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DPM and WEP analyzed the experimental data and phenolic content in wheat forage, collected solar radiation, and wrote the manuscript; DP and BRM conducted analysis of foam strength and wrote corresponding sections

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ORIGINAL RESEARCH PAPER

Solar radiation affects bloat potential of wheat forage

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Abstract

Frothy bloat is a serious digestive disorder in cattle (*Bos taurus* L.) grazing winter wheat (*Triticum aestivum* L.) pastures in the Southern Great Plains of the USA. Wheat plant metabolism may be one of the factors involved in bloat occurrence. In a series of experiments conducted during 2004–2007, we evaluated the effects of solar radiation intensity (ambient, 100% vs. reduced, 25%), a short-time (24 h vs. 48 h) exposure to solar radiation, and forage allowance (high, 18 kg vs. low, 6 kg DM/100 kg body weight) on seasonal concentration of phenolic compounds and foam strength (a measure of bloat potential) of wheat forage 'Cutter'. Reduced solar radiation decreased total phenolic concentration and increased foam strength when compared to ambient solar radiation. Forage allowance interacted with solar radiation and short-term exposure treatments in determining phenolic concentrations; however, the effects were inconsistent during and among growing seasons. Concentration of phenolic compounds responded rapidly to sudden changes in weather patterns (passing cold fronts) that were usually associated with significant decrease in solar radiation intensity and temperature. Solar radiation intensity was positively correlated with total phenolic concentration and explained 62% to 72% of the variation in total phenolic concentration. Correlation between temperature and total phenolic concentration varied among growing seasons and explained 9–17% of the variation in total phenolic concentration. Results suggest that phenolic concentration in wheat forage is correlated with solar radiation. The decrease in phenolic concentration and resulting increase of bloat potential are especially pronounced during sudden changes in weather patterns during winter.

Keywords

bloat; phenolics; solar radiation; *Triticum*; wheat

Introduction

Hard red winter wheat (*Triticum aestivum* L.) is often used as a source winter forage in environments with mild winters, such as the Southern Great Plains of the USA [1], Australia [2], China [3], Argentina [4], Uruguay [5], Pakistan [6], and the Mediterranean Basin [7]. About half of the total area planted to winter wheat in the Southern Great Plains (2.5 million hectares annually) is for dual-use (forage and grain) and graze-out (forage only) [1]. In addition to tolerance to cold and drought, wheat forage has excellent nutritive value, being high in protein, energy, and mineral content, and low in fiber [8]. The quality of winter wheat is comparable with alfalfa (*Medicago sativa* L.) forage produced during summer growing season [9].

Total and soluble forage proteins have been identified as precursors to frothy bloat in cattle grazing on wheat forage [10]. Frothy bloat is a digestive condition caused by the capture of ruminal gases in a polysaccharide biofilm that forms a matrix with ingesta. This matrix leads to an increase in intraruminal pressure, suppression of nerve receptors at the esophagus-reticulorumen juncture regulating eructation, and a cessation of eructation leading to death from pulmonary or cardiac arrest [11]. The annual impacts of frothy bloat on cattle production in the United States and Australia are estimated to be greater than $300 million and $180 million, respectively [12].

Frothy bloat is a multiaxes complex, comprised of both animal and plant responses to environmental variables. The animal axis is comprised of genotypic, phenotypic, and in vivo components. There is evidence that frothy bloat is heritable in cattle [13]. Heritability has been postulated to affect saliva production and chemical characteristics, rumen motility, and gut chemistry [14]. Min et al. [15] reported that bloated cattle had different grazing patterns from those of nonbloated animals. Rumen bacterial populations also differed between bloated and nonbloated cattle in specific bacteria that produce substantially greater amounts of low-gas permeable biofilms when cattle were grazing wheat pasture [15,16]. The plant axis of frothy bloat is comprised of the presence and abundance of bloat precursors, i.e., total and soluble proteins, soluble carbohydrates, and fibers [10,17], in addition to Rubisco activity and chlorophyll content [18]. Studies evaluating cause-and-effect data on bloat precursors' availability and bloat occurrence are limited. There is evidence that precursor intake and/or ruminal availability are closely correlated with bloat incidence and severity [15]. Environmental variables play a role in the occurrence of frothy bloat in ruminants that graze alfalfa [19]. In contrast, bloat does not occur at all times on wheat pasture. In the Southern Great Plains, increased incidence of bloat occurs during grazing periods in fall to midwinter [17]. Anecdotal observations suggest that bloat occurrences in cattle that graze wheat forage are usually prevalent during sudden changes in weather patterns, e.g., shortly after a change from a period of mild and sunny to cold and cloudy weather as a result of a passing cold front.

Malinowski et al. [20] reported that a decrease in UV radiation and temperature were associated with a decrease in production of phenolic compounds in wheat forage that, at normal concentrations, might interfere with protein digestion in the rumen and prevent bloat [21]. Although the role of condensed tannins (both as forage constituents and feed additives) in bloat prevention has been documented [19,22–24], the possible role of simple phenolic compounds in wheat forage in preventing bloat in grazing cattle is a relatively new aspect of the multiaxes bloat paradigm [20,25,26]. Wheat forage contains a range of simple phenolic compounds [27–29] that may affect rumen microflora activity and reduce the amount of produced gases [30], thus, reducing the potential for bloat [20,21,31].

Malinowski et al. [20] also reported that phenolic concentrations in wheat forage and foam strength (an in vitro measure of bloat potential) expressed a diurnal cycle that corresponded to the diurnal pattern of solar radiation. In this series of experiments, we hypothesized that phenolic concentration in wheat forage might respond to sudden changes in solar radiation and temperature that are characteristic of short-lasting cold fronts that occur during the winter-spring grazing season applied to wheat in the Southern Great Plains. The objectives of the studies were to determine short-term and seasonal changes in total phenolic concentration and foam strength in wheat forage under ambient and reduced solar radiation and contrasting forage allowance (grazing pressure) during the winter-early spring grazing season.

Material and methods

During 2004–2007 growing seasons, a series of experiments were conducted at the West Smith and Walker Research Unit near Vernon, Texas (34°02′ N, 99°16′ W, elevation 383 m). A growing season referenced in this study is the period from October through May. Wheat 'Cutter' was planted in a no-till soil with a John Deere planter at 67 kg ha^{-1} seeding rate in early October each year. Wheat was planted on six 6-ha paddocks. Prior to planting wheat, the plots were treated with glyphosate [*N*-(phosphono-methyl) glycine] at 2.5 kg active ingredient ha^{-1} during late summer each growing season to control weeds and broadcast fertilized with 72 kg ha^{-1} N, 22 kg ha^{-1} P, 0 kg ha^{-1} K, and 22.5 kg ha^{-1} S.

Grazing commenced when wheat had generated sufficient standing crop to support grazing, usually 6 to 12 weeks after sowing. Over the experimental period, high-forage allowance paddocks (n = 3) were stocked with steers (average initial body weight, BW = 200 ±6 kg) per paddock to an initial forage allowance of 18 kg DM 100 kg^{-1} BW day^{-1}. Low-forage allowance paddocks (n = 3) were stocked with steers (average initial BW = 209 ±6 kg) per paddock to an initial forage allowance of 6 kg DM 100 kg^{-1} BW day^{-1}. Forage biomass and allowance were measured at 14- and 35-day intervals. Forage allowance was estimated by hand-clipping wheat standing crop from five 1-m^2 quadrats per paddock to ground level. Samples were oven dried at 60°C to a constant weight.

Reduced solar radiation treatment was imposed by installing enclosures (2.1 m diameter, 0.6 m height) covered with a standardized, woven black shade cloth (International Greenhouse Company, Danville, IL, USA) intercepting 75% of ambient sunlight. The enclosures were installed in each forage allowance treatment and replication 24 h before sampling forage for total phenolic and foam strength analysis, and remained in place for 72 h. The enclosures were placed on new locations within the paddocks before each measurement and forage harvest dates. Solar radiation flux density was measured inside the enclosure (reduced solar radiation treatment corresponding with 25% of ambient solar radiation) and outside in the field (ambient solar radiation treatment, Tab. 1) using silicon pyranometers (Spectrum Technologies, Inc., Plainfield, IL, USA). Temperature was measured with external temperature sensors (Spectrum Technologies, Inc., Plainfield, IL, USA) inside the enclosures and outside in the field. Solar radiation and temperature data were recorded to quantify their relationships to total phenolic concentration and foam strength of wheat forage.

