


Cattle select against the invasive grass tall fescue in heterogeneous pastures managed with prescribed fire

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Abstract

Tall fescue (*Festuca arundinacea*) is a Eurasian forage grass extensively planted in the United States. However, an endophytic fungus in tall fescue, *Epichloë coenophiala*, causes health problems in cattle. We predicted that cattle prefer to graze alternative forages when available. We also predicted that cattle use tall fescue more intensively in recently burned areas, as fire can increase forage quality. We tested these predictions in four diverse-forage pastures in Iowa, comparing use by cattle of tall fescue and four alternative forages (non-fescue cool-season grasses, native warm-season grasses, non-leguminous forbs and legumes) to their availabilities at the pasture scale. We also examined how tall fescue influences the distribution of grazing at a fine scale (0.1-m² quadrats). Tall fescue was the most abundant forage (46% of plants), but composed only 26% of grazed vegetation. In contrast, legumes composed 12% of available forage but 25% of grazed vegetation. Other forages were used in proportion to availability. At a fine scale, total grazing frequency (proportion of plants grazed) was lower in quadrats containing abundant tall fescue, and higher in quadrats with abundant warm-season grasses. Grazing frequency of tall fescue and other cool-season grasses was greatest in recently burned quadrats, but total grazing frequency did not increase after burning. Our results show that although cattle graze tall fescue, particularly following burns, they limit their use of this grass. Given that tall fescue is underused, creates health risks for cattle, and degrades wildlife habitat quality, it may be advisable to reduce tall fescue in pastures.

KEYWORDS

cattle, *Festuca arundinacea*, grazing selectivity, legumes, patch-burn grazing, tall fescue

1 | INTRODUCTION

The increasing prevalence of invasive plants on rangelands is a critical issue in resource management and livestock production (DiTomaso, Monaco, James, & Firn, 2017). In the United States, tall fescue (*Festuca arundinacea* (Schreb.); syn. *Schedonorus arundinaceus* (Schreb.) Dumort.) is an introduced, cool-season grass considered

invasive in multiple states because of its increasing dominance on millions of grassland hectares (Barnes, DeMaso, & Bahm, 2013) and its negative effects on wildlife, such as small mammals (Coley, Fribourg, Pelton, & Gwinn, 1995), northern bobwhite (*Colinus virginianus*; Osborne, Sparling, & Hopkins, 2012), and grassland songbirds (Lyons, Miller, Debinski, & Engle, 2015; Maresh Nelson et al., 2018). Even so, it is one of the most widely used livestock forages in the country due to its high herbage production and drought tolerance—benefits conferred by a mutualistic relationship with a fungal endophyte, *Epichloë coenophiala* (Arachevaleta, Bacon, Hoveland, &

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Radcliffe, 1989; Ball, Lacefield, & Hoveland, 1991). Despite its agricultural benefits, this endophyte produces ergovaline toxins that can cause weight loss in cattle (*Bos taurus*), as well as decreased milk production, tail loss, lameness and poor thermal regulation (Mays et al., 2013; Schmidt et al., 1982; Stuedemann & Hoveland, 1988).

Given the potential negative health consequences of tall fescue, cattle may prefer alternative forages when given a choice (Boland et al., 2012). In species-rich rangelands, cattle have multiple forage options, including other cool-season grasses, native warm-season grasses, legumes and forbs (Soder, Rook, Sanderson, & Goslee, 2007; Tracy & Sanderson, 2000). Unfortunately, despite the resilience and grazing potential of diverse-forage pastures (Sanderson, Goslee, & Soder, 2013; Soder et al., 2007), few data are available on cattle selectivity for tall fescue versus other forages in such systems. To date, research has focused on the preferences of steers for tall fescue versus legumes in two-species systems, finding that steers consume more legumes than tall fescue and achieve greater weight gain as a result (Boland et al., 2012; Schaefer, Albrecht, & Schaefer, 2014). Although to our knowledge, there are no reports on selectivity with respect to tall fescue in pastures with higher plant diversity, cattle have been shown to frequently graze warm-season grasses (e.g., switchgrass *Panicum virgatum* (L.)), big bluestem *Andropogon gerardii* (Vitman) relative to their availability during the summer, while grazing cool-season grasses (e.g., Kentucky bluegrass *Poa pratensis* (L.)) disproportionately less (Plumb & Dodd, 1993). Cattle preferences for warm-season grasses during the summer, when these grasses are actively growing and cool-season grasses are mature or senescing, may improve livestock performance (Burns, Mochrie, & Timothy, 1984; Paterson, Belyea, Bowman, Kerley, & Williams, 1994).

If cattle do prefer alternative forages over tall fescue, these preferences may not be fixed and instead may vary with management context. In particular, cattle tend to graze heavily in recently burned areas, either to avoid dead plant stalks (Willms, Bailey, McLean, & Tucker, 1980) or take advantage of new plant growth with high forage quality (Allred, Fuhlendorf, Engle, & Elmore, 2011). If the advantages cattle receive from grazing on burned areas outweigh the potential health impacts of tall fescue, selectivity may diminish following prescribed fire. This could lead to increased tall fescue consumption in recently burned areas, as is the case with invasive sericea lespedeza (*Lespedeza cuneata* (Dumont) G. Don; Cummings, Fuhlendorf, & Engle, 2007).

