | NS | NS | NS | 0.001 |

^aPercentage of total protein; ISP = insoluble protein N; SP = soluble protein N.

^bVS = vegetative stage (January to February); RS = reproductive stage (March to April). Forage allowance expressed as kg of DM/(100 kg BW·d) = high (18 kg) and low (6 kg).

^cTime of day = morning (AM = 0800) and afternoon (PM = 1500).

^{e,f}Within a column, means without a common superscript letter differ, $P < 0.05$.

collected in the afternoon had greater ($P < 0.05$) IVDMD than when collected in the morning. The NDF content tended to be greater ($P = 0.07$) in the morning- vs. afternoon-harvested wheat forage (Table 3).

Forage allowance had no effect on CP, insoluble protein, or soluble protein N of the wheat forage (Table 3). The NDF content was lower ($P < 0.03$) in high forage allowance than low forage allowance during the vegetative stage and comparable in the reproductive stage (Table 3).

Effect of Condensed Tannin Addition on Total and Cumulative In Vitro Gas Production

The effects of CT on in vitro ruminal gas and methane gas production are summarized in Table 4. Addition of CT above 15 mg/g of DM decreased the rate of ruminal gas production ($P < 0.01$) and methane gas production ($P < 0.05$; Table 4). There was no effect on average hourly rate of ruminal gas at 15 mg of CT/g of DM;

however, the average hourly rate of methane production was lower ($P < 0.05$) than controls and similar to 10 and 20 mg of CT/g of DM treatments. The overall effects of forage allowance and stage of growth on average hourly gas production in the CT experiment were similar in magnitude but quantitatively lower than in Exp. 1 (Table 1), reflecting the addition of CT. Methane production varied in response to stage of growth ($P < 0.01$) and forage allowance ($P < 0.01$). Methane production was 61% greater in the reproductive stage than the vegetative stage growth phase. Low forage allowance methane production was 20% greater than for high forage allowance.

Cumulative ruminal gas production was decreased ($P < 0.01$) at all levels of CT after 5 h of incubation (Table 5). Addition of 20 mg of CT/g of DM tended to decrease ($P = 0.08$) gas production at 1 h. Maximum reduction of cumulative ruminal gas production (55%) occurred at 5 h in the 20 mg of CT treatments.

Table 4. The influence of stage of growth (SG) and forage allowance (FA) on the effect of condensed tannins (CT) on in vitro ruminal gas production and ruminal methane gas emission (mL/h) from fresh wheat forage during January 29 to April 4, 2003

| Item ^a | n | Rate of gas production, c, ML/h | Potential gas production, a + b, mL/12 h | Methane gas, mL/h |
|-----------------------|----|---------------------------------|--|-------------------|
| CT^b | | | | |
| 0.0 | 32 | 13.8 ^d | 64.6 | 4.5 ^d |
| 10 | 32 | 12.1 ^{de} | 62.8 | 3.7 ^{de} |
| 15 | 32 | 11.7 ^{de} | 65.9 | 3.5 ^e |
| 20 | 32 | 9.3 ^e | 65.1 | 3.3 ^e |
| SEM | | 1.26 | 4.57 | 0.52 |
| SG^c | | | | |
| VS | 16 | 13.6 ^d | 53.1 ^e | 2.1 ^e |
| RS | 16 | 9.8 ^e | 76.1 ^d | 5.4 ^d |
| SEM | | 0.89 | 4.04 | 0.37 |
| FA | | | | |
| Low-FA | 16 | 11.7 | 66.9 | 4.1 ^d |
| High-FA | 16 | 11.8 | 62.3 | 3.3 ^e |
| SEM | | 0.86 | 4.04 | 0.36 |
| VS^c | | | | |
| Low-FA | 8 | 13.7 | 57.6 | 2.4 |
| High-FA | 8 | 13.6 | 48.5 | 1.7 |
| RS^c | | | | |
| Low-FA | 8 | 9.6 | 76.2 | 5.9 ^d |
| High-FA | 8 | 9.9 | 75.9 | 5.2 ^e |
| SEM | | 1.23 | 5.72 | 0.52 |

^aLeast squares means for each collection period in vitro ruminally incubated with CT treatment. The in vitro ruminal gas production (Y) was calculated using the following exponential equation (Ørskov and McDonald, 1979): $Y = a + b(1 - e^{-ct})$, where Y = ruminal gas production in time t, and a, b, and c are constants of the exponential equation, where a = the ruminal gas production at time 0, b = the proportion gas production during time (t), and c = the rate of gas production of the b fraction. Potential ruminal gas production was calculated as a + b.

^bCondensed tannins concentration, mg of CT/g of DM.

^cVS = vegetative stage (January to February); RS = reproductive stage (March to April).

^{d,e,f}Within a column, means without a common superscript letter differ, $P < 0.05$.

