The role of grass stems as structural foraging deterrents and their effects on the foraging behaviour of cattle

Michael Drescher a,b,*, Ignas M.A. Heitkö nig a, Jan G. Raats c, Herbert H.T. Prins a

a Resource Ecology Group, Wageningen University, 6708 PD Wageningen, The Netherlands
b Department of Integrative Biology, University of Guelph, Guelph, Ont. N1G 2W1, Canada
c Faculty of Agricultural and Environmental Sciences, University of Fort Hare, Alice 5700, South Africa

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Abstract

Little quantitative information is available about the role of stems as structural foraging deterrents for large grazers and the actual mechanisms by which such deterrents affect foraging behaviour. We measured bite size, bite rate and the rate of forage intake of cattle foraging on artificial micro-swards of the tropical, broad-leaved guinea grass. These micro-swards varied in total forage mass density, in forage quality, defined as the proportion of high-quality plant parts (leaves) and of foraging deterrents (stems), and in the spatial pattern of plant parts. We hypothesized that stems interfere with the process of grasping of leaves and predicted that decreasing forage quality, by reducing bite size and bite rate, depresses the slope and the asymptotic maximum of the functional response curve. Further we hypothesized that increasing cluster size of leaves increases the accessibility of leaves to cattle, thus alleviating the negative effects of decreasing forage quality, and predicted that increasing leaf cluster size has positive effects on bite size and on the rate of forage intake.

The slope of the functional response curve decreased with decreasing forage quality, mainly because of depressed bite size. These effects were also found when the amount of leaves in the grass sward was kept constant while only the amount of stems increased. Thus, the observed effects are not merely the result of decreased availability of leaves, but at least in part caused by the increasing

* Corresponding author at: Ministry of Natural Resources, Ontario Forest Research Institute, 1235 Queen Street East, Sault Ste. Marie, Ont. P6A 2E5, Canada. Tel.: +1 705 946 7406; fax: +1 705 946 2030.
E-mail address: michael.drescher@mnr.gov.on.ca (M. Drescher).

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interference of stems with the grasping of leaves. Leaf cluster size had a positive effect on bite size. However, this effect did not show in the rate of forage intake, because for small leaf clusters high bite rates compensated for decreased bite sizes. Instead of the familiar negative relationship of bite rate with bite size, we found a positive relationship. We speculate that this effect is the result of decreased chewing times for small bites and increased time needed to grasp these bites, effectively changing the limitation of bite rate from chewing time to a limitation by the time needed to grasp bites.

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1. Introduction

The functional response (i.e., the relationship of forage intake rate with forage availability, Holling, 1959) plays a central role in the interaction of a forager with a forage resource. Because forage intake has consequences for animal fitness and production (e.g., Romney et al., 2000; Smallegange and Brunsting, 2002; Landete-Castillejos et al., 2003), quantifying the effects of resource structure on the rate of forage intake and the shape of the functional response curve (e.g., Durant et al., 2003) is critical for furthering our understanding of foraging ecology.

Theoretical studies have shown that the rate of forage intake in large herbivores is mainly determined by bite size (Spalinger and Hobbs, 1992; Parsons et al., 1994; Farnsworth and Illius, 1996). This notion is in line with various empirical studies in mostly temperate environments (Spalinger et al., 1988; Gross et al., 1993a, 1993b; Ginnet and Demment, 1995). However, when processing capacity is not limiting, bite rate also has the potential to affect the rate of forage intake (Spalinger and Hobbs, 1992).

Nevertheless, explaining the variation in the rate of forage intake with bite size is only a proximate answer. The ultimate question is which characteristics of the forage resource determine bite size and bite rate and thus, ultimately, the rate of forage intake.