Our objective was to assess selectivity of cattle for five plant categories: tall fescue, other cool-season grasses, native warm-season grasses, non-leguminous forbs and legumes. First, we assessed forage selectivity at a broad spatial scale (pasture scale), testing whether cattle graze each of the five plant categories in proportion to their relative abundances on pastures. Second, we examined selectivity within 0.1-m² quadrats, testing whether plant use by cattle at a fine spatial scale is mediated by local botanical composition, time-since-fire or stocking density. With this second assessment, we aimed to explore the spatial distribution of grazing within pastures. These patterns will reveal whether cattle restrict their use of tall fescue when provided with alternative forages and will clarify the impacts of fire and stocking density on selectivity. Given that tall fescue is often viewed as problematic

due to its negative economic and ecological effects (Barnes et al., 2013), clarifying its value to cattle will indicate whether tall fescue could be replaced on rangelands without losing preferred forage.

2 | MATERIALS AND METHODS

2.1 | Study region

This study was conducted on four pastures (21.6–31.4 ha) with high plant species diversity in Ringgold County, Iowa—part of the Grand River Grasslands of southern Iowa and northern Missouri (McGranahan et al., 2012; Miller, Morton, Engle, Debinski, & Harr, 2012). This region is characterized by rolling hills, with loess soils occurring along ridgetops and glacial till on hillslopes (United States Department of Agriculture, 2017). Average annual precipitation in Ringgold County is 923 mm, of which 38% falls from June to August (PRISM Climate Group, 2015). The average temperature from June to August is 22.9°C (National Weather Service, 2018). The four pastures were managed by the Iowa Department of Natural Resources.

2.2 | Pasture management

Within the four pastures, we examined grazing selectivity by cattle among tall fescue, other cool-season grasses, native warm-season grasses, legumes and non-leguminous forbs. Pasture canopies were dominated by tall fescue and other exotic cool-season grasses, including Kentucky bluegrass and smooth brome (*Bromus inermis* (Leyss.)). Native warm-season grasses, including big bluestem and Indiangrass (*Sorghastrum nutans* (L.) Nash), and native and non-native forbs and legumes (e.g., white clover *Trifolium repens* (L.), birdsfoot trefoil *Lotus corniculatus* (L.)) were also common (see Appendix S1 for dominant species).

Since 2007, the four pastures have been managed using patch-burn grazing, a system in which each pasture is delineated into three patches of approximately equal size. One patch per pasture is burned in late March or early April on a rotating basis, such that the entire pasture is burned over a three-year cycle (Scasta et al., 2016). Consequently, the three patches in each pasture represent a gradient of time-since-fire (zero, one and two years; Figure 1).

A herd of either Black Angus or mixed Black Angus and Charolais beef cattle had free access to all patches in each pasture (Table 1). Two of the pastures were stocked from early April to early September at a moderate stocking rate (season-long stocking) and two were stocked more heavily from early April to early July (intensive-early stocking). Because aboveground plant production differed among pastures, stocking rates were set to attain comparable standing crops of approximately 5,000 kg DM/ha on all pastures by early November, the end of the growing season (Table 1). Thus, while instantaneous grazing pressure (AU/T DM of plant biomass) on intensive-early stocking pastures was 2.7–4.3 times greater than that of season-long stocking pastures (based on estimates of standing biomass in early July 2016), end-of-season biomass was expected to be similar. Even so, grazing pressure in both treatments was low relative to many commercial operations, allowing cattle to express their grazing preferences.

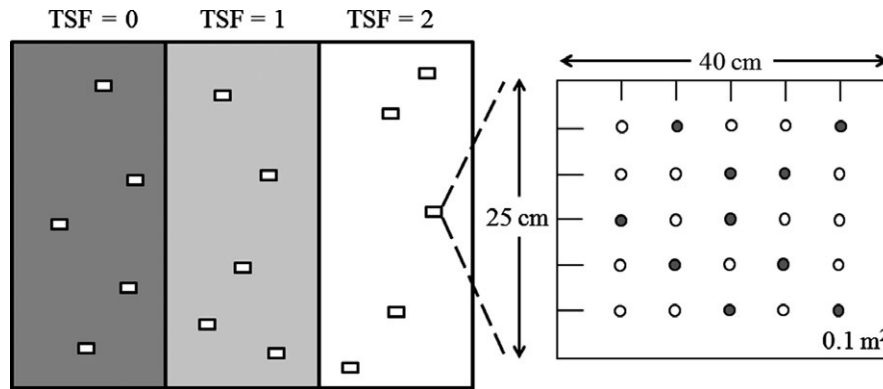


FIGURE 1 Sampling design used to measure the relative abundances of five plant categories, as well as grazing by cattle on those plants, in four pastures in Ringgold County, Iowa, USA. Each pasture was divided into three patches, burned sequentially such that each pasture had one patch burned in 2016 (time-since-fire, or TSF = 0), one patch burned in 2015 (TSF = 1) and one patch burned in 2014 (TSF = 2). We took plant measurements in five 0.1-m² quadrats per patch. We measured relative abundances in each quadrat using a 25-point grid (open and shaded circles), and then randomly selected two points per grid-row (10 points total; shaded circles) at which to measure total and per-category grazing frequencies

