

Sward structural resistance and biting effort in grazing ruminants

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Abstract — Grazing ruminants face complex decisions in searching for and harvesting adequate forage to meet their requirements in the face of heterogeneity in the abundance, nutritive value and distribution of resources. Some of the major decisions which affect the bite mass and therefore, forage intake adjustments in bite depth, bite area and exerted bite force, are made in relation to heterogeneity in sward structure. A number of relationships have been established linking the adjustment of bite mechanics in response to variations in sward height and bulk density on temperate forages for animals of a range of body sizes. However, there is less consistency in the response of the bite mechanics to the greater variations in structural resistance that arise from the vertical and horizontal arrangements of the plant morphological organs of leaf, pseudostem and stem. Furthermore, only limited progress has been made in quantifying the biting forces involved in grazing, the linkages between the plant morphological organs and their effect on bite force and, the interaction with body mass. In this paper, we discuss the different hypotheses that have been proposed to explain the regulation of bite depth and provide evidence for their acceptance or rejection. We comment on the knowledge gap in understanding biting force mechanisms across animal species of contrasting body mass, and stress the need for differentiation between the concepts of biting force and biting effort.

bite / effort / force / ruminants / structure

Résumé — **Résistance de structure du couvert végétal et effort de prélèvement des bouchées chez les ruminants au pâturage.** Face à l'hétérogénéité de la ressource en abondance, en valeur nutritive et en répartition, les ruminants au pâturage doivent prendre des décisions complexes pour rechercher et récolter les fourrages nécessaires à leurs besoins. Certaines de ces décisions affectent la masse de la bouchée et donc, l'ajustement de l'ingestion en terme de profondeur et de surface de la bouchée, ainsi que de force de prélèvement. Ces décisions sont prises en relation avec l'hétérogénéité de la structure du couvert végétal. Nombre de relations ont été mises en évidence liant l'adaptation de la mécanique de la bouchée aux variations de la hauteur et de la densité du couvert végétal de fourrages tempérés pour des animaux de différentes tailles corporelles. En revanche, les grandes variations

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de résistance des végétaux, qui résultent des arrangements verticaux et horizontaux des organes morphologiques de la plante (feuille, gaine et tige), ont des effets variables sur la mécanique de la bouchée. De plus, seuls des progrès limités ont été accomplis pour quantifier les forces de prélèvement des bouchées impliquées au pâturage, les liens entre les organes morphologiques de la plante et leurs effets sur les forces de prélèvement, ainsi que l'interaction avec le format des animaux. Dans cet article, nous discutons les différentes hypothèses qui ont été proposées pour expliquer la régulation de la profondeur des bouchées, et nous proposons des éléments pour leur acceptation ou leur rejet. Nous exposons les lacunes qui subsistent pour comprendre les mécanismes des forces de prélèvement à travers différentes espèces animales de formats distincts et nous soulignons le besoin de différencier deux concepts : la force de prélèvement et l'effort de prélèvement.

bouchée / effort / force / ruminants / structure

1. INTRODUCTION

The harvesting of forage is a particularly time-consuming exercise for ruminants; a large number of bites, of a relatively small bite mass, are required to meet the nutrient intake requirements for maintenance, growth and reproduction. A number of reviews have discussed the mechanisms of foraging behaviour [7, 9, 45, 50, 59, 60], including the considerable advances that have been made in understanding the influence of the independent effects of sward height and sward bulk density on the components (e.g. bite mass and bite rate) of daily herbage intake [19, 30, 38, 59]. However, despite the comprehensive information available, researchers are still unable to predict the intake responses of grazing animals to changes in the vegetation structure and morphology of more complex swards. Illius and Hodgson [41] suggested that this lack of predictive power emphasised the abundance of descriptive studies, and called for studies to actively seek a mechanistic explanation of sward-bite interactions. Descriptive and mechanistic approaches are, however, essentially intertwined due to the difficulty of clarifying the many confounding, and indeed complex sward-bite interactions.

Our aim is to focus attention on the importance of the interaction between the

morphological plant organs encompassed within the bite, and biting effort, an area that has received considerably less attention, even though the effects of the distribution of plant morphological organs on the feeding strategy in ruminant species has recently been stressed [59]. The principles should have direct relevance to ruminants foraging in both temperate and tropical ecosystems.