In simple, uniformly leafy swards, grass sward height (m), grass surface density (g m$^{-2}$), and grass bulk density (g m$^{-3}$) were found to determine bite size of grazers (Black and Kenney, 1984; Arias et al., 1990; Ungar et al., 1991; Laca et al., 1992a, 1992b, 1994; Gong et al., 1996; Bakker et al., 1998; WallisDeVries et al., 1998; Wilmshurst et al., 1999). However, mature natural grass swards are a complex mixture of various plant parts (e.g., leaves and stems). The structural and chemical properties of plant parts in grasses differ (Van Soest, 1994), though not as markedly as in woody plants. Some studies have indicated that grass stems can act as structural foraging deterrents in grasses, much like thorns in shrubs, and can limit bite size (Arias et al., 1990; Ginnet et al., 1999; Bergman et al., 2000). However, most of these studies were restricted to investigating the effects of grass stems in sub-canopy horizons of the grass sward on bite depth. To our knowledge, only the study of Hongo (1998) dealt with the effects of grass stems in the grass sward canopy itself. Unfortunately, his experimental design did not lend itself to clearly distinguishing between the effects of a number of sward characteristics. Past studies on the effects of grass stems on bite rate yielded contradictory results because some studies found a negative effect (Ryule et al., 1987; Ginnet et al., 1999), while other studies found no effect (Arias et al., 1990;
Neither of these studies addressed the question whether the spatial pattern of structural foraging deterrents in the sward canopy determine bite size and bite rate, and thus the rate of forage intake.

The objectives of this paper are to show that grass stems in the grass sward canopy can act as structural foraging deterrents to cattle by depressing both bite size and bite rate, thus decreasing the rate of forage intake and changing the shape of the functional response curve. Further, we want to show how this effect varies with the spatial pattern of the plant parts in the grass sward canopy and with season.

If we define forage quality as the proportion of high-quality forage parts (i.e., grass leaves) in the grass sward, then a decrease in forage quality means an increase in the proportion of foraging deterrents (i.e., grass stems) in the grass sward canopy. For a given total forage mass density, decreasing forage quality means an increase in the density of foraging deterrents. Given that cattle select for leaves, we hypothesized that stems interfere with the process of grasping of leaves and that therefore the proportion of stems in the grass sward has negative effects on forage ingestion. More specifically, we predicted that decreasing forage quality has the following effects: (i) because foraging deterrents stand closer together, cattle decrease bite size showing in a reduced slope of the bite size–forage mass relationship; (ii) because foraging deterrents stand closer together, cattle have to spend more time to locate and crop interspersed leaves, thus decreasing bite rate; (iii) mainly because of the effect on bite size, the slope and the maximum potential rate of forage intake of the functional response curve will be depressed.

For a given forage quality (i.e., the same proportion of grass leaves and grass stems) we define spatial pattern as the size (surface area) of clusters of high-quality forage parts (grass leaves) in a matrix of foraging deterrents (grass stems). We hypothesized that increasing cluster size of leaves increases the accessibility of these forage parts and alleviates the negative effects of decreasing forage quality, as outlined above. In other words, for a given forage mass and forage quality, with increasing cluster size, we expected to observe: (i) an increase in bite size, because the cropping of leaves is less hindered by the surrounding stems; (ii) a change in bite rate that can either be positive, if bite rate is limited by cropping, or negative, if bite rate is limited by the time between the cropping of bites; (iii) an increase in the rate of forage intake mainly due to the effect of cluster size on bite size.

2. Materials and methods

The study was conducted at the Research Farm of the University of Fort Hare, at Alice, Eastern Cape, South Africa. We performed experiments with cattle (*Bos taurus* L.), foraging on hand-constructed micro-swards of the (sub-)tropical guinea grass (*Panicum maximum* Jacq.), an erect, broad-leaved species. The experimental swards differed in total mass, in the proportion of grass leaves and grass stems, and in the size (surface area) of clusters of leaves surrounded by grass stems. The experiments were performed during the late wet season and repeated during the early dry season to additionally investigate potential effects of season on foraging behaviour.
2.1. Experimental swards