TABLE 1 Herd composition and cattle breeds, stocking treatments, rounds sampled, stocking rate (animal-unit-months per hectare) and instantaneous grazing pressure (animal-units per ton of dry matter; measured in early July 2016) applied to each grazing pasture in the study. An AUM is 360 kg dry matter (DM)—the amount of plant biomass that an AU (an animal weighing 450 kg) is expected to consume in one 30-day month (Society for Range Management, 1998)

Pasture ID	Herd composition and cattle breeds	Stocking treatment	Rounds sampled	Stocking rate (AUM/ha)	Instantaneous grazing pressure (AU/T DM)
KLN	Cow-calf pairs (Black Angus)	Intensive-early	R1	3.85	0.27
PYN	Heifers (Black Angus)	Intensive-early	R1	3.31	0.30
PYS	Heifers (Black Angus)	Season-long	R1, R2	2.10	0.07
RIS	Cow-calf pairs (Black Angus and Charolais)	Season-long	R2	2.72	0.10

2.3 | Sampling design

All data were collected over two sampling rounds between June and August 2016 (Table 1). In Round 1 (10 June–5 July), we measured vegetation in three pastures—one season-long stocked pasture and two intensive-early stocked pastures. In Round 2 (24 July–10 August), we measured vegetation on two season-long stocked pastures (one of which was also measured in Round 1). In each round, we collected data on plant abundance and use by cattle within 0.1-m² quadrats. We placed five quadrats in each patch of each pasture per round (three patches per pasture; Figure 1), for a total of 45 quadrats measured in Round 1 and 30 quadrats measured in Round 2. Quadrats were placed randomly along a range of hillside aspects, avoiding hilltops and swale bottoms to reduce effects of wind and moisture accumulation on grazing distribution (Bailey et al., 1996).

2.3.1 | Assessing plant abundance

We used a modified version of the point-quadrat method (Levy & Madden, 1933) to measure the relative abundance of plants in the five categories: tall fescue, other cool-season grasses, native warm-season grasses, legumes and non-leguminous forbs.

Quadrats were marked with gridlines, creating 25 evenly spaced grid-points. We laid the quadrat flat on the soil surface, placed a 2-mm-diameter pin in the ground at each of the 25 grid-points, and classified the plant rooted nearest to each pin-drop into a plant category (Figure 1).

In each quadrat, we calculated the relative abundances of the five categories as the proportion of all sampled plants belonging to each (i.e., number of plants of each category/25). We then calculated the relative abundance of each category at the pasture scale as the average per-category abundance across all quadrats in a given pasture (equivalent to the proportion of all plants in each pasture belonging to each category). Although plant abundance does not directly reflect biomass, it is an index of forage availability.

2.3.2 | Assessing plant use by cattle

In addition to measuring plant abundances, we estimated the percentage of all plants grazed in each quadrat (total grazing frequency). To measure total grazing frequency, we randomly selected 10 of the 25 grid-points per quadrat and recorded whether the plant rooted nearest to each point had been grazed (Figure 1). To determine this, we examined all

shoots on those plants (or all leaves, on plants forming a leaf rosette). If at least two shoots were sheared in a straight line, we counted the plant as grazed. We set the threshold at two shoots to reduce the likelihood of false positives (i.e., a shoot appeared grazed but had been damaged by another cause). If a plant only formed one shoot, as is true of many forbs, we considered it grazed if that shoot was sheared.

We calculated total grazing frequency in each quadrat as the number of plants grazed divided by 10—the number of plants examined for grazing. This method could be biased if some grazed plants were unobservable due to complete consumption, but this was likely rare since cattle tend not to defoliate plants to ground level (Griffiths, Hodgson, & Arnold, 2003).

After measuring total grazing frequency, we measured grazing frequency of each of the five plant categories. At the same 10 grid-points per quadrat (Figure 1), we documented whether the nearest-rooted plant of *each plant category* had been grazed. Thus, in every quadrat we determined the grazing status of up to 10 tall fescue plants, 10 non-fescue cool-season grasses, 10 warm-season grasses, 10 non-leguminous forbs and 10 legumes. We never documented the grazing status of the same plant more than once, so if an individual plant was the closest representative of a given category to more than one grid-point, we would document its grazing status once for the first point, and then record the grazing status of the second-nearest representative for the other points. We calculated per-category grazing frequency in each quadrat as the number of plants of each category that were grazed divided by the number of plants in that category assessed for grazing (10, if at least 10 individual plants of the given category were present in the quadrat; fewer, if there were fewer than 10).