Approximately 250 g fresh weight (FW) of wheat forage was harvested to ground level at 24 and 48 h after imposing the solar radiation treatment, both from shaded and unshaded sections of the paddocks. Harvest dates were based on forecasted changes in weather patterns, i.e., sudden transitions from warm and sunny to cold and cloudy weather. If no significant change in weather pattern was expected, wheat forage was harvested monthly during December (or January) through March each growing season. Forage samples were immediately placed on ice and transported to the laboratory within 45 min after harvest. A portion (50 g FW) of each forage sample was placed in a plastic Zip-Lock bag and frozen at −20°C until analyzed for concentration of total phenolics and foam strength. The remainder of samples were used to determine dry matter (DM) content.

Concentrations of total phenolics in wheat forage were determined using the modified Price and Butler method [32]. The method quantifies the total concentration of phenolic hydroxyl groups present in the assayed extract. Approximately 5 g of frozen wheat forage was homogenized in 50 mL of ethanol:water solution (50:50 vol) for 30 s and subsequently filtered using Whatman No. 1 filter paper. One mL of the collected supernatant and 49 mL of distilled water were added to a 150-mL flask and mixed thoroughly. Ferric chloride (3 mL) was added to flasks containing the diluted supernatant and flasks with blank (water) and standards, followed by potassium ferricyanide (3 mL) 3 min later. After 15 min of incubation in darkness, the absorbance of samples and standards against the blank was determined at 720 nm with a Helios UV-Visible Spectrophotometer (Thermo Fisher Scientific, Inc., Waltham, MA, USA). Standards within a range of concentrations of 0–0.02 mg/mL tannic acid were prepared. The total phenolic concentration, expressed on DM basis, was calculated from a calibration curve.

Estimation of the bloat potential of wheat forage was based on determination of foam strength [33,34]. Approximately 5 g FW forage samples were homogenized with 60 mL of artificial saliva [35] and filtered through three layers of cheesecloth. Subsequently, 40 mL of the filtrate was aerated with carbon dioxide gas in a 250-mL glass cylinder through a bottom inlet at 6.2 MPA for 20 s. Heights of both initial and the final foam columns, and the time required for the foam column to collapse to initial volume, were recorded to calculate foam strength according to the equation:

$Foam\ strength = T/(HF - HI) \times 100$,

where T is the time (min) taken for the foam column height to collapse, HF is the final foam column height (mm), and HI is the initial foam column height (mm).

Tab. 1 Temperature (*T*) and ambient solar radiation (SR) values measured on days corresponding with measurements of total phenolic concentration and foam strength in wheat forage during 2004–2007 growing seasons.

Growing season	Date	Hours	T_{min} (°C)	T_{max} (°C)	T_{mean} (°C)	SR_{mean} (W m^{-2})
2004–2005	2005-01-16	24	−6.9	3.7	−3.1	345
	2005-01-17	48	−7.2	7.8	−1.2	323
	2005-01-20	24	−0.2	25.3	10.1	320
	2005-01-21	48	1.8	21.8	10.9	227
	2005-02-21	24	11.2	24.6	17.9	458
	2005-02-22	48	8.1	20.9	13.9	440
	2005-02-24	24	3.9	9.4	8.2	112
	2005-02-25	48	3.5	12.5	7.3	467
	2005-03-02	24	1.2	11.7	6.8	449
	2005-03-03	48	1.2	15.0	7.6	337
2005–2006	2005-12-14	24	−4.7	13.3	4.0	234
	2006-12-15	48	−6.2	13.0	1.6	277
	2006-01-19	24	−5.2	22.0	5.8	380
	2006-01-20	48	−0.8	27.7	9.0	407
	2006-02-15	24	−0.3	25.3	12.5	445
	2006-02-16	48	8.5	23.0	14.2	438
	2006-02-17	24	−1.7	3.2	0.0	176
	2006-02-18	48	−9.0	−3.2	−6.3	171
	2005-03-09	24	16.5	28.7	21.1	276
	2006-03-10	48	8.7	21.2	15.2	492
2006–2007	2006-12-12	24	2.0	18.0	9.0	338
	2006-12-13	48	0.0	16.0	7.3	260
	2007-01-17	24	−3.3	1.2	−1.2	151
	2007-01-18	48	−1.7	4.2	0.3	170
	2007-02-20	24	2.1	25.1	13.2	431
	2007-02-21	48	6.9	23.3	14.5	444
	2007-03-20	24	12.7	28.7	19.9	454
	2007-03-21	48	16.0	25.5	19.6	294

Measured values for foam strength were correlated with total phenolic concentrations determined in the same samples.

The experiments were set up as completely randomized designs. In each experiment, treatments were forage allowance, measurement date, solar radiation, and time of exposure (24 vs. 48 h) to solar radiation replicated three times and conducted during three growing seasons. Data for total phenolic concentration and foam strength were analyzed using PROC MIXED techniques [36] separately for each growing season (Tab. 2). Forage allowance, measurement date, solar radiation, and time of exposure to solar radiation were considered fixed effects, whereas replications were considered random effects in the analysis of variance (ANOVA). Significance of means was declared at $p = 0.05$. Correlation and stepwise regression analyses of total phenolic concentration with foam strength of wheat forage, solar radiation, and temperature were performed using the CORR and REG procedures of the SAS software [36]. All variables left in the model of the stepwise REG procedure were significant at $p = 0.15$.

Tab. 2 Combined analysis of variance (PROC MIXED): probabilities ($p > F$) for the main effects and interactions of measurement date (D), forage allowance (A), solar radiation (S), and short-term exposure to solar radiation (H) on total phenolic concentration (tannic acid equivalent) and foam strength of wheat forage. NS – not significant at $p = 0.05$.

Year	Variable	Total phenolic conc.	Foam strength
2005	Date (D)	<0.01	<0.01
	Exposure time to shading (H)	NS	NS
	D × H	<0.01	<0.01
	Forage allowance (A)	NS	NS
	D × A	<0.01	NS
	H × A	NS	0.03
	D × H × A	0.04	NS
	Shading (S)	<0.01	<<0.01
	D × S	<0.01	0.03
	H × S	NS	NS
	D × H × S	0.03	NS
	A × S	NS	NS
	D × A × S	NS	NS
	H × A × S	NS	NS
	D × H × A × S	NS	NS
2006	Date (D)	<0.01	<0.01
	Exposure time to shading (H)	NS	NS
	D × H	<0.01	0.01
	Forage allowance (A)	<0.01	NS
	D × A	NS	NS
	H × A	NS	NS
	D × H × A	NS	<0.01
	Shading (S)	<0.01	<0.01
	D × S	<0.01	NS
	H × S	NS	0.04
	D × H × S	NS	<0.01
	A × S	NS	NS
	D × A × S	<0.01	NS
	H × A × S	NS	NS
	D × H × A × S	NS	NS
2007	Date (D)	<0.01	<0.01
	Exposure time to shading (H)	<0.01	NS
	D × H	NS	NS
	Forage allowance (A)	<0.01	NS
	D × A	<0.01	<0.01
	H × A	NS	NS
	D × H × A	NS	NS
	Shading (S)	<0.01	<0.01
	D × S	<0.01	<0.01
	H × S	<0.01	NS
	D × H × S	<0.01	NS
	A × S	<0.01	<0.01
	D × A × S	<0.01	0.03
	H × A × S	NS	NS
	D × H × A × S	NS	NS

Results

Weather patterns

The annual long-term (1981–2010) average precipitation for the experimental location is 711 mm, with 224 mm received during September–December and 122 mm received during January–March. Precipitation received during the early growing season and wheat establishment phase (September–December) was 37% and 27% higher than the average in 2004–2005 and 2006–2007 growing seasons. Most of the recorded rainfall occurred during November (2004) or October (2006) with no or marginal precipitation in the other months (Fig. 1). Severe soil moisture deficits occurred during September–December of 2005–2006, when was 49% of the average precipitation. Precipitation amounts during January–March of 2004–2005 and 2006–2007 growing seasons were similar to the long-term average (122 mm). In contrast, 58% less precipitation occurred during these months of 2005–2006 growing season. Average temperatures during wheat establishment and early growth (September–December) were 1.1°C above normal in 2004–2005 and 2005–2006, and 0.3°C higher in 2006–2007. Average temperatures later in the growing season (January–March) were 0.9, 2.4, and 1.9°C above normal, respectively for 2004–2005, 2005–2006, and 2006–2007.