All experimental work was performed using hand-constructed swards (Black and Kenney, 1984; Laca et al., 1992b). Each morning between 07:30 and 09:30 h, tillers of guinea grass were clipped in the field. At all times, plant parts were kept in water, sprayed and, if necessary, covered with plastic to prevent wilting. Grass leaves and grass stems were separated and then threaded through holes in wooden blocks. In each hole we inserted either three leaves (subsequently we call this one leaf tiller), or one stem, or holes were left empty. In each block of 10 cm x 10 cm there were 16 holes in a square grid at equal distance. In each block a minimum of one hole and a maximum of eight holes were filled with leaves or stems, with the remaining holes left empty. Plant parts were clamped to the wooden block by shifting a plastic plate underneath the block and screwing it tightly against it. We fastened between 40 and 50 blocks on a large plastic board, to produce one hand-constructed sward of between 0.4 and 0.5 m². Leaf tillers and stems were always trimmed to produce a uniform canopy height of 15 cm. Hand-constructed swards were offered to the animals in a shed between 11:00 and 15:00 h.

2.2. Animals

We used four Nguni oxen of 1.5 to 2 years, weighing 250–320 kg. Two of the oxen were oesophageally fistulated more than 4 months earlier for other experiments. All animals were duly cared for by a veterinarian. When not in experimental trials and between experimental series, the animals were kept on a rangeland, but had daily contact with the experimenters. During the period of the experiments, the animals were not fed dietary supplements.

2.3. Experimental design

The experiments were performed from February to March 2000, during the late wet season, and from May to June, during the subsequent early dry season. Before each experimental series, the animals were trained for at least 3 weeks to accustom them to the experimental set-up. Each day, before beginning with the experimental trial, the animals were collected from the rangeland and brought to a shed, where they were fasted for 2.5–5 h. Subsequently, one animal was led to the hand-constructed sward and allowed to graze. The grazing process was video taped and the observation was ended after 50–90% of the high-quality forage parts were removed.

Swards differed in total mass (i.e., g leaf + g stem), forage quality (i.e., the proportion of leaves = g leaf/g total × 100%), and spatial pattern of leaves and stems (Fig. 1). All masses in this study are given as dry matter. We varied total mass by changing the number of filled holes (i.e., by changing the bulk density). Because of logistic constraints, we used incomplete factorial designs. We offered swards of: low (approximately 20 g m⁻²), medium (approximately 80 g m⁻²), or high (approximately 180 g m⁻²) total mass. Forage quality was low (approximately 25% leaves), medium (approximately 45% leaves), or high (100% leaves). The spatial pattern of leaf tillers and grass stems was varied by building leaf clusters of varying surface area: small (25 cm²), medium (100 cm²), large (200 cm²), and
very large (400 cm²). A leaf cluster, in this study, is one leaf tiller or a number of leaf tillers directly adjacent to one another. The perimeter of a leaf cluster is spatially defined by the stems surrounding it.

In the first experiment on forage quality, leaf tillers and stems were always arranged uniformly over the grass sward, thus avoiding clustering of leaf tillers or stems. The combinations of total forage mass and forage quality used for this experiment were: 20 g m⁻² with 45% and 100% leaves, 80 g m⁻² with 25%, 45%, and 100% leaves; 180 g m⁻² with 25% and 45% leaves. The arrangement of leaf tillers and stems in these treatments are shown in Fig. 1.

In the second experiment on spatial pattern of plant parts, we arranged tillers of leaves in various degrees of clustering in a matrix of grass stems. Total forage mass (approximately 80 g m⁻²) and forage quality (approximately 45% leaves) were kept constant over all treatments. The arrangement of leaf tillers and stems in these treatments are shown in Fig. 1.

2.4. Measurements

We measured the time of active grazing (s) and counted the number of bites using the video recordings; periods when animals engaged in other activities were excluded from the measurements. Bite rate (s⁻¹) was calculated as active grazing time divided by the number of bites.