Finally, we quantified per-category use by cattle at the pasture scale. First, we summed the number of plants of each plant category grazed across all quadrats in each pasture to determine the total number of plants grazed per category per pasture. Next, we summed these category-specific use levels to calculate the total number of plants grazed per pasture. For each pasture, we then divided each category-specific use level by the total number of plants grazed to quantify what percentage each plant category composed of all grazed plants. These values do not refer to biomass consumed, but rather to the proportion of plants grazed. We also point out that our measurements are not estimates of use by individual animals, but rather of use by the entire herd on each pasture.

2.4 | Data analysis

We first examined whether cattle used the five plant categories in proportion to their abundances on pastures. We conducted this analysis at the pasture scale, as opposed to the quadrat scale, to determine overall patterns of forage use. To test whether abundance differed from use for any plant categories, we constructed a general linear mixed model in PROC GLIMMIX (SAS, 2013) and compared the relative abundance of each plant category to the proportion of all grazed plants comprised of each category. We chose a Gaussian distribution for this model and included “PastureID” as a random variable.

We next quantified selectivity at the quadrat scale. Focusing on forage use at this fine scale enabled us to understand which local factors determined the spatial distribution of grazing. For these analyses, we assembled candidate model sets to predict total grazing frequency within our 0.1-m² quadrats, as well as grazing frequency of tall fescue, other cool-season grasses, and warm-season grasses. Candidate models included predictor variables chosen based on a priori hypotheses (Table 2), and candidate sets were identical for each of the four response variables (total grazing frequency and the three per-category grazing frequencies). We included quadrat sampling date as a model in each set to assess whether within-season changes in plant biomass, size, stage of growth or palatability influenced forage use. We also included time-since-fire (with quadrats classified based on years since last burn) and stocking treatment (with quadrats classified based on whether they were in an intensive-early or season-long stocking pasture) in the model sets. We did not, however, include sampling round (with quadrats classified based on whether they were measured in Round 1 or Round 2) in the model sets because a general linear mixed model with “Round” as a fixed effect predicting grazing frequencies (“PastureID” included as a random variable) indicated that there were no differences between rounds ($p > 0.15$).

Candidate models for fine-scale selectivity were constructed as generalized linear mixed models with “PastureID” as a random variable. Analyses were completed using PROC GLIMMIX with a lognormal response distribution, identity link function and Laplace maximum likelihood estimation for each candidate model. We used an AIC_c framework to rank models in each set (Burnham & Anderson, 2002) and obtained predicted values and 85% confidence intervals (Arnold, 2010) from the top-ranked models in each set (i.e., models with AIC_c lower than a random-effect-only model and with weight contributing to the top 90% of model-set weights).

3 | RESULTS

3.1 | Selectivity at the pasture scale

Cattle used some plant categories disproportionately to their relative abundance ($F(9, 27) = 9.71, p < 0.001$; Figure 2). Although tall fescue was the most abundant category in the pastures, composing on average 46.4% of all plants, it composed only 26% of all grazed plants. In contrast, legumes composed only 12.3% of all plants, but composed 24.6% of all grazed plants—similar to use of both tall fescue and other cool-season grasses (Figure 2). Other cool-season grasses, warm-season grasses, and forbs were used in proportion with their abundances (i.e., confidence intervals around relative abundance and use estimates overlapped).

3.2 | Selectivity at the quadrat scale

Total grazing frequency in the 0.1-m² quadrats was primarily related to the quadrat-scale abundance of warm-season grasses and tall fescue, and to measurement date (Table 3A). There is model-selection uncertainty for these effects, but the models associated

TABLE 2 Models included in all candidate model sets for AIC analyses of which variables influence total grazing frequency and category-specific grazing frequencies by cattle at the quadrat scale in the Grand River Grasslands. Biological justifications provide context for why we included each model

Model	Justification
Non-fescue cool-season grass relative abundance	Many non-fescue cool-season grasses provide palatable forage and thus could influence spatial patterns of grazing. At the same time, they may be less palatable in late summer since they reach maturity in early summer.
Tall fescue relative abundance	Tall fescue infected with the fungal endophyte <i>Epichloë coenophiala</i> can cause health problems in cattle, so cattle may avoid grazing areas of high tall fescue abundance. Also, being a cool-season grass, they may be less preferred in the later summer.
Non-leguminous forb relative abundance	These include a broad diversity of species that could provide either highly nutritious or unpalatable forage.
Legume relative abundance	Legumes often have high levels of protein and may counteract the negative effects of alkaloids in endophyte-infected fescue. Cattle may therefore be attracted to areas with abundant legumes.
Warm-season grass relative abundance	Warm-season grasses grow primarily in mid-to-late summer months when we sampled, and thus may be preferred over more mature cool-season grasses. Moreover, these grasses are recommended as drought-tolerant summer forages and are planted for wildlife conservation, so it is important to understand their use by cattle.
Ordinal date	Forage use by cattle may vary during the summer with changes in forage quantity, forage quality, biomass of individual plants and dietary needs.
Time-since-fire	Fires remove dead plant material and may increase forage quality, so patches burned more recently are predicted to experience higher levels of forage use.
Stocking treatment (intensive-early vs. season-long stocking)	Forage use should be greater in pastures stocked at higher grazing pressures.
Null	This random-effect-only model provides a baseline for comparison. Pasture identity is the random effect.