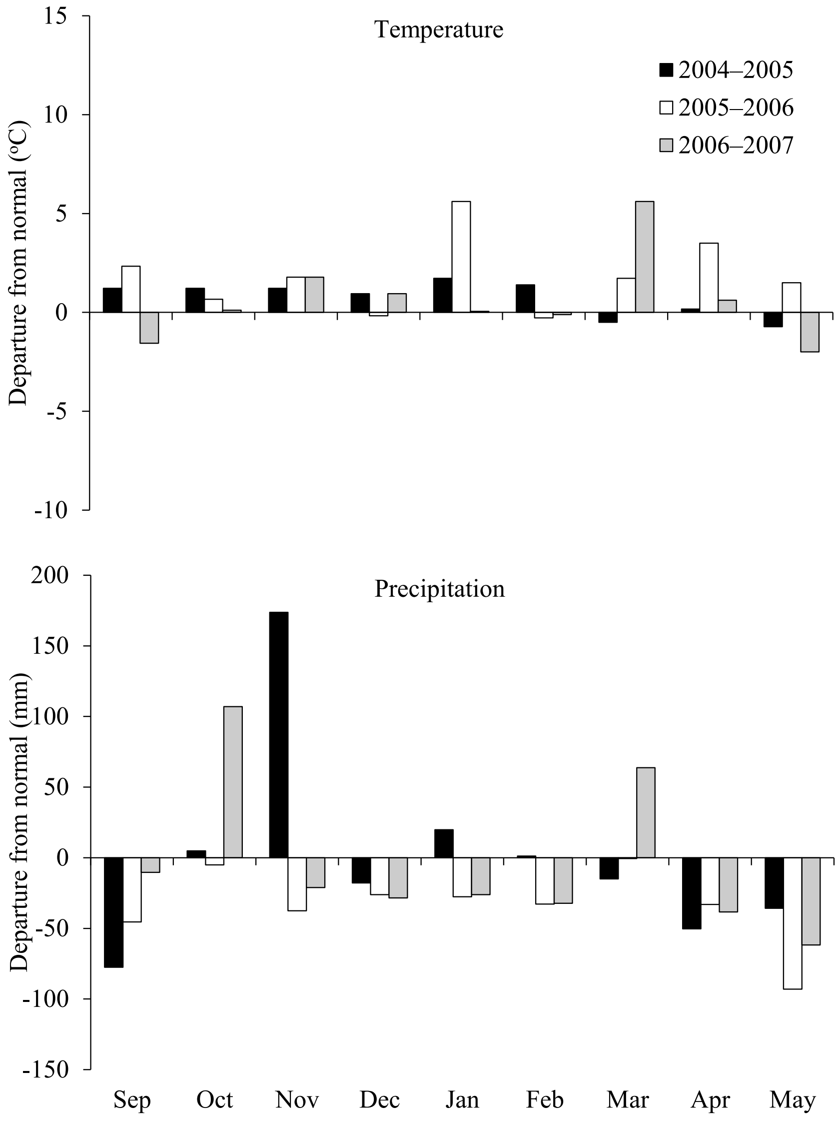

Fig. 1 Temperature and precipitation departures from long-term averages during three growing seasons of 2004–2007.

Total phenolic concentrations and foam strength of wheat forage

The experimental treatments, i.e., forage allowance, measurement date, solar radiation intensity, and time of exposure to solar radiation, all interacted to influence both total phenolic concentration and foam strength in wheat forage each growing season. This was expected because of contrasting weather patterns, especially precipitation amounts.

Concentration of total phenolics during 2004–2005 was affected by (***i***) a three-way interaction among measurement date, intensity of solar radiation, and time of exposure to solar radiation and (***ii***) a three-way interaction among measurement date, forage allowance, and time of exposure to solar radiation (Tab. 2). Phenolic concentrations in wheat forage increased in response to increasing solar radiation during January and February, and it were always higher in plants grown at ambient vs. reduced solar radiation, regardless of forage allowance (Fig. 2A). The short-term changes in phenolic concentration (24 and 48 h from initiation of measurements) were not consistent among the measurement dates and radiation treatments. During the 2004–2005 growing season, there was one incidence of a cold front passing on February 24, 2005, resulting in a sudden decrease in the average daily temperature and reduction in the average daily ambient solar radiation compared to the period preceding the weather change (Tab. 1). Concentrations of total phenolics in wheat forage were significantly reduced during that weather event, regardless of radiation treatments and time of exposure to solar

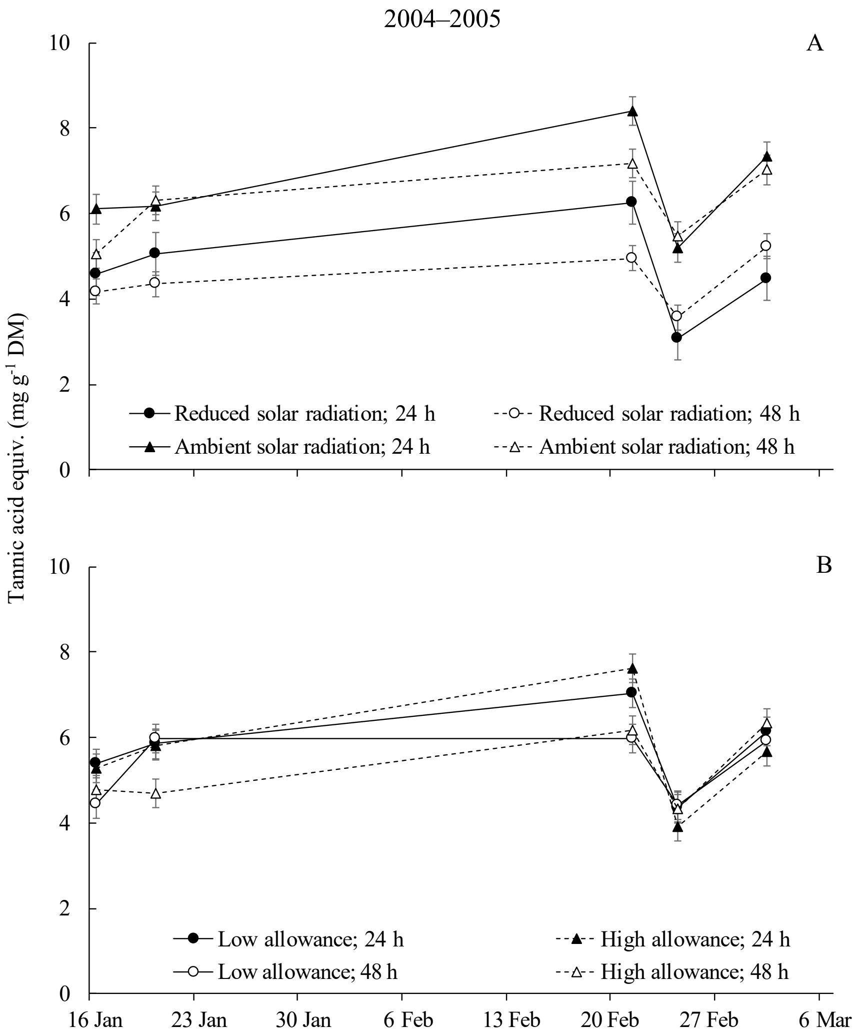

Fig. 2 The effects of short-term exposure (24 vs. 48 h) to ambient (100%) and reduced (25%) solar radiation (**A**) and forage allowance (**B**) treatments on total phenolic concentration (measured as tannic acid equivalent) in wheat forage during the 2004–2005 growing season. Bars indicate ± 1 *SE*.

radiation immediately following the weather pattern change. The temperatures did not rebound in the next 7 days, but solar radiation reached and exceeded values observed during the period preceding the cold front. As a result, phenolic concentration in wheat forage increased to levels comparable with those measured prior to the cold front. The effects of forage allowance on phenolic concentration during 24 and 48 h exposure to solar radiation treatments were inconsistent during the growing season (Fig. 2B). On January 20, 2005, phenolic concentration was lower at 48 h vs. 24 h at high vs. low forage allowance; however, forage allowance did not affect short-term dynamics of phenolic concentration in wheat forage on other measurement dates.