Available pre-grazing forage mass (g) was estimated via randomly selected and removed blocks. Total ingested forage mass (g) was calculated as pre-grazing forage mass minus the residual forage mass after grazing. Bite size (g) was calculated as total ingested forage mass divided by the number of bites. Average intake rate (g s⁻¹) was calculated as
totally ingested forage mass divided by active grazing time. In the remainder of this paper, forage mass is expressed as mass per area, thus as forage mass density (g m\(^{-2}\)). Each of the four animals was exposed to each treatment and animals were treated as replicate measurements.

2.5. Statistical analyses

In the first experiment, we examined the effects of forage quality and total forage mass density on the rate of forage intake, bite size, and bite rate using mixed ANCOVAs. We treated season and forage quality as fixed factors, individual as random factor, and total forage mass density as covariate. We limited our analyses to main factors and two-way interactions and excluded non-significant terms. When a significant interaction effect of forage quality with total forage mass density on forage intake rate or bite size was found, we performed unplanned pairwise comparisons of slopes between forage qualities to identify significant differences between slopes with sequential Bonferroni correction (Rice, 1989). For bite rate, we performed unplanned pairwise comparisons of least squares means with sequential Bonferroni correction between forage qualities to identify significant differences between means. In the second experiment, for a given total forage mass density, we examined the effects of the spatial pattern of plant parts on the rate of forage intake, bite size, and bite rate using mixed ANOVAs. We treated season and leaf cluster size as fixed factors, and individual as random factor. We limited our analyses to main factors and two-way interactions and excluded non-significant factors. We performed unplanned multiple comparisons between least squares means of leaf cluster sizes and identified significant differences between means with sequential Bonferroni correction.

3. Results

3.1. Forage quality

Our analysis indicated that the slope of the bite size-total forage mass density relationship varied between forage qualities (\(F = 128.51, P < 0.0001\), Fig. 2a). Comparison of slopes ((−0.29, 5.51, and 75.91) \(\times 10^{-4}\) m\(^{-2}\), for 25%, 45%, and 100% leaf, respectively) showed that decreasing forage quality depressed the slope of this relationship (Table 1). Bite size increased with forage mass density for 100% and 45% leaf (\(t = 11.83, P = 0.001; t = 3.60, P = 0.037\), respectively), but there was no significant effect of total forage mass density on bite size for 25% leaf (\(t = −0.14, P = 0.901\)). There was no effect of season on bite size (\(F = 1.83, P = 0.269\)).

The relationship of bite rate with total forage mass density varied between forage qualities (\(F = 5.61, P = 0.009\), Fig. 2b). However, none of the slopes of this relationship was significantly different from zero (all |\(t\)| < 2.87, all \(P > 0.064\)). Comparison of least squares means (28.58, 36.82, and 57.21 min\(^{-1}\), for 25%, 45%, and 100% leaf, respectively) showed that decreasing forage quality depressed bite rates for all contrasts (Table 1). There was no effect of season on bite rate (\(F = 6.66, P = 0.082\)).
Fig. 2. Effects of forage quality on the relationship between bite size, bite rate, and forage intake rate and total forage mass density for cattle. Shown are the experimental data and regression lines for the different forage qualities: (a) the relationship between bite size and forage mass density (100% leaf: $y = 1.8 \times 10^{-1} g + 7.6 \times 10^{-3} m^2 \times x$; 45% leaf: $y = 1.6 \times 10^{-1} g + 5.5 \times 10^{-4} m^2 \times x$); (b) the relationship between bite rate and forage mass density; (c) the functional response, i.e., the relationship between the rate of forage intake and forage mass density (100% leaf: $y = -1.7 g \ min^{-1} + 4.5 \times 10^{-1} m^2 \ min^{-1} \times x$).
The pattern of response of forage intake rate to changing total forage mass density was very similar to the pattern shown by bite size (Fig. 2a and c). The slope of the functional response curve varied between forage qualities ($F = 128.51, P < 0.0001$, Fig. 2c). Comparison of slopes ($(-0.33, 1.48, \text{ and } 44.99) \times 10^{-2}$ m$^2$ min$^{-1}$, for 25%, 45%, and 100% leaf, respectively) showed that decreasing forage quality depressed the slope of the functional response curve (Table 1). Forage intake rate increased with total forage mass density for 100% leaf ($t = 10.15, P = 0.002$), but for neither 45% leaf nor 25% leaf the slope of the functional response curve was significantly different from zero over the investigated ranges ($t = 1.73, P = 0.182$; $t = -0.46, P = 0.680$, respectively). Our analysis did not indicate an effect of season ($F = 2.52, P = 0.211$).