with these variables composed 66% of AIC weight. Total grazing frequency increased with warm-season grass abundance (Figure 3a; $F(1, 38) = 5.27, p = 0.027$), but decreased as tall fescue abundance increased (Figure 3b; $F(1, 38) = 3.88, p = 0.056$). Total grazing frequency was greater in quadrats measured earlier in the growing season, suggesting that forage use decreased over time within the season (Figure 3c; $F(1, 38) = 4.04, p = 0.052$).

Time-since-fire did not influence total grazing frequency, but use of both tall fescue (Table 3B; Figure 4a; $F(1, 41) = 14.11, p < 0.001$) and other cool-season grasses (Table 3C; Figure 4a; $F(1, 40) = 15.54, p < 0.001$) was greater in more recently burned patches. Use of tall fescue was also lower in quadrats with high tall fescue abundance (Figure 4b; $F(1, 41) = 5.93, p = 0.019$). Although this model composed only 5% of AIC weight, it was ranked much higher than the null model (Table 3B).

Similar to total grazing frequency and use of tall fescue, use of warm-season grasses within quadrats decreased with increasing abundance of tall fescue (Table 3D; Figure 5a; $F(1, 20) = 3.38, p = 0.08$). In contrast, warm-season grass use increased as legume abundance increased within quadrats (Figure 5b; $F(1, 20) = 15.44, p < 0.001$).

4 | DISCUSSION

Cattle used some plant categories disproportionately to their abundances on pastures. Although tall fescue was far more abundant than

all other categories, it was grazed less than expected—at a frequency comparable to both legumes and other cool-season grasses. In contrast, legumes were grazed more frequently than expected. These results are consistent with two prior studies conducted in two-species pastures containing tall fescue and either alfalfa (*Medicago sativa* (L.); Boland et al., 2012) or white clover (Schaefer et al., 2014), which showed that cattle prefer legumes when grazing in legume-tall fescue mixtures. Our results extend these findings, demonstrating this pattern in heterogeneous pastures containing many more forage species. This is notable because the other plant categories we measured—non-fescue cool-season grasses, warm-season grasses, and forbs—were grazed in proportion to their abundances, indicating that cattle specifically restricted grazing of tall fescue, and not of non-legume forages more generally. Cattle may prefer legumes in part because they have high leaf-to-stem ratios and contain high levels of protein (Van Soest, 1994), but legumes may be particularly beneficial in pastures with abundant tall fescue because some species—in particular, alfalfa and birdsfoot trefoil—produce compounds that counteract the negative health impacts of ergovaline alkaloids in endophyte-infected tall fescue (Lyman, Provenza, Villalba, & Wiedmeier, 2011). Our pasture-scale data were consistent with these mechanisms since cattle avoided grazing tall fescue.

Our fine-scale data—measurements of plant composition and use within 0.1-m² quadrats—also indicated cattle avoidance of tall fescue. Quadrats with abundant tall fescue exhibited low total grazing frequency (percent of all plants grazed), showing that cattle

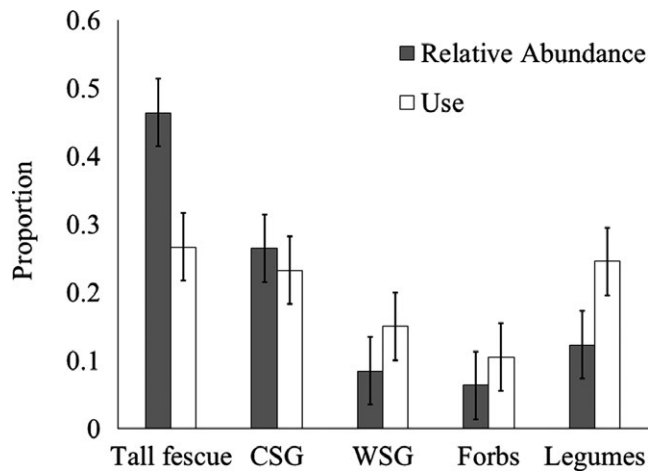


FIGURE 2 Comparison of relative abundance versus use by cattle of five plant categories—tall fescue, other cool-season grasses (CSG), native warm-season grasses (WSG), non-leguminous forbs (forbs) and legumes—in four Iowa pastures. Relative abundance of each plant category (dark bars) was measured as the proportion of all plants comprised of each plant category. Use (light bars) was measured as the proportion of all grazed plants comprised of each category. Confidence intervals (85%) are shown

limited grazing in parts of pastures with large amounts of tall fescue. Moreover, as tall fescue abundance within a quadrat increased, use of tall fescue within that quadrat decreased, indicating that even when cattle chose to graze in areas with abundant tall fescue, they selected against it. This pattern suggests that cattle may attempt

to limit consumption of tall fescue, and thus, the spatial distribution of tall fescue influences the distribution of grazing within pastures.