In this paper we define sward structure and the terminology associated with the study of bite mechanics, describe the anatomy of the grass leaf with respect to severance, and highlight the potential contrasts in severance action across animals of different body mass. The inconsistency in terminology, the methodologies and their suitability for assessing bite force are identified. Evidence of the hypothesised linkage between bite depth, bite area and bite force is discussed, and lastly the idea of assessing biting effort is introduced.

2. SWARD STRUCTURE AND BITING FORCE TERMINOLOGY

Studies investigating the linkages between the structural organs and food comminution in the mouth have been reviewed [56], but there is comparatively less information on the linkages between sward structure and biting effort. Further progress

within this field calls for a review of the definitions of the terminology used in this area. Morphological changes that occur with plant maturation lead to different proportions, and relative age, of leaf, pseudostem, stem, and inflorescence in the vertical dimension of the sward [13]. The architecture of these organs within the sward canopy is termed *sward structure*. *Sward bulk density*; the weight of herbage per unit volume, increases with increasing sward depth. This pattern is more pronounced for tropical pastures than for temperate pastures [28, 67], and the slope of the relationship can also vary markedly across swards of different structure within temperate pastures [see 25]. The volume of a bite is the major contributor of intake rate, and comprises *bite depth*, which is the vertical distance that animals insert their muzzle into the sward, and measured as the difference between sward surface height and the residual height post-grazing, and *bite area*, which is the horizontal area of herbage encompassed within a single bite [38, 48]. Evidence from temperate swards shows that bite area exhibits less sensitivity to sward variation than does bite depth [12, 48, 53], although Wade and Carvalho [74] suggest that bite area is the primary parameter that animals adjust to increase bite mass.

In linking the disciplines of plant mechanics with foraging behaviour we define five plant-based terms: (i) *fracture force in tension*, which is a measure of herbage strength and is estimated from the maximum force that produces fracture of the plant organ/s [80]; (ii) *tensile strength*, which is the fracture force in tension per unit cross-sectional area of the plant specimen [80, 81]; (iii) *maximum force in shear*, also a measure of herbage strength and is the maximum force required to fracture the plant organ/s, and is determined from the height of the highest peak on the force displacement curve (N.B.: it does not represent the force to fracture the whole plant organ) [80]; (iv) *specific work to fracture*,

equally known as *toughness* as it is measured by the energy required to shear the test specimen per unit cross-sectional area of the plant specimen [18, 80] and (v) *resistance*, which is the theoretical, accumulated force required for severing all of the plant organs encompassed within a bite. Two important animal-based terms are: (i) *bite force*, which represents the three-dimensional force applied in severing a bite (N.B.: this term does not represent the force exerted during chewing as given by Pérez-Barbería and Gordon [57]) and (ii) *biting effort*, which represents the power applied by the animal to sever a bite and includes components of resistance, bite force and head acceleration (N.B.: the importance of the individual components may interact with species body mass and species differences in severance action, see below SEVERANCE ACTION).

3. GRASS LEAF ANATOMY

Plants are the primary producers in most food chains, and animal subsistence and production is dependent upon them. Forages, like all plants, however, have evolved structures that resist ingestion by grazing animals (grazing resistance; [11]), as a means of ensuring their own continued existence within ecosystems.

The grass leaf anatomy responsible for protection against herbivory can be modelled as a three component system [71], consisting of sclerenchyma tissue, vascular bundles and epidermal cells covered by a protective cuticle. These components comprise the 'fibre' fraction, along with a matrix consisting of thin-walled parenchyma cells found in the leaf mesophyll. However, these thick-walled cells that are heavily lignified, and hence confer mechanical strength to the plant by way of attachment to chained bundles of vascular tissue only account for a small proportion of leaf cross-sectional area. Despite this, the fibre

component accounts for 90–95% of the longitudinal stiffness of grass leaves [71].

The critical disparity between the leaf anatomy of grasses from the C_3 and C_4 photosynthetic pathways lies in the greater number of veins, and smaller interveinal distance [62, 78], and a higher proportion of sclerenchyma [1, 78] in C_4 species. These structural characteristics strengthen plant tissues [72]. In tropical ecosystems, environmental temperature increases the rate of plant growth, which increases plant strength [72], and also reduces the moisture content between the sclerenchyma fibres [72], which leads to increased herbage strength [34, 36]. Nevertheless, despite possible categorical groupings of plants, plant anatomy will vary between plant groups, genera, species and even lines within a species [77], but while some plants may be stronger in tension, fracture properties will be more dependent on the organisation of the bundles of sclerenchyma which determines brittleness [73].