Foam strength was affected by two-way interactions between (***i***) measurement date and solar radiation, (***ii***) measurement date and time of exposure to solar radiation, and (***iii***) forage allowance and time of exposure to solar radiation (Tab. 2). During the 2004–2005 growing season, foam strength was always higher in response to the reduced vs. ambient radiation treatment and declined as the growing season progressed from January through March (Fig. 3A). During the passing cold front on February 24, 2005, foam strength in wheat forage rapidly increased in the reduced vs. ambient radiation treatment, likely due to the low amount of ambient solar radiation associated with significant cloudiness. Foam strength changes were not significant for the ambient radiation treatment during the cold front. Foam strength declined rapidly once the cold front passed and reached levels measured prior to the cold front. The difference in foam strength at 24 and 48 h after initiation of the measurements was not significant during January 2005. However, it declined at 48 vs. 24 h in response to the passing cold front on February 24, 2005 (Fig. 3B). During the following day, foam strength declined because of high solar radiation. Later in the season (March 2005), the difference in short-term dynamics of foam strength was not significant in response to time of exposure to solar radiation. At low forage allowance, foam strength was lower at 48 vs. 24 h, regardless of measurement date, but the difference was not significant at high forage allowance (Fig. 3C). At 48 h, foam strength was higher in the high vs. low allowance treatments, but the difference was not significant at 24 h, regardless of measurement date.

Phenolic concentration in wheat forage was affected by (***i***) a two-way interaction between measurement date and time of exposure to solar radiation, and (***ii***) a three-way interaction among measurement date, solar radiation intensity, and forage allowance (Tab. 2) during 2005–2006. During December–February, the short-term (24 vs. 48 h) changes in phenolic concentration were not significant. In response to a strong cold front on February 17, 2006, phenolic

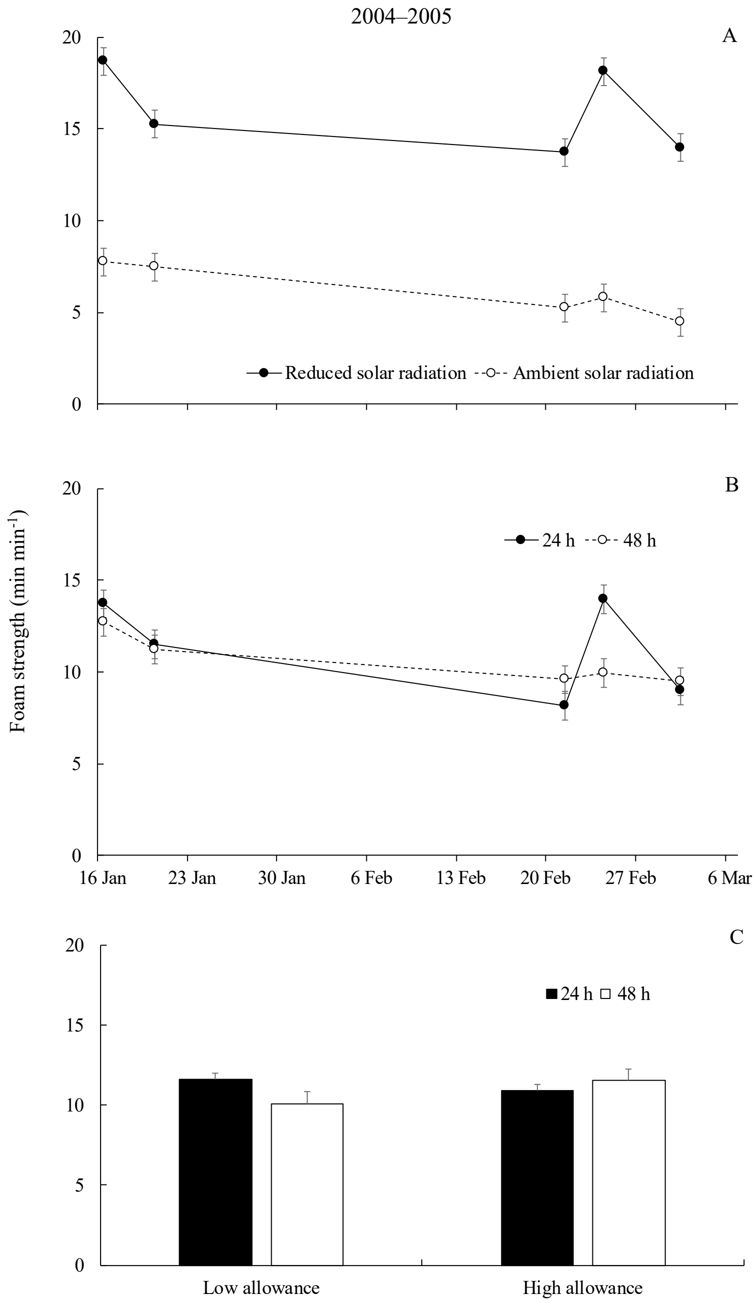

Fig. 3 The effects of interactions between measurement date and solar radiation (**A**), measurement date and short-term exposure to solar radiation (**B**), and forage allowance and short-term exposure to solar radiation (**C**) on bloat potential (measured as foam strength) of wheat forage during the 2004–2005 growing season. Bars indicate ± 1 *SE*.

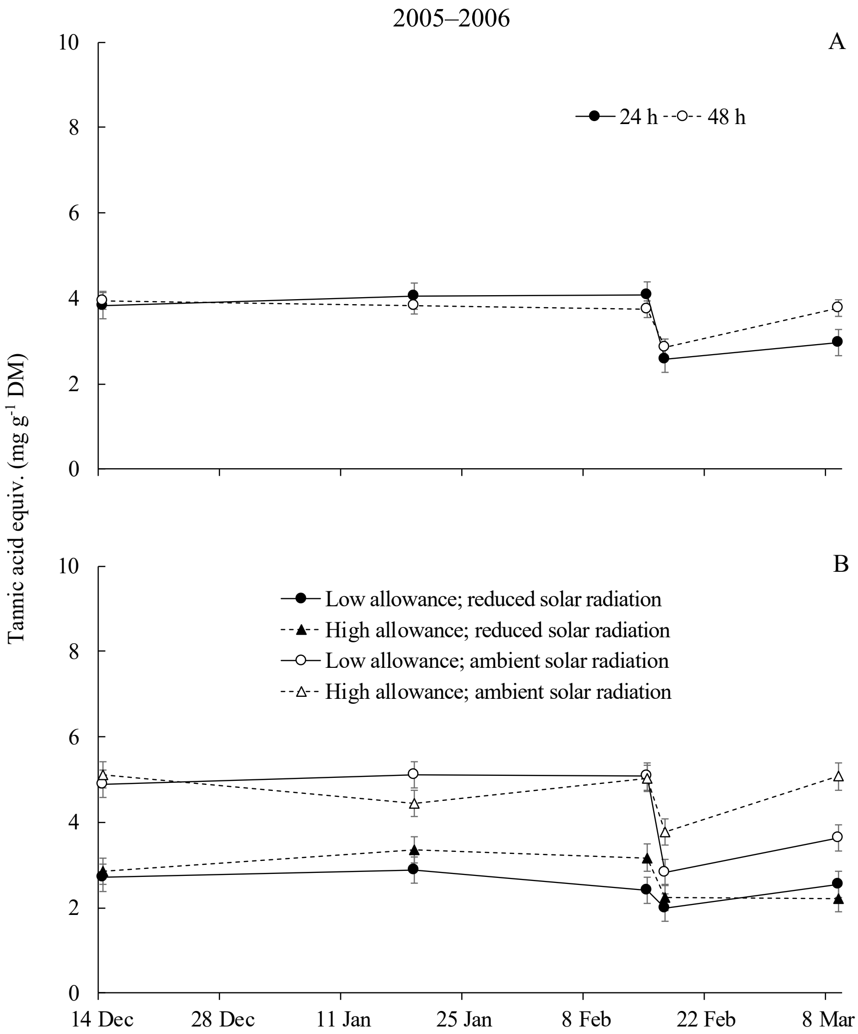

Fig. 4 The effects of interactions between measurement date and short-term exposure to solar radiation (**A**), and among measurement date, solar radiation, and forage allowance (**B**) on total phenolic concentration (measured as tannic acid equivalent) in wheat forage during 2005–2006 growing season. Bars indicate ± 1 *SE*.

concentrations were reduced by 30% when compared with those prior to the cold front event. After the cold front passed, phenolic concentrations in wheat forage increased and were higher at 48 vs. 24 h after the initiation of measurements on March 9, 2006.