In contrast to the effects of tall fescue, total grazing frequency was greater in 0.1-m² quadrats with abundant warm-season grasses. This may have been because the timing of data collection (June–August) corresponded with periods of cool-season grass maturity and high warm-season forage quality (Burns et al., 1984; Paterson et al., 1994). The effects of warm-season grasses on grazing intensity at fine spatial scales may be less marked in the cooler months of April and May when growing conditions are not favourable for warm-season grass growth.

We also found that total grazing frequency was greater earlier in the season (i.e., more plants were grazed in quadrats measured in June vs. August). This result could have been a product of plant growth and size; if plants tended to be larger later in the season, as expected, cattle may have needed to graze fewer of them to achieve intake requirements. We thus caution against generalizations about temporal patterns of cattle biomass consumption based on our data.

In contrast to vegetation composition and time within season, time-since-fire did not influence total grazing frequency. We had expected that total grazing frequency would be higher in more recently burned patches because fire removes dead plant material, making it easier for cattle to graze (Willms et al., 1980), and because forage protein content may be higher in more recently burned areas (Allred et al., 2011). Instead, we found that cattle only increased use of tall fescue and other cool-season grasses following a fire. On one hand, this may indicate that fire leads to a particularly strong increase in the palatability of cool-season grasses. Fire may also reduce endophyte infection

Response variables and candidate models	-2LL ^a	K ^b	AIC _c	ΔAIC	Weight ^c
(A) Total grazing frequency (% of all forage grazed)					
Warm-season grass relative abundance	80.11	3	89.16	0	0.300
Ordinal date	81.08	3	90.13	0.97	0.185
Tall fescue relative abundance	81.14	3	90.2	1.04	0.178
Null (random-effect only)	85.08	2	91.69	2.53	0.0847
(B) Grazing frequency of tall fescue (% tall fescue grazed)					
Time-since-fire	92.5	3	101.47	0	0.885
Tall fescue relative abundance	98.16	3	107.14	5.67	0.0519
Null (random-effect only)	110.66	2	110.66	9.19	0.0088
(C) Grazing frequency of other cool-season grasses (% cool-season grasses grazed)					
Time-since-fire	69.53	3	78.53	0	0.918
Null (random-effect only)	82.5	2	89.09	10.56	0.00468
(D) Grazing frequency of native warm-season grasses (% warm-season grasses grazed)					
Legume relative abundance	49.26	3	59.26	0	0.468
Tall fescue relative abundance	54.16	3	61.3	2.04	0.169
Null (random-effect only)	57.59	2	62.13	2.87	0.111

TABLE 3 Results for generalized linear mixed model sets for each response variable (A–D). Models were ranked using AIC_c. All models include “PastureID” as a random effect. Only the null model and models with cumulative AIC_c weight ≥ 0.90 are displayed for the model sets with low model selection uncertainty (B and C). Only models ranked above the null are shown for sets with higher uncertainty (A and D)

^aModel deviance; a metric of goodness of fit. ^bNumber of estimable parameters in the model. ^cAkaike weight; interpreted as the probability that the model is the best-approximating model in the candidate set.