Wright and Vincent [81], in their review of the mechanics of fracture in plants, discussed the three modes of crack propagation in a leaf; shear, tension and torsion, and it is the modes of shear and tension that have attracted interest from plant and animal scientists alike. Assessment of the mechanical properties of grass leaves is far from new. It has provided information for the design and improvement of the cutting mechanisms in forage harvesting machines [34, 51], and for plant breeding programmes where the primary objective is to increase forage intake [20, 36, 52], through increasing the forage's feeding value [70]. These studies have focussed primarily on the properties of fracture in shear. The interest in relating the tensile properties of plants to aspects of foraging behaviour, particularly prehension, is of more recent origin [42, 68, 80], and has led to a clearer definition and use of tensile strength to quantify fracture properties in tension and the specific work to fracture (i.e. toughness) in shear

for determining properties such as those associated with food comminution in the mouth. Henry et al. [35] contended, however, that there was a lack of evidence to support the partitioning of the fracture mechanics between prehension and chewing.

The sclerenchyma tissue content is often reported in biomechanical studies where the structural and fracture properties of plants have been extensively evaluated [73, 80]. Fracture force in tension is well correlated with the volume-fraction of sclerenchyma tissue [80] when the sclerenchyma tissue is below 15% of the volume-fraction of the leaf, and the fibres are laterally separated [71, 73]. Above 15%, the fibres can be continuous across the leaf, rendering the leaf brittle [81], and thus more susceptible to fracture since the leaf will lose a large proportion of its strength with only a very small applied force [72]. The plant properties that increase mechanical resistance, chiefly the fibre component, are essentially the same as those that reduce plant digestibility [66, 80]. However, to rely on the nutritional indices of Neutral Detergent Fibre (NDF) or Acid Detergent Fibre (ADF) to provide measures of herbage strength and resistance would be inappropriate since fracture force in tension (the maximum force that produces fracture) is poorly correlated with both NDF and ADF [80], whereas, for example, the work to fracture in shear (the area under the displacement curve) is well correlated with both NDF and ADF, as well as the lignin content of the leaf [80].

4. SEVERANCE ACTION

All ruminant species have a common dental structure that consists of four paired incisors set on the lower jaw, with a thick pad of connective tissue, also known as the dental pad, positioned on the upper jaw. The act of severance entails the incisors closing against the dental pad to grip each mouthful of herbage before fracture of

plant tissue occurs, although cattle have been observed to grip herbage against the incisors using the tongue [16].

The structural arrangement of parallel venation in grass leaves, ensures that leaves exhibit little fracture sensitivity, thus the damage at the point of incisor insertion does little to act as a concentrator of stress [72]. Wright and Vincent [81] commented that unlike small herbivores which can avoid the problems of indigestible fibres in plant tissues, by eating around them (e.g. larvae of the gum-leaf skeletoniser moth, *Uraba lugens*) or cutting the lamina with their mandibles or incisors (e.g. rabbits have upper and lower incisors), ruminants must use their strength. If strength scales with body mass [42], then how do small-bodied ruminants cope with the same constraints as large-bodied ruminants? Vincent [72] suggested that sheep (*Ovis aries*), like geese, probably use a strategy that involves creating a crease on the lamina, through pulling the lamina at an angle across the incisors, and thereby reducing the force required to create fracture. There is no known quantitative evidence for this severance action in sheep, and there is the puzzling concern, as Vincent noted, that it is difficult to create creases across multiple lamina. Cattle (*Bos taurus*), sheep and goats (*Capra hircus*) foraging on a range of swards have been observed to insert and/or move their mouth sideways into swards to gather herbage [21, 28, 61]. In these examples it is likely that animals were making use of the shearing cusps on the molars to grip and sever plant tissue [see also 63], thereby obtaining a bite mass above what would otherwise be possible.