Plotting the rate of forage intake against bite size again shows the effects of forage quality on foraging behaviour (Fig. 3). The slope of the forage intake rate-bite size relationship can be interpreted as representing bite rate. The graph illustrates the decrease in bite rate with forage quality, which is significantly higher for 100% leaf compared to 45% leaf ($t = -3.30, P = 0.002$). However, the remaining contrasts in this analysis give no evidence for any further differences in bite rate (100% versus 25%: $t = -1.52, P = 0.136$; 45% versus 25%: $t = -0.01, P = 0.999$).

Through pairwise comparison of treatments of equal leaf mass density but different stem mass densities, we uncoupled the effects of foraging deterrents and of high-quality forage mass (Table 2). After controlling for individual effects and for season, increasing stem mass density always decreased the rate of forage intake and bite rate. However, bite size only decreased with stem mass density in the higher leaf mass density treatments. Over all comparisons, the effect of the foraging deterrents increased with leaf mass density.

### Table 1

<table>
<thead>
<tr>
<th>Foraging behaviour variable</th>
<th>Contrasted forage qualities</th>
<th>d.f.</th>
<th>$t$</th>
<th>$P$</th>
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<tr>
<td>Bite size</td>
<td>100% vs. 45%</td>
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<td>-14.43</td>
<td>&lt;0.0001**</td>
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<tr>
<td></td>
<td>100% vs. 25%</td>
<td>37</td>
<td>-13.97</td>
<td>&lt;0.0001**</td>
</tr>
<tr>
<td></td>
<td>45% vs. 25%</td>
<td>26</td>
<td>-2.04</td>
<td>0.026</td>
</tr>
<tr>
<td>Bite rate</td>
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<td>6</td>
<td>-4.78</td>
<td>0.002**</td>
</tr>
<tr>
<td></td>
<td>100% vs. 25%</td>
<td>6</td>
<td>-5.96</td>
<td>0.001**</td>
</tr>
<tr>
<td></td>
<td>45% vs. 25%</td>
<td>6</td>
<td>-2.48</td>
<td>0.024</td>
</tr>
<tr>
<td>Forage intake rate</td>
<td>100% vs. 45%</td>
<td>37</td>
<td>-14.01</td>
<td>&lt;0.0001**</td>
</tr>
<tr>
<td></td>
<td>100% vs. 25%</td>
<td>37</td>
<td>-13.04</td>
<td>&lt;0.0001**</td>
</tr>
<tr>
<td></td>
<td>45% vs. 25%</td>
<td>26</td>
<td>-1.21</td>
<td>0.118 ns</td>
</tr>
</tbody>
</table>

A unplanned multiple comparisons of slopes for bite size and forage intake rate, and of least squares means for bite rate. Uncorrected $P$-values for 1-tailed $t$-test.

ns: No significant difference after sequential Bonferroni correction.

* Significant difference at $\alpha = 0.05$ after sequential Bonferroni correction.