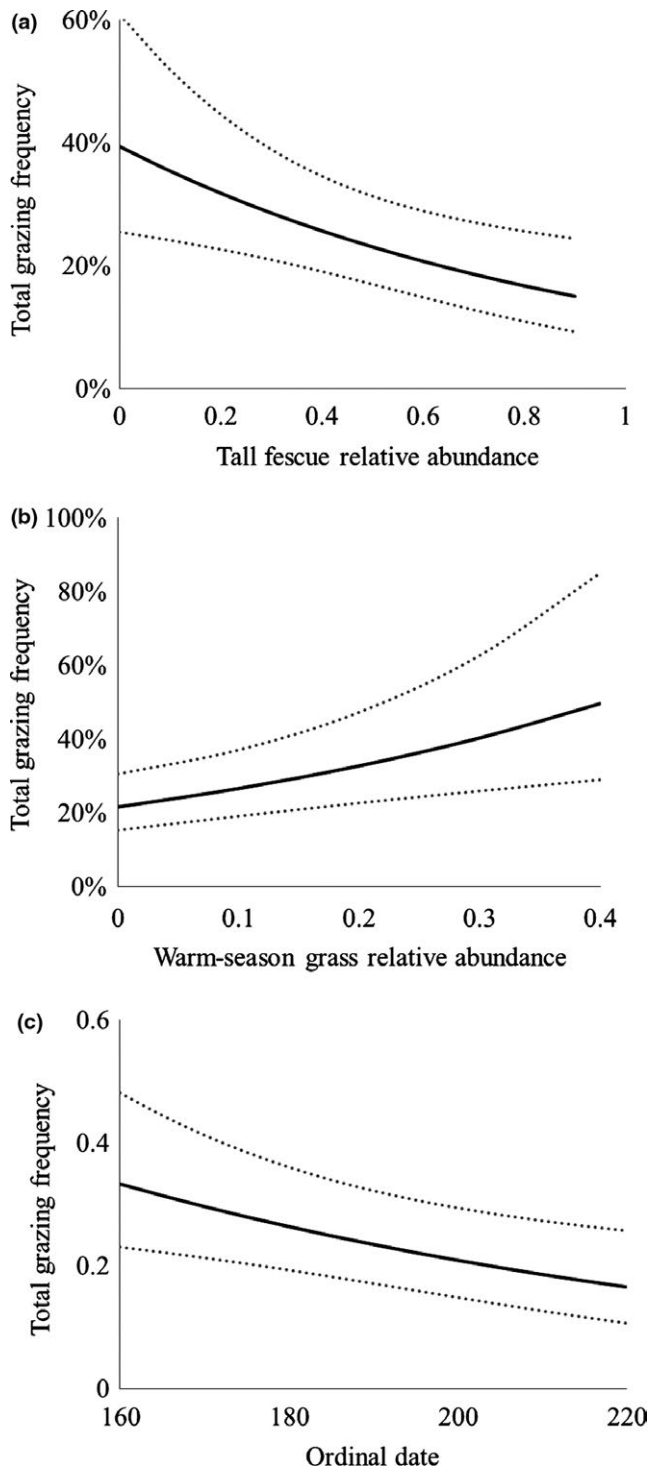


FIGURE 3 Total grazing frequency (proportion of plants grazed) within a given 0.1-m² quadrat as a function of the relative abundance of (a) tall fescue and (b) warm-season grasses in the quadrat, as well as (c) ordinal date of measurements (10 June–10 August). Confidence intervals (85%) are shown

in tall fescue—a hypothesis supported by the fact that detectability of ergovaline alkaloids in cattle faeces in our study region decreased after fire (Debinski, Jokela, McCulley, Engle, & Scasta, 2015). Another possibility may be that all forages were consumed in greater quantities

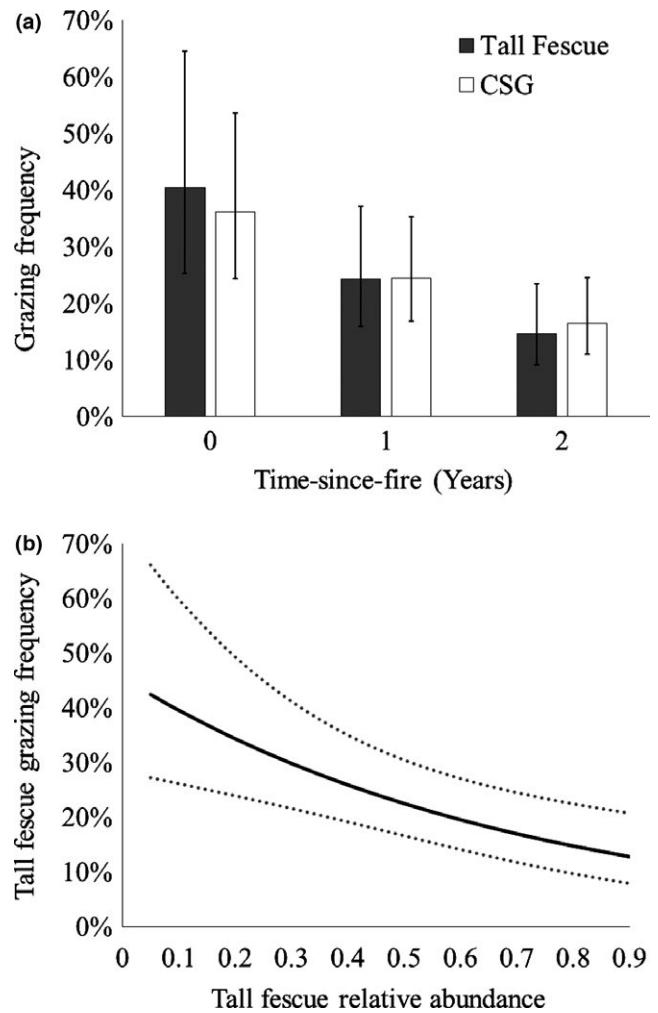


FIGURE 4 Grazing frequency of tall fescue within a given 0.1-m² quadrat as a function of (a) time-since-fire and (b) relative abundance of tall fescue in the quadrat. Panel (a) also shows use of non-fescue cool-

in more recently burned patches, but this manifested through increased biomass consumption rather than grazing frequency. This explanation is consistent with our observation that plant biomass on our study pastures (estimated in July by visual obstruction measurements with a Robel pole; $N = 30$ per patch) was lower in more recently burned patches (J. Coon and W. Schacht, unpublished data). A final explanation may be that total grazing frequency was not higher in recently burned patches because stocking rates on intensive-early stocking pastures were too high for this pattern to manifest; high stocking rates have been seen to limit focal grazing of burned areas in our patch-burn-grazing system (Scasta et al., 2016).