5. QUANTIFYING BITE FORCE

The idea of measuring the mechanical resistance of plants is far from new, but the motivation, approach and reporting have varied considerably [5, 18, 22, 32, 35, 51,

52, 73, 80]. One consequence has been the number of different descriptive terms that have surfaced and these are often used interchangeably. 'Strength' and 'toughness' are both biological terms that have been adopted in quantifying plant mechanical resistance [e.g. 17, 22], possibly since they represent a physical attribute that is easily understood. There is, however, some confusion since toughness commonly implies strength. Correctly defined, toughness is a measure of the energy required to propagate a crack, and not a measure of the force involved in fracturing material [81]. This definition is crucial since it implies that toughness is an important mechanical parameter for the chewing dynamics, but not for the process of severance of plant material.

Other inconsistencies have emerged in the definition of tensile strength and the use of the term shear strength, which has no clear definition in its own right, and, therefore, varies in terms of its units of expression [e.g. 23, 69, 80 for tensile and 20, 43 for shear]. According to Wright and Vincent [81] tensile strength should be reported as the force for crack propagation per unit cross-sectional area of plant material, and consistent expression of tensile strength would greatly facilitate across-study comparisons. However, it is not always a feasible use of resources to conduct laborious estimates of tensile strength within the context of animal-based studies. Fracture force is a measure of the maximum force required to fracture a test specimen [80]. It takes no account of cross-sectional area of the plant material [80], and so has less acceptability for comparison across different plant species with contrasting tiller size-density relationships, and thus potentially contrasting lamina cross-sectional area. Fracture force measurements, however, can be carried out more quickly since they omit the additional laborious cross-sectional area measurement, and thus can provide objective information on herbage

strength, as long as the above constraints are borne in mind.

When answering questions on the causal relationship between bite force and bite mechanics, an area of concern lies with the estimates on single, whole or separated fractions of plant organs and their relation with clumped plant material encompassed within a bite. For single tests to have direct relevance, one question of particular importance, and that does not appear to have been answered, is the potential error associated with estimates using a constant multiplier [e.g. 42]. In practical terms, it is unlikely that the bite force required for the severance of 10 leaves together will be the summation of the strength of 10 single leaves, unless a correction for the packing effect of leaves encompassed within the bite is applied. The absence of a constant multiplier would have implications for the scaling of bite force with modulations in bite area [e.g. 42, 68]. Other factors worthy of consideration are that the number of leaves able to be created i.e. running at an angle over the incisors, would be of a magnitude lower than the total number grasped. This is of particular importance for the severance action in small ruminants [see 72]. Furthermore, it is difficult to conceive that integrating the estimates of fracture force in tension from single, separate tests of leaf, pseudostem and stem can model the predicted force for a bite encompassing two or more morphological components, unless measurements are made at a very fine level of precision (i.e. 1 cm strata), forming serious constraints for swards more applicable for testing with large-bodied animals.

Indirect assessments of bite force [42, 68] are derived from estimates of the force required to fracture plant organs in the vertical dimension. Although the contribution from Illius et al. [42] predicted bite forces indirectly from regressions based on a separate set of swards, they amassed their data from three studies, which may not be possible where time is a major constraint. Small-

scale apparatus' that provide direct, quick and reliable estimates from field conditions would aid progress. There has been some recognition of the need for the development of portable field operated devices that measure fracture force in tension [68] and tensile strength [76] in situ, providing an estimate of the magnitude of the contrast in resistance, for a given bite volume. Progress has nonetheless been slow and fraught with difficulties; Westfall et al. [76] in a short communication described a portable tensiometer with hand-operated modified pliers and an electronic recording system, and Tharmaraj [68] discussed a portable lever operated clamping apparatus mounted on a tripod frame, which expressed the peak fracture force reading (Fig. 1). However, for neither apparatus was it clear how the rate of acceleration during fracture was controlled.