** Significant difference at $\alpha = 0.01$ after sequential Bonferroni correction.
3.2. Cluster size

Bite sizes were significantly larger in the wet season than in the dry season ($F = 14.77$, $P = 0.031$). Within seasons, bite size increased with leaf cluster size ($F = 10.20$, $P = 0.003$; $F = 5.87$, $P = 0.017$, wet and dry season, respectively, Fig. 4a). Comparison of bite sizes between leaf cluster sizes indicated that in both seasons bite sizes increased from 25 to 100 cm$^2$ leaf cluster size (0.26–0.50 g, and 0.23–0.38 g, for the wet and dry season, respectively), but not thereafter (Table 3).
Fig. 4. Effects of leaf cluster size on bite size, bite rate, and forage intake rate of cattle. Shown are means with standard deviation. Means were compared within each season (pooled over both seasons for bite rate) and
There was no significant effect of season on bite rate ($F = 3.94, P = 0.141$), but bite rate changed with leaf cluster size ($F = 5.87, P = 0.017$, Fig. 4b). The analysis indicated that bite rate for the 25 cm$^2$ leaf cluster size was higher than for the 100 cm$^2$ leaf cluster size (39.9 and 27.0 min$^{-1}/C_0$, for 25 and 100 cm$^2$, respectively), but not different from the 200 to 400 cm$^2$ leaf cluster size treatments. Bite rates did not differ between any of the 100, 200, and 400 cm$^2$ leaf cluster size treatments (Table 3).

Wet season rates of forage intake were significantly higher than in the dry season ($F = 12.92, P = 0.037$). The analysis of variance did not indicate an effect of leaf cluster size on the rate of forage intake within seasons ($F = 1.27, P = 0.341; F = 1.51, P = 0.277$, wet and dry season, respectively, Fig. 4c). Comparison of mean forage intake rate between leaf cluster sizes (wet season: 11.7 and 16.9 g min$^{-1}/C_0$, dry season: 7.7 and 11.4 g min$^{-1}/C_0$, for 25 and 400 cm$^2$, respectively), did not indicate any significant differences either (Table 3).

significant differences after sequential Bonferroni correction ($P < 0.05$) are indicated by different letters: (a) the relationship between bite size and leaf cluster size for the wet and for the dry season; (b) the relationship between bite rate and leaf cluster size pooled over both seasons; (c) the relationship between forage intake rate and leaf cluster size for the wet and for the dry season.
4. Discussion

The results of this study are in line with our prediction that decreasing forage quality has negative effects on bite size, bite rate, and the rate of forage intake of cattle, thus reaching our first objective. Decreasing forage quality decreased the slope of the functional response curve (Table 1 and Fig. 2c). Whereas the rate of forage intake responded strongly to an increase in forage mass density for a forage quality of 100% leaf, there was no significant increase in forage intake rate for a forage quality of either 45% leaf or of 25% leaf. In the light of the already high densities of total forage mass offered in the 45% leaf and 25% leaf treatments, which scale up to about 2 tonnes of dry mass per hectare, we do not anticipate that there would be any increases in forage intake rate if total forage mass density was to be increased further. This implies that decreasing forage quality did not only decrease the slope of the functional response curve, but likely also depressed its asymptotic maximum. Also in agreement with our predictions is the decreasing slope of the bite size-total forage mass density-relationship, and the decrease in mean bite rate with decreasing forage quality. Our results are supported by the study of Hongo and Akimoto (2004), who investigated the grazing behaviour of horses and cattle. They found that exchanging half of the leaves of a uniformly leafy sward for grass stems, reduced bite size, bite rate, and the rate of forage intake of both species. When comparing the pattern of variation between the different behavioural variables (Fig. 2a–c), the similar responses of forage intake rate and bite size give evidence that changes in the functional response curve were mainly caused by the response of bite size to forage quality. The plot of forage intake rate against bite size (Fig. 3) supports this latter notion, as indicated by the increasingly strong limitation of bite size with decreasing forage quality and the comparatively weaker response of bite rate.