Discussion

Across forage allowances, bloat incidence (9 to 41%) was lower than reported by Horn et al. (1977; 40%) and Branine and Galyean (1990; 50%). Similarly, average bloat scores in this experiment were lower (0.20 to 0.43) than previously reported (0.88; Horn et al., 1977). Unlike previous reports, steers in our study were provided (ad libitum) a free-choice mineral containing 150 mg of lasalocid/113.4 g mineral that probably decreased bloat frequency and severity (McGuffey et al., 2001).

Bloat scores varied in response to forage allowance and wheat growth stage. Bloat occurred primarily during the vegetative growth stage and at the high forage allowance. Wheat forage in the vegetative growth stage had greater CP, soluble protein N concentrations, and IVDMD than in the reproductive stage of growth but had lower insoluble protein and NDF contents. These findings agree with the data of Mader et al. (1983), who reported that wheat forage in vegetative stage (January to March) had higher CP content and IVDMD value and a lower NDF content than in reproductive stage

Table 5. The effect of increasing levels of condensed tannins (CT) on cumulative in vitro ruminal gas production (mL/h) from fresh wheat forage

| Item | n | In vitro ruminal incubation times, h | | | | | | |
|-----------------------|----|--------------------------------------|------|------|-------|--------------------|-------------------|--------------------|
| | | 1 | 2 | 3 | 4 | 5 | 6 | 12 |
| CT^a | | | | | | | | |
| 0 | 32 | 1.7 | 10.0 | 21.0 | 28.9 | 32.5 ^b | 34.9 ^b | 40.5 ^b |
| 10 | 32 | 1.5 | 7.8 | 18.1 | 24.9 | 29.9 ^c | 31.7 ^c | 36.7 ^c |
| 15 | 32 | 1.7 | 7.8 | 17.5 | 25.5 | 30.4 ^{bc} | 32.5 ^c | 37.3 ^{bc} |
| 20 | 32 | 1.1 | 5.5 | 14.6 | 21.4 | 26.8 ^d | 29.2 ^d | 34.3 ^c |
| SEM | | 0.20 | 3.41 | 9.33 | 11.38 | 1.30 | 1.16 | 1.84 |

^aCondensed tannins concentration, mg/g of DM.

^{b,c,d}Within a column, means without a common superscript letter differ, $P < 0.05$.

(March to April). The data indicate that wheat forage maturity or age of forage growth is an important factor affecting the incidence of bloat.

Forage allowance had a profound effect on bloat dynamics within and among vegetative growth stages of wheat. Average bloat scores were 4 and 2.5 times greater in steers grazing at a high forage allowance than at a low forage allowance in the vegetative and reproductive growth stage of wheat, respectively. Across wheat growth stages, cattle grazing at a low forage allowance experienced a 9% incidence of bloat compared with a 41% incidence in cattle grazing at the high forage allowance. No previous research has reported relationships between forage allowance and bloat on wheat pasture. There was no difference in season-long ADG between low and high forage allowances. Similarly, there was no appreciable difference in the nutrient composition of wheat forage from high and low forage allowance treatments. Based on these similarities, we believe daily forage intake was similar among forage allowances. We propose that increased bloat at the high forage allowance resulted from those cattle having greater forage intake rates than cohorts grazing at the low forage allowance. Intake rate is directly related to the quantity of forage available per animal at an individual feeding station (Ungar, 1996). Research with sheep consuming alfalfa reported that bloat was correlated to intake rate or appetite (Quin, 1943; Stifel and Vetter, 1967). Increased intake rates would lead to the rapid addition of soluble nutrients and fermentable substrates to the reticulorumen that could promote formation of the polysaccharide slime precursor required for frothy bloat to develop (Hungate et al., 1955; Cole and Boda, 1960).

Horn et al. (1977, 1993) reported that bloat-promoting wheat pastures had greater concentrations of CP (35 vs. 25% CP) and soluble protein (62 vs. 45%) compared with nonpromoting pastures. Mangan (1959) concluded soluble proteins were the primary foaming agents and affected foam strength. Subsequent work reported that wheat forage from bloat-provocative pastures contained less DM (22 vs. 28%) and markedly lower NDF (35 vs. 45%) content (Horn et al., 1977). These results are consistent with our study where CP, soluble protein-N, NPN, NDF, and IVDMD were correlated to ruminal gas production rate and bloat severity.

Wheat forage protein may degrade rapidly *in vitro*, but possibly less quickly after denaturation of soluble protein by foaming. The delay in destruction of soluble protein denatured at the foam surface may be important in bloat (Clarke and Hungate, 1971). In our experiment, potential gas production and rate of gas production were not directly correlated to bloat; however, ruminal gas production was positively correlated with CP, soluble protein N, NPN, and IVDMD that are associated with bloat. Fay et al. (1980) reported that birdsfoot trefoil (*Lotus corniculatus*) would not cause bloat because it does not give rise to enough gas. Conversely, cicer milkvetch (*Astragalus cicer* L.) acts as a

bloat-safe legume because it does not produce enough foam even though it generates a large amount of gas during digestion. Collectively, these relationships indicate that frothy bloat was influenced not only by forage chemical composition (CP, soluble protein N, NDF, and IVDMD), but also by accumulation of ruminal gas and the propensity to produce foam.