Furthermore, an indirect estimate of bite force from fracturing plant organs in tension does not fully mimic the mode of the characteristic jerk action in the horizontal plane during severance. By comparison, direct quantification of the forces involved in severing herbage in grazing animals yields potentially more valuable information as biomechanical force plates [75], such as those used by Hughes et al. [40] and Laca et al. [47] record three dimensional forces (Figs. 2 and 3). Consequently, some disparity between values obtained from indirect estimates as compared with direct methodology must be expected (Griffiths and Gordon, in preparation). In the foreseeable future, such technical difficulties will become inconsequential if effort is made to partition and present the force according to the Cartesian coordinates. This is also a critical point of evaluation as animal species of contrasting body mass may allocate the force between the Cartesian coordinates differently. It is important to recognise that bite force predicted indirectly from estimates of fracture force and tensile strength, provide only a theoretical framework for

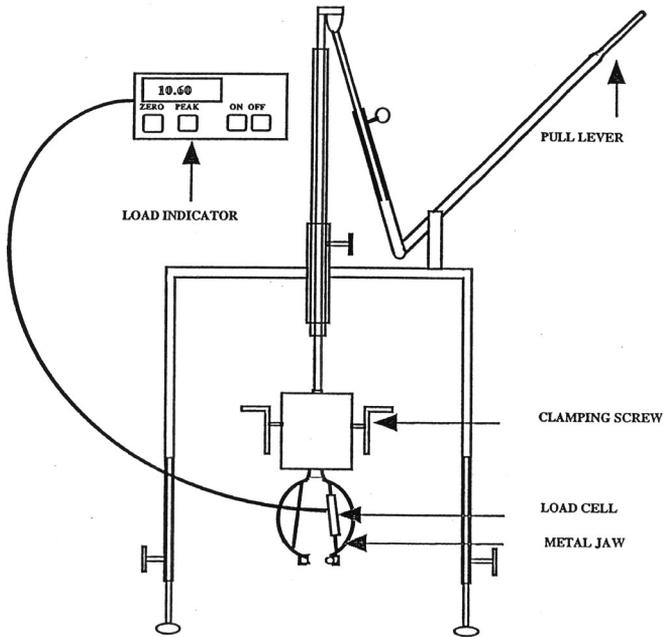


Figure 1. Tensile bite fracture force apparatus (from Tharmaraj [68]).

comparative purposes. These predictions also leave many unanswered questions as to the effort exerted, particularly as evidence does not suggest a 1:1 response in bite geometry with plant resistance (see below **SUMMIT FORCE HYPOTHESIS**).

6. BITE DEPTH AND THE LINKAGE WITH BITE AREA AND BITE FORCE

An increasing number of studies have focussed on the responses of the bite mechanics to the structural complexity and the rigidity of plant organs, but can we draw any consistency between studies and quantitatively relate the response patterns to bite force? Three hypotheses have been proposed for the regulation of bite depth penetration:

- Summit Force (6.1).
- Balancing reward against cost of bite procurement (6.2).
- Marginal Revenue (6.3).

In discussing the available evidence to support or reject the above three hypotheses we pull together studies which have provided supporting data on fracture force in tension, tensile strength and leaf toughness and/or bite force when examining the parameters of bite volume. There are relatively few studies that meet this criterion, and all of these come from the vegetative temperate forages. Only a few studies [e.g. 54, 69] have assessed tensile strength on forages in more extensive grassland environments, but these studies have not provided parallel data on bite volume. There is a need to evaluate the hypotheses for swards displaying greater structural complexity