For a given total forage mass density, we decreased forage quality by decreasing the mass density of high quality forage (leaves) and at the same time increasing the mass density of foraging deterrents (stems) in the grass sward. This caused the depression of bite size, bite rate, and of the rate of forage intake. However, these changes were not merely a response to a decreasing availability of high-quality forage. We also compared grass swards, which had equal densities of leaves and differed only in the amount of stems. The results show that even when the mass density of leaves was kept constant, just increasing the amount of stems already depressed bite size, bite rate, and the rate of forage intake (Table 2). Thus, the observed changes in the foraging behaviour are not simply the consequence of decreased availability of high-quality forage parts, but are at least in part caused by the interference of stems with the foraging process.

We also partially reached our second objective, which was to show that the spatial arrangement of forage parts, i.e., different degrees of clustering of leaves, affects foraging behaviour of cattle. Increasing leaf cluster size had the predicted positive effect on bite size (Table 3 and Fig. 4a). Bite size increased from leaf cluster sizes of 25–100 cm² and reached a plateau at a cluster size of 100 cm². Also as predicted, we found that bite rates responded to changes in leaf cluster size. Bite rate was highest for the smallest leaf clusters (25 cm²), decreasing with increasing cluster size (100 cm²), but then increasing again (200–400 cm²). However, based on our analysis, there is no evidence that increasing leaf cluster size has a positive effect on the rate of forage intake,
though visual inspection suggests such an effect (Table 3 and Fig. 4c). It appears that despite the negative response of bite size to decreasing cluster size, the high bite rates at small leaf cluster sizes alleviated the negative effect of decreasing cluster size on the rate of forage intake. Though we see a consistent trend of increasing forage intake rate with cluster size in both seasons, given the observed mean difference and sample variance, we would have had to increase our sample size at least eight-fold to have a probability of about 75% of finding a significant effect.

Bite size reached its maximum at a leaf cluster size area of 100 cm$^2$, which was approximately equal to the maximum bite area of our cattle. We interpret this result as an indication that stems surrounding clusters of leaves can impose an upper limit on bite size as long as leaf cluster size is smaller than the maximum bite area. Because maximum bite area is largely determined by muzzle width (or incisor arcade width: Gordon and Illius, 1988), it can be expected that the interaction between grass sward structure and grazers depends on muzzle size. Because of the allometric relationship of muzzle size and body size (Gordon and Illius, 1988), different sized foragers may be affected differently by grass stems: smaller grazers may reach their maximum bite size at higher densities of foraging deterrents and at smaller leaf cluster sizes. Therefore, we suggest that the observed interaction between grass sward structure and forager may vary during an individual’s ontogeny and between species.

We propose, that the negative effect of grass stems on bite size in cattle is comparable to the effects of thorns and spines on bite size in browsers. In browsers, larger bites tend to contain more woody support material. The large differences in structural and chemical properties between plant parts in shrubs (i.e., leaves and branches), therefore lead to a positive correlation of fibre content with bite size. Consequently, bite size selection is effectively limited by a trade-off between forage intake and diet quality (Shipley et al., 1999; Wilson and Kerley, 2003). Structural foraging deterrents, like thorns or spines, can reduce bite size to below its optimum as set by the intake-quality trade-off (Gowda, 1996; Haschick and Kerley, 1997; Illius et al., 2002; Wilson and Kerley, 2003). Bite size can also be affected by branch architecture and the spatial distribution of leaves along the branches (Dziba et al., 2003). We caution, however, that the negative effect of grass stems on bite size and forage intake could be less pronounced in softer grass species. Smit et al. (2005) found no negative effect of stem mass on forage intake in cattle grazing ryegrass, though this might also be explained by the low proportion of stems in their study (around 15%) and the positive correlation of pseudostem mass and total forage availability.

The mixed response of bite rate to leaf cluster size, which is defined as the surface area of leaf clusters, can be interpreted as an indication of two distinct domains of influence of cluster size (Fig. 4b). We speculate that bite rate was highest for the smallest leaf clusters (25 cm$^2$) because small bites were located close to each other. If the time between cropping of bites depends on the distance between bites, this would mean that the time between cropping was shortest for the smallest leaf clusters and could thus explain the higher bite rates. For larger leaf clusters, bite size and the distance between bites increased, thus increasing the time between cropping and decreasing bite rate. For the largest cluster size however, we speculate that several bites can be located next to each other within one leaf cluster, thus decreasing the distance between bites and the time between cropping, as well as that cropping time is minimal, thus increasing bite rate.
A manuscript of a detailed investigation of the effects of cropping time and time between cropping on bite rate is in preparation.