Phenolic concentrations in wheat forage were higher at ambient vs. reduced solar radiation during December 2005 through early February 2006, regardless of forage allowance (Fig. 4B). Phenolic concentrations declined sharply in response to a sudden decrease in temperature and solar radiation associated with the cold front on February 17, 2006, especially in response to the ambient solar radiation and low forage allowance treatments. Wheat forage in the ambient solar radiation and high allowance treatments maintained higher phenolic concentrations during the cold front, compared to low forage allowance. After the cold front passed, phenolic concentrations were restored faster under ambient vs. reduced solar radiation and under in high forage allowance compared to the low forage allowance.

Foam strength was higher in the reduced vs. ambient solar radiation treatments through most of the growing season (Fig. 5A). In the reduced solar radiation treatment, foam strength was higher at 48 vs. 24 h after initiation on all measurement dates except December 14, 2005. In contrast, foam strength did not change significantly between 24 and 48 h under ambient solar radiation treatment on any date except February 17, 2006. The sudden cold front passing on February 17, 2006 resulted in a rapid increase in foam strength in wheat forage regardless of experimental treatments. After the cold front passed, foam strength declined regardless of radiation treatment.

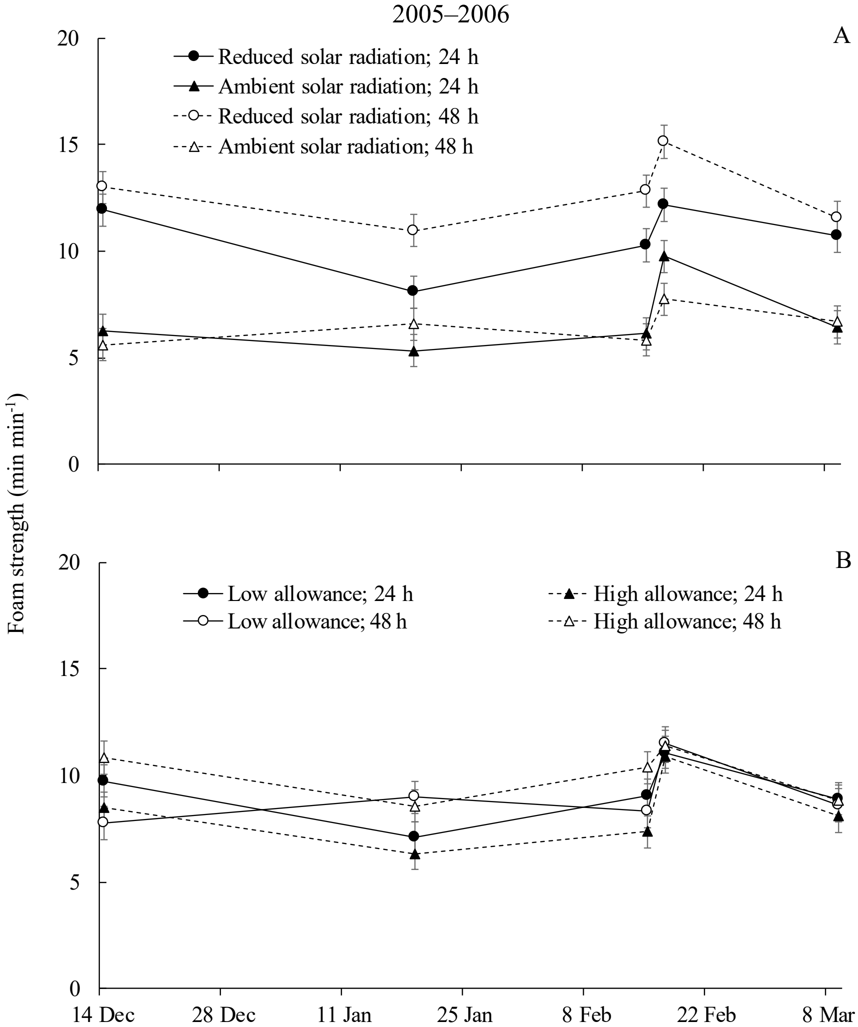

Fig. 5 The effects on interactions among measurement date, solar radiation, and short-term exposure to solar radiation (**A**) and measurement date, forage allowance, and solar radiation (**B**) on total phenolic concentration (measured as tannic acid equivalent) during the 2006–2007 growing season. Bars indicate ± 1 *SE*.

The interaction of forage allowance and time of exposure to solar radiation on foam strength were inconsistent throughout the growing season (Fig. 5B). On December 14, 2005, forage allowance did not affect foam strength within 24 h after initiating observations. However, foam strength was greater under the high forage allowance than low forage allowance treatment at 48 h after initiating the observation, regardless of radiation treatment. On January 19, 2006, foam strength increased at 48 vs. 24 h, regardless of forage allowance. During the cold front (February 17, 2006) and after (March 9, 2006), neither forage allowance or short-term exposure to solar radiation affected foam strength.

During 2006–2007 growing season, phenolic concentrations in wheat forage were affected by (***i***) a three-way interaction among measurement date, solar radiation intensity, and time of exposure to solar radiation and (***ii***) a three-way interaction among measurement date, intensity of solar radiation, and forage allowance (Tab. 2). Phenolic concentrations were similar for all measurement dates under the reduced radiation treatment and did not differ among 24 and 48 h from initiation of the measurements (Fig. 6A). At ambient solar radiation, phenolic concentrations were increasing at 48 vs. 24 h on December 15, 2006 and February 21, 2007, but no significant differences were noted on other measurement dates.

Phenolic concentrations were higher at ambient vs. reduced solar radiation, and the effects of forage allowance were more pronounced during January–March 2007 than early (December 2006) in the growing season (Fig. 6B). On January 17, 2007, phenolic