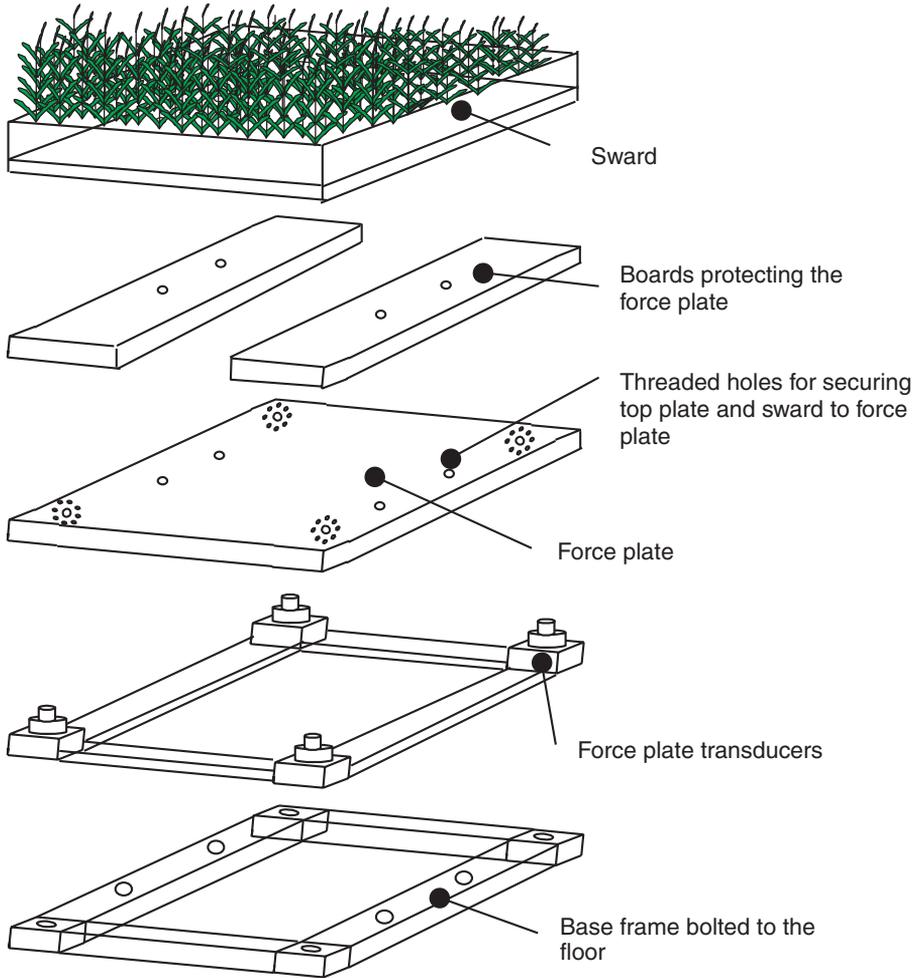


Figure 2. Exploded view of a force plate apparatus (adapted from Webb and Clark [75] and Griffiths and Gordon, unpublished).

including those present in extensive grass-land environments.

6.1. Summit force

The Summit Force hypothesis [37] was originally offered as an explanation for the association between bite depth and pseudostem height [8, see also 2, 3] with the rational response being one of animals being

constrained by the effort required to sever pseudostem within the lower stratum. The estimated fracture force of pseudostem was later quantified [80] as approximately three times that measured for a single leaf, and arose from the complex arrangement of concentric sheaths around the immature leaves and growing points. In order to maintain consistency in bite force, the Summit Force hypothesis implied that once the limit in force had been reached, that animals