The sward structure of natural grasslands commonly changes in the course of the seasons due to phenology and forage consumption. Especially towards the end of and after the growth season, a general pattern is the decrease in the proportion of green and of leafy material. During this time free-ranging, non-supplemented cattle tend to show a decrease in live weight gain or even a loss of live weight (e.g., WallisDeVries, 1996). Our results show the negative effects of decreased proportion of grass leaves on the rate of forage intake. If cattle are not able to sufficiently increase daily grazing time after the growth season, the decreased rate of forage intake will therefore cause the daily forage intake to drop. Because of the positive relationship of forage intake with live weight gain, we can also expect live weight gain to decrease during this period. Our findings therefore illustrate an additional link between seasonal changes in sward structure and decreased live weight gain after the growth season, besides of the commonly recognized effect of a drop in nutritive value of the plants.

The results of the current study have implications for the modeling of herbivore foraging behaviour. In their landmark paper, Spalinger and Hobbs (1992) described models of the functional response in sparse and food-concentrated patches. According to their definition, forage intake in food-concentrated patches is exclusively regulated by forage handling. They proposed that the dynamics of forage intake in such patches arise from the competition between cropping and processing of bites. Because larger bites need to be chewed longer than smaller ones, bite size and bite rate show a negative relationship. However, they also mentioned that it is believed that the degree of protection of bites by spines and thorns influences handling time and thus bite rate. The results of our study illustrate circumstances in which bites are protected by grass stems to various degrees. Fig. 5 shows the relationship of bite rate with bite size for a given total forage mass density of about 80 g m$^{-2}$ and changing forage quality. Higher forage quality means an increase in the availability of preferred leaves and leads to larger bite sizes. If the effect of bite size on

![Fig. 5. Effect of forage quality on the relationship between bite rate and bite size of cattle, given a total forage mass density of 80 g m$^{-2}$.](image)
handling time were predominant as assumed by Spalinger and Hobbs (1992), then we would expect a decrease in bite rate with increasing bite size. However, our results show an increase of bite rate with increasing bite size. This finding is line with the study of Orr et al. (2004), who found that both bite size and bite rate of cattle were decreasing during increasing depletion of a ryegrass sward. It appears that in our study the mechanistic control of foraging deterrents over bite size and bite rate was so strong that it outweighed the proposed effect of the competition between cropping and processing of bites. We speculate that the presence of grass stems suppressed bite size so far and inflated the time needed to grasp bites so much, that the chewing time of bites was shorter than the minimal time between the cropping of bites. Then, with decreasing stem density, bite size increases and grasping time decreases, leading to the observed positive relationship between bite rate and bite size. We therefore suggest that the presence of stems in the grass sward in our experiment transformed the foraging process from a situation where bite rate was limited by chewing time, to a situation where bite rate was limited by grasping time. The density and spatial pattern of high-quality plant parts (leaves) and foraging deterrents (stems), therefore deserves more attention in the modeling of herbivore foraging behaviour.

5. Conclusion

Forage quality, as the proportion of high-quality forage parts, and the spatial pattern of high-quality forage parts have strong effects on the rate of forage intake in cattle. Primarily, these effects are caused by the strong negative response of bite size to the presence of structural foraging deterrents, but to some extent also by the negative response of bite rate. The presence of grass stems in the grass sward can transform the relationship of bite rate with bite size from the familiar negative form to a positive one. The proportion and spatial pattern of preferred forage parts and of foraging deterrents therefore deserves more attention in the modeling of foraging behaviour of large herbivores in complex grasslands.

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