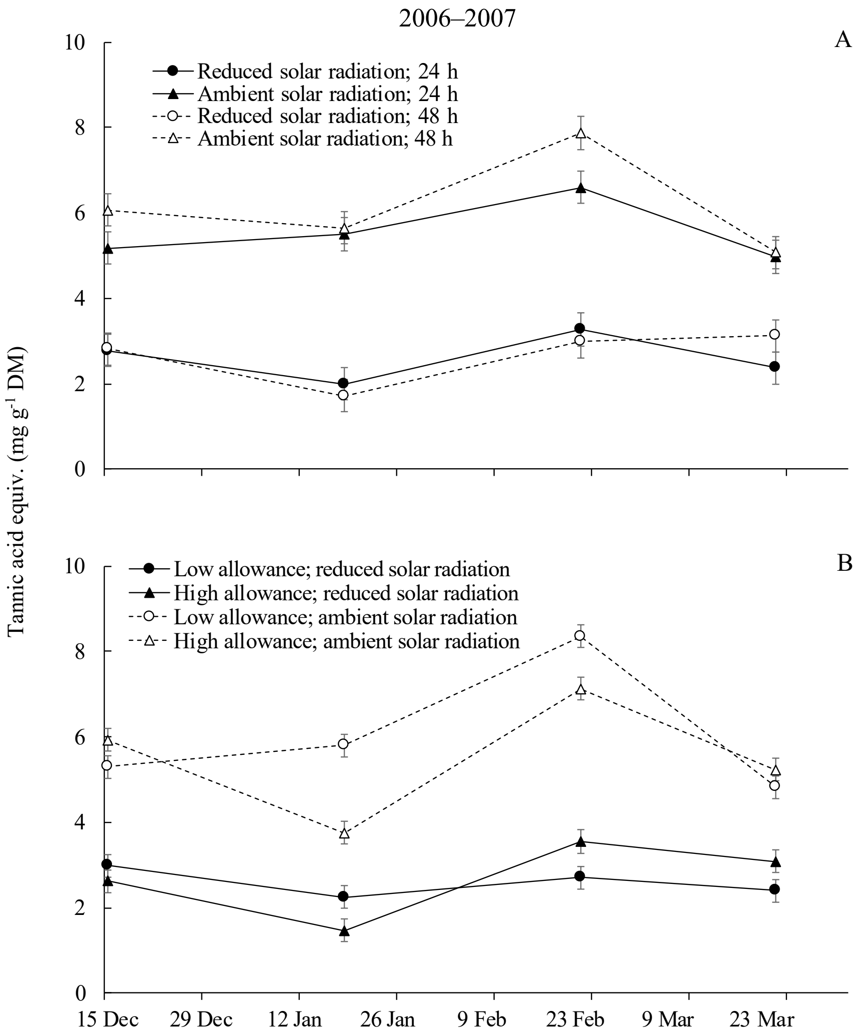

Fig. 6 The effects on interactions among measurement date, solar radiation, and short-term exposure to solar radiation (**A**) and measurement date, forage allowance, and solar radiation (**B**) on total phenolic concentration (measured as tannic acid equivalent) during the 2006–2007 growing season. Bars indicate ± 1 *SE*.

concentrations were higher in wheat subjected to more intense grazing (low allowance) than these in the less intense grazing (high allowance), regardless of intensity of solar radiation. Note that a cold front was passing through the area on this date, which was reflected in decreasing concentrations of phenolic compounds, compared to concentrations measured in December 2006. On February 21, 2007, a reverse effect of forage allowance on phenolic concentrations was observed under reduced solar radiation, compared to concentrations measured on January 17, 2007 and lasted throughout the remaining measurement dates. Phenolic concentrations increased under ambient amounts of solar radiation when compared with phenolic concentrations measured on January 17, 2007, and they were higher at low forage allowance than high allowance. However, the effect of forage allowance was not significant on March 21, 2007, when phenolic concentrations decreased in response to a period cloudy weather.

Foam strength was also affected by the three-way interaction among measurement date, solar radiation treatment, and forage allowance (Tab. 2), and responses to experimental treatments generally occurred in an opposite fashion to phenolic concentration (Fig. 7). Foam strength was higher at reduced vs. ambient solar radiation and the effects of forage allowance were more pronounced during January through March 2007 than in December 2006. On January 17, 2007, foam strength was lower in wheat subjected to more intense grazing (low allowance) than under less intense grazing (high allowance), regardless of intensity of solar radiation. A cold front passing through the area on this date resulted in an increase in foam strength when compared to that measured

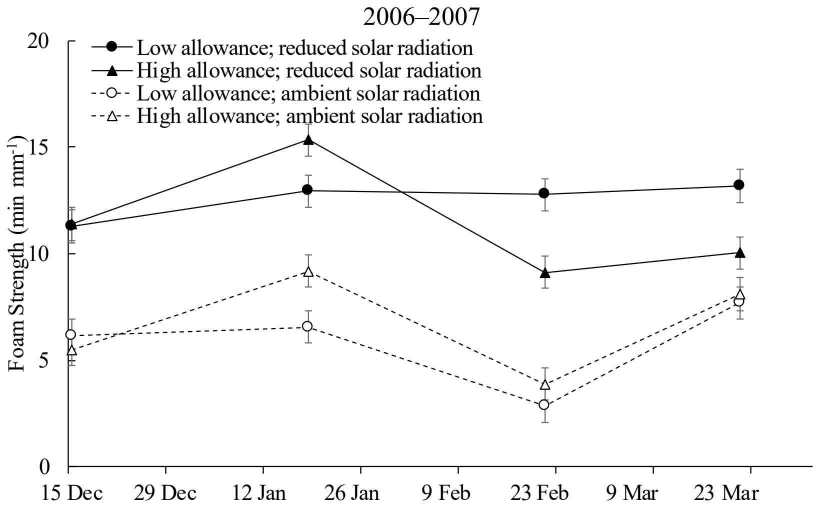

Fig. 7 The effects of measurement date, forage allowance and solar radiation on bloat potential (measured as foam strength) during the 2006–2007 growing season. Bars indicate ± 1 *SE*.

in December 2006, except for the low forage allowance under ambient solar radiation. On February 21, 2007, a reverse effect of forage allowance was observed under reduced solar radiation when compared to measurement on January 17, 2007 and lasted until March 21, 2007. Foam strength decreased on February 21, 2007 under ambient solar radiation, compared to responses on January 17, 2007 and did not differ among allowance treatments. Cloudy weather on March 21, 2007 resulted in an increase in foam strength under ambient solar radiation compared to the previous measurement date, but remained similar under reduced solar radiation.

Correlations between total phenolic concentration, foam strength, and weather variables

Correlation coefficients indicated significant inverse associations between concentration of total phenolics and foam strength of wheat forage in each growing season (Tab. 3). This suggested that higher concentration of phenolic compounds in wheat forage was correlated with lower potential for bloat (Fig. 8). Depending on the growing season, concentration of total phenolics in wheat forage explained 64% to 86% of the variation in foam strength (Tab. 4). Furthermore, concentrations of total phenolics in wheat forage was positively associated with intensity of solar radiation each growing season (Tab. 3). Intensity of solar radiation explained 62% to 72% of the variation in total phenolic concentration (Fig. 9). The correlation between temperature and phenolic concentration was significant only in the 2004–2005 growing season (Tab. 3). Temperature explained 17% of the variation in phenolic concentrations in 2004–2005 growing season and 9% of the variation in 2006–2007 growing season (Fig. 10). The correlation between foam strength and phenolic concentration was significant in each growing season, and the correlation between foam strength and solar radiation was significant in two of the three growing season (Tab. 5)

Discussion

Results of our studies suggest that intensity of solar radiation affects the concentration of phenolic compounds in wheat forage. We have evidenced a strong positive correlation between solar radiation and phenolic concentration, and an inverse relationship between phenolic concentration and foam strength. These findings agree with results presented by Malinowski et al. [20,37]. Accumulation of phenolic compounds in plants has been well documented as a response plant stress caused by UV radiation [38], which is known

Tab. 3 Correlation coefficients and probabilities among total phenolic concentration (tannic acid equivalent), foam strength, solar radiation, and temperature calculated from experiments conducted during 2004–2007 growing seasons.

Season	Trait	Total phenolics	Foam strength	Solar radiation	Temperature
2004–2005	Total phenolics	-	−0.80 [a] <0.01 [b]	0.79 <0.01	0.42 <0.01
	Foam strength		-	−0.85 <0.01	−0.29 0.07
	Solar radiation			-	0.16 0.31
	Temperature				-
2005–2006	Total phenolics	-	−0.82 <0.01	0.85 <0.01	0.12 0.47
	Foam strength		-	−0.79 <0.01	−0.13 0.42
	Solar radiation			-	0.26 0.10
	Temperature				-
2006–2007	Total phenolics	-	−0.93 <0.01	0.83 <0.01	0.30 0.10
	Foam strength		-	−0.78 <0.01	−0.23 0.20
	Solar radiation			-	0.46 <0.01
	Temperature				-

[a] Correlation coefficients; [b] probabilities.

to occur in wheat [39,40]. However, the effects of environmental variables on phenolic compounds in wheat forage and the association between phenolic concentration and the occurrence of bloat in grazing cattle have not been well documented.

Malinowski et al. [20] showed that phenolic compounds in wheat forage responded to diurnal changes in UV radiation in an opposite fashion to foam strength, a measure of bloat potential. The authors concluded that reduced UV radiation may be associated with a decrease in production of phenolic compounds in wheat forage, thus interfering with protein digestion in rumen and contributing to the occurrence of bloat [21]. Our results may help explain the anecdotal observations of a relationship between increased bloat incidences and sudden changes in weather patterns associated with passing cold fronts in the Southern Great Plains during early and midwinter [17].