Previous research has shown that cows fed fresh alfalfa expressed maximal bloat during the morning and afternoon periods (Bartley, 1965). Conversely, other studies have reported that both cattle and sheep bloat more severely in the afternoon than in the morning (Cole and Boda, 1960; Davis and Essig, 1972). Our study revealed no clear diurnal pattern to bloat severity, despite DM, soluble protein N, and IVDMD levels that were greater in the afternoon than in the morning, which was similar to those measured in other grasses (Ciavarella et al., 2000).

Environmental conditions in the 24 to 48 h before wheat forage is consumed may affect bloat severity based on our results and from historical evidence of bloat outbreaks. The episodic occurrence of frothy bloat on wheat pasture clearly points to interactions between environmental conditions, wheat stress physiologic responses, and wheat chemical composition. Recently, it was reported that heat increments from 24°C d/21°C night to 38°C d/34°C night for 24 h increased the accumulation of soluble protein (Fraction 1- leaf protein) in wheat plants (Law and Craft-Brandner, 2001). Long-term (48 h) heating increased the amounts of *de novo* synthesized soluble protein, leading to accumulation of soluble protein in wheat during a series of warm days. Soluble protein levels remained elevated in wheat leaves during cold nights (Law and Craft-Brandner, 2001), suggesting soluble protein may have been irreversibly physically denatured (Feller et al., 1998). Recent research at our laboratory (D. P. Malinowski, unpublished data) suggests that wheat under high solar radiation conditions has greater levels of total phenolics than under low solar radiation conditions. Plant phenolics often increase with increased solar radiation stress (Hakala et al., 2002). The potential role of phenolics in wheat and associated interactions with soluble proteins or ruminal microbes in altering bloat potential is unknown at this time.

In irrigated alfalfa forage, bloat occurred in spring, early and late summer, and fall, increasing with cool weather, frost, and frequent heavy dew (Majak et al., 2003). Bloat was observed after killing frosts of less than -2.2°C (Majak et al., 1995). The response of alfalfa soluble proteins to changes in temperature (Feller et al., 1998) and solar radiation (Sage et al., 1993) seemed to affect frothy bloat potential, but how these environmental factors affected bloat in alfalfa was not clear.

Our research suggests that the action of quebracho CT (15 to 20 mg CT/g of DM) consistently decreased both the rate of ruminal gas (33%) and methane gas (23%) production. Like most other CT, quebracho tannins precipitate soluble protein (Martin and Martin,

1983). In sheep fed a grass hay with addition of quebracho CT, in sacco digestibility was decreased for DM (17%), OM (17%), CP (16%), NDF (20%), and ADF (21%) components of the diet (Salawu et al., 1997b). The decreased digestibilities associated with CT probably resulted from the formation of complexes between CT and dietary carbohydrates and proteins, decreased ruminal proteolytic enzyme activities, and decreased ruminal protozoa numbers (Makkar et al., 1995; Min et al., 2002, 2003).

Li et al. (1996) reported that CT-containing forages with greater than 1 to 5 mg of CT/g of DM were bloat-safe. However, the minimal CT level in the diet for bloat avoidance is 10 mg/g DM for sheep (Wang, 1995; McAllister et al., 2002). In our study, the addition of less than 10 mg CT to in vitro ruminal incubation was insufficient to decrease ruminal gas production. Decreases in cumulative ruminal gas production over time with quebracho CT additions occurred as early as 3 h of incubation at 20 mg of CT/g of DM and as late as 5 h of incubation at 10 mg of CT/g of DM. The effects of CT addition remained for up to 12 h. Salawu et al. (1997a) and Roth et al. (2003) also documented that the addition of CT decreased cumulative in vitro gas production over time in forages and mixed-feeds, respectively.

Major ruminal gas components are carbon dioxide (CO₂; 45%) and methane (CH₄; 30%), with N₂, O₂, and H₂S as minor components (Clarke and Reid, 1974). As judged by the response to CT addition (20 mg of CT/g of DM) into in vitro ruminal incubation, approximately 64% of the decrease in methane gas production could be explained by action of CT (Waghorn, 1996). Supplementation of CT between 15 and 20 mg of CT/g of DM decreased ruminal gas and methane gas accumulation and may decrease ruminant bloat during grazing. Nonetheless, the mechanism for decreasing methane production in ruminants is unknown at this time, and the potential value of CT-containing forages for decreasing ruminal methane production needs to be tested experimentally. Our findings emphasize the need to further test assumptions underlying the role of CT in ruminant bloat interactions.

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