Overall, our data show that cattle consume a broad variety of forages. Non-fescue cool-season grasses, native warm-season grasses, and forbs were grazed in proportion to their abundances, but cattle grazed more legumes and less tall fescue than expected. At a fine spatial scale, areas of pastures with abundant tall fescue exhibited low use levels, indicating avoidance of tall fescue by cattle. These results suggest that tall fescue is not a preferred forage in heterogeneous

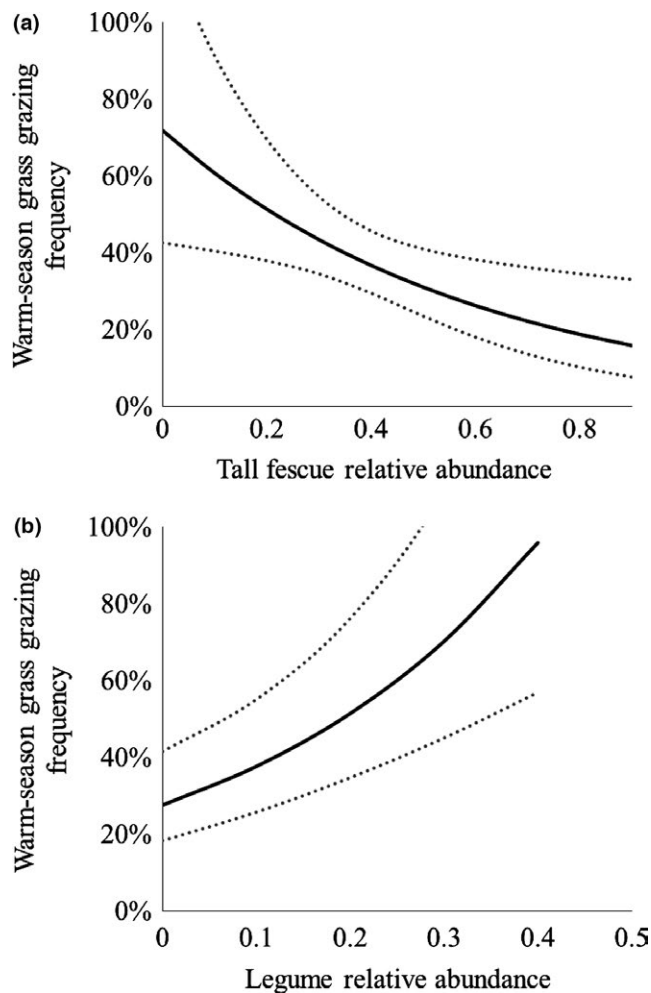


FIGURE 5 Grazing frequency of warm-season grass within a given 0.1-m² quadrat as a function of the relative abundance of (a) tall fescue and (b) legumes in the quadrat. Confidence intervals (85%) are shown

pastures—not only relative to legumes, but to other cool-season and warm-season grasses. The mechanisms behind this pattern, however, warrant further research. In particular, we did not analyse plants in this study for nutritive contents or infection by the fungal endophyte, so we cannot discern whether tall fescue was avoided because of endophyte infection or because it is relatively unpalatable in mid-to-late summer. In examining these mechanisms, quantifying nutritive value, endophyte content, and use by cattle among different parts of individual tall fescue plants could provide insight on within-plant-scale interactions between forage quality and selection.

Given the known negative effects of tall fescue on cattle health (Mays et al., 2013; Schmidt et al., 1982; Stuedemann & Hoveland, 1988), some cattle producers are concerned that tall fescue could adversely affect livestock production and are open to reducing its abundance on their lands (Coon, Morton, & Miller, 2018). Our results show that tall fescue is underutilized relative to other forages, and thus maintaining high levels on pastures may be counterproductive to production goals in the Midwestern United States. We do not urge tall fescue eradication, given its cool-season productivity and resilience under stress

(Tracy et al., 2018), but we suggest that ensuring that other forages are highly abundant on pastures may improve forage quality. In particular, warm-season grasses may enhance summer grazing (Paterson et al., 1994; Tracy et al., 2018). In addition to providing preferred forages, increasing plant diversity on pastures may increase forage production under variable environmental conditions, as well as resilience to invasive plants (Sanderson et al., 2013). Reducing tall fescue could also provide ecological benefits, given that the grass has been shown to reduce habitat suitability for wildlife (Barnes et al., 2013; Osborne et al., 2012). If tall fescue reduction is not an option, however, our finding that cattle increase use of tall fescue and other cool-season grasses following burning indicates that prescribed fire may increase the value of tall fescue as livestock forage in the summer following a burn.

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CONFLICT OF INTEREST

None.

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