Our results also suggest a positive correlation between temperature and phenolic concentration, which was noted during one of the three growing seasons of this study. Production of phenolic compounds can vary among wheat genotypes in response to temperature under controlled environmental conditions [41]. Studies by Malinowski et al. [25,37] and MacKown et al. [26] revealed a wide variability in total phenolic and tannin concentrations in forage among wheat cultivars and breeding lines grown in north Texas and southern Oklahoma (USA). This result suggests there is some potential for selection of forage-type wheat cultivars with higher phenolic concentrations for grazing. Thus, we suggest that a sudden decrease in temperature, especially below the freezing point, may contribute to rapid decreases in phenolic concentration in wheat forage and result in the occurrence of bloat, especially in cattle grazing low-phenolic dual-purpose wheat cultivars.

Short-term changes (24 and 48 h after the initiation of measurements) in phenolic concentrations and foam strength were often inconclusive and could likely be affected by growth stages of wheat, sward composition, or precipitation patterns. Although forage allowance (i.e., removal of biomass through grazing) did not affect phenolic concentrations or foam strength during the experiments, it interacted with short-term exposure to solar radiation to modify phenolic concentrations in wheat forage. For

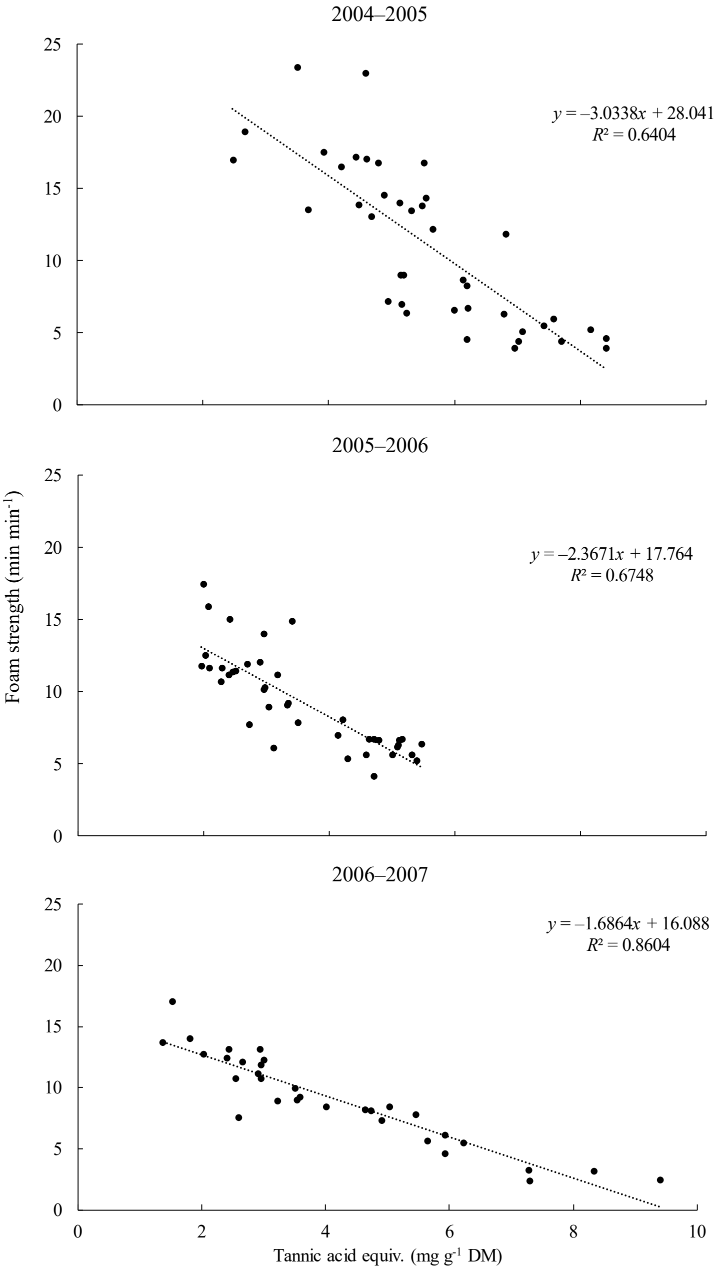

Fig. 8 Correlations between total phenolic concentration (measured as tannic acid equivalent) and the potential of bloat (measured as foam strength) in wheat forage during 2004–2005, 2005–2006, and 2006–2007 growing seasons.

Tab. 4 Analysis of stepwise regression of total phenolic concentration (tannic acid equivalent) with foam strength, solar radiation, and temperature in experiments conducted during 2004–2007 growing seasons.

Season	Variable entered	Partial R^2	Model R^2	Cp	F value	$p > F$
2004–2005	Foam strength	0.64	0.64	13.22	67.68	<0.01
	Solar radiation	0.04	0.68	9.38	4.98	0.03
	Temperature	0.05	0.74	4.00	7.38	0.01
2005–2006	Solar radiation	0.73	0.73	10.74	102.21	<0.01
	Foam strength	0.06	0.78	3.10	9.61	<0.01
2006–2007	Foam strength	0.86	0.86	6.96	184.97	<0.01
	Solar radiation	0.03	0.89	2.04	7.16	0.01

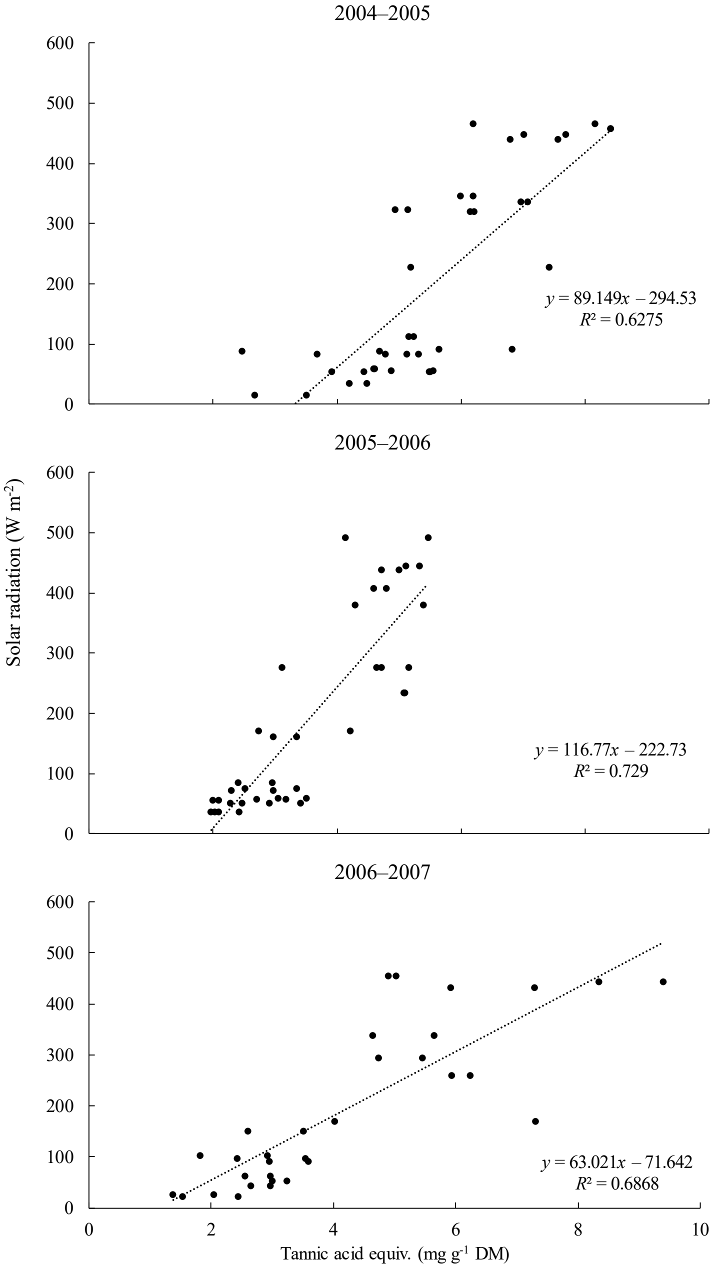

Fig. 9 Correlations between total phenolic concentration (measured as tannic acid equivalent) and solar radiation intensity during 2004–2005, 2005–2006, and 2006–2007 growing seasons.

example, bloat potential (higher values of foam strength) decreased in a short term in wheat subject to high grazing intensity (low forage allowance) when compared with less intensively grazed plants (high forage allowance). Although we did not measure parameters related to plant morphology, one would assume that intensively grazed plants had lower proportion of leaf vs. stem tissues (shorter residual sward height) than plants subject to less intensive grazing. These morphological differences resulting from contrasting grazing pressures could contribute to differences in phenolic concentrations in wheat forage [42,43].

Further research is needed to determine which phenolic compounds are synthesized in wheat forage in response to amount of solar radiation and define the mechanism of interactions between phenolic compounds and forage constituents that promote bloat and activity of rumen microflora.

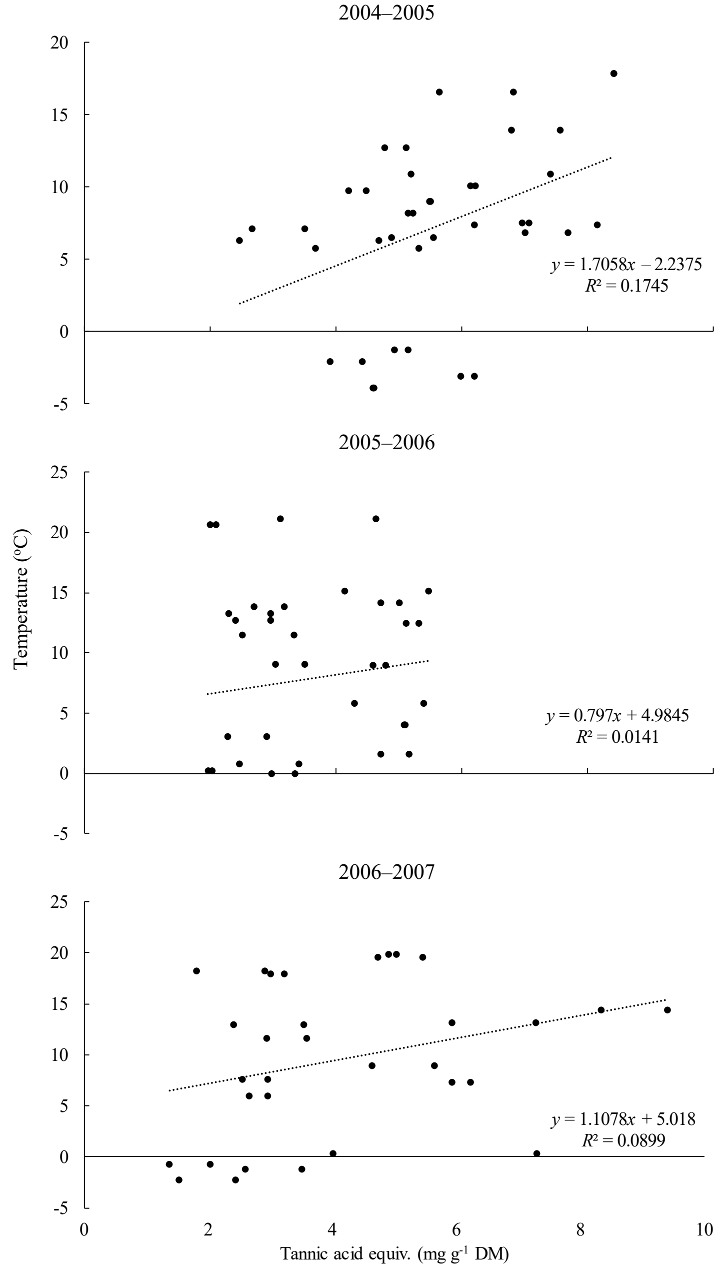

Fig. 10 Correlations between total phenolic concentration (measured as tannic acid equivalent) and temperature during 2004–2005, 2005–2006, and 2006–2007 growing seasons.

Tab. 5 Analysis of stepwise regression of foam strength with total phenolic concentration (tannic acid equivalent), solar radiation, and temperature in experiments conducted during 2004–2007 growing seasons.

Season	Variable entered	Partial R^2	Model R^2	Cp	*F* value	$p > F$
2004–2005	Solar radiation	0.73	0.73	7.14	104.77	<0.01
	Total phenolics	0.04	0.77	2.69	6.50	0.01
2005–2006	Total phenolics	0.67	0.67	3.92	78.86	<0.01
	Solar radiation	0.03	0.71	2.06	3.96	0.05
2006–2007	Total phenolics	0.86	0.86	0.91	184.97	<0.01

Conclusions

Results of our studies provide further evidence for the presence of phenolic compounds in wheat forage and an inverse correlation between total phenolic concentration and foam strength (a measure of bloat potential). We suggest that synthesis of phenolic compounds in wheat is accelerated by greater amount of solar radiation and, to lesser degree, by increasing temperatures. Results suggest that sudden changes in weather patterns resulting in significant decreases in solar radiation and temperature, which are conditions often associated with passing cold fronts in winter and early spring in the Southern Great Plains, cause a rapid decrease in concentrations of phenolic compounds and an increase in foam strength (bloat potential). Such short-term metabolic changes in wheat forage may be associated with observed increases in frequency of bloat during sudden changes in weather in the Southern Great Plains.

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Promieniowanie słoneczne wpływa na wzrost potencjału paszowego pszenicy (*Triticum aestivum* L.)

Streszczenie

Wzdęcia są poważnym zaburzeniem trawienia u bydła (*Bos taurus* L.) spasanego na pastwiskach pszenicy ozimej (*Triticum aestivum* L.) w południowych rejonach Stanów Zjednoczonych. Metabolizm pszenicy może być jednym z czynników związanych z występowaniem wzdęć. W serii eksperymentów przeprowadzonych w latach 2004–2007 oceniono wpływ (***i***) natężenia promieniowania słonecznego (naturalne natężenie, 100% w stosunku do zmniejszonego natężenia, 25%), (***ii***) krótkotrwałego (24–48 godz.) wystawienia na działanie promieniowania słonecznego i (***iii***) ilości dostępnej masy zielonej (wysoki poziom, 18 kg DM / 100 kg w porównaniu z niskim poziomem, 6 kg DM / 100 kg masy ciała) na sezonowe stężenie prostych związków fenolowych i stabilność pęcherzyków powietrza w homogenacie z zielonej masy pszenicy 'Cutter' (miara potencjału wzdęcia). Zmniejszone promieniowanie słoneczne wywołało redukcję stężenia związków fenolowych i zwiększyło stabilność pęcherzyków powietrza w homogenacie z zielonej masy pszenicy w porównaniu do naturalnego stężenia promieniowania słonecznego. Stężenie związków fenolowych określone było przez współdziałanie między natężeniem promieniowania słonecznego, czasem działania promieniowania słonecznego i ilością dostępnej paszy zielonej, jednak efekty były zmienne podczas i pomiędzy sezonami wegetacyjnymi. Stężenie związków fenolowych szybko reagowało na nagłe zmiany pogody (przechodzące zimne fronty), które zwykle wiązały się ze znacznym spadkiem natężenia promieniowania słonecznego i temperatury. Natężenie promieniowania słonecznego było dodatnio skorelowane z całkowitym stężeniem związków fenolowych i wyjaśniało 62% do 72% zmian w stężeniu związków fenolowych w masie zielonej pszenicy. Korelacja pomiędzy temperaturą a całkowitym stężeniem związków fenolowych zależała od sezonu wegetacyjnego i wyjaśniała 9–17% zmian w całkowitym stężeniu związków fenolowych. Wyniki sugerują, że stężenie związków fenolowych w masie zielonej pszenicy jest

skorelowane z natężeniem promieniowania słonecznego. Spadek stężenia związków fenolowych i wynikający z tego wzrost potencjału wzdęć u bydła spasanego na pszenicy są szczególnie wyraźne podczas nagłych zmian pogodowych w okresie zimowym.