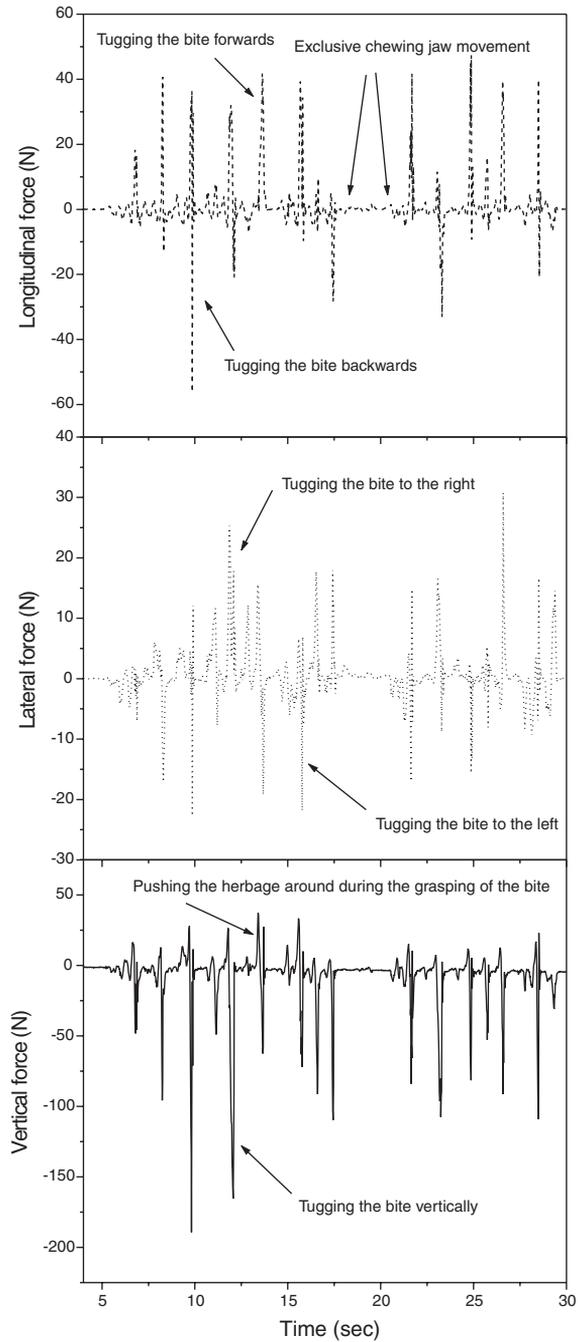


Figure 3. An example of the output from a force plate apparatus for a series of 15 bites (from Griffiths and Gordon, unpublished).

would adjust bite area to maintain a constant bite force in the face of increasing strength or tiller density.

There are comparatively few reports documenting tiller, or leaf and stem strength, and tiller density on bite area. Despite this, there appears to be general consistency across studies in that the rate of reduction in bite area is much lower than the rate of increase in tiller density or tiller strength [39, 48, 53, 68]. This suggests that there is only a partial adjustment in bite area in relation to sward structure, and furthermore, the adjustment has little effect in reducing the energy required to sever a bite [79]. This partial compensation in bite area also explains, at least in part, the absence of significant patterns in sweeping tongue movements in cattle in response to decreased lamina length across swards of different structure [25]. Mitchell [53] demonstrated, using pooled data from sheep and red deer (*Cervus elaphus*), that bite area was only 35% greater on wheat (*Triticum aestivum*) swards than ryegrass (*Lolium perenne*) swards of identical height, despite the ryegrass swards exhibiting 110% stronger tissues (measured by shear). The reduction of bite area in an attempt to maintain the biting force momentum can thus be considered to be a small effect. This inference is supported by the few direct evaluations of biting force. Hughes and colleagues [39, 40], using boxed swards anchored to a force plate, found no supporting evidence for a maximum force that goats or sheep exerted across a range of sward arrangements within immature swards and across sward species. Similarly, cattle grazing from hand-constructed swards mounted on a force plate were not observed to exhibit a maximum force per bite [46]. Furthermore, Illius et al. [42], in a study with goats, found appreciable variation in the indirect estimates of bite force, derived by substituting the grazed heights into polynomial regression equations summarising force-canopy structure relationships, across broad- and

fine-leaved plant species. More recently, Tharmaraj [68] indirectly estimated bite forces using a field-operated bite force meter and found no indication of a maximum force that cattle exerted across a range of plant species and tiller densities. The absence of a maximum bite force that animals exert, irrespective of how the bite dimensions are balanced in the face of tiller structural rigidity and bulk density constraints, does not, therefore, lend support to the Summit Force hypothesis. This is also consistent with the fact that not all leaves within the bite are severed simultaneously but rather in close succession (W.M. Griffiths and I.J. Gordon, unpublished data). In practical terms obtaining a measure of the peak bite fracture force is of little importance, and it is the average force applied for a given bite that needs to be assessed. Furthermore, rejection of the Summit Force hypothesis is supported by the consistent findings that, across a wide range of body sizes, animals do not always fully exploit the available depth of regrowth [sheep and guanacos (*Lama guanicoe*) [6], bison (*Bison bison*) [10], cattle [27, 33]].

6.2. Balancing reward against cost of bite procurement

A second hypothesis utilising economic principles described an efficient forager as one that forages to maximise, or at the very least, balance the reward against the cost of bite procurement i.e. force per bite [40]. However, as with the Summit Force hypothesis there does not appear to be any constancy in the force per bite. Hughes [39] found that sheep were more willing to increase the force exerted if the force was compensated by a greater reward, while Illius et al. [42] found that the expenditure:reward ratio for goats was not consistent across a range of plant species. More recently, Tharmaraj [68] found a fluctuating

expenditure: reward ratio across short and tall swards, but a constant ratio when swards varied in tiller density only. The calculation that the energy gain from increased penetration will always exceed the energy cost [42], implies that the greatest gain will be achieved from severance of material encompassed within the buccal cavity at the base of the sward, in the absence of uprooting. Why then, do cattle and other species, restrict their grazing depth to some fraction of sward height, even when the sward is composed solely of lamina [48]? Furthermore, goats have been found to be insensitive to the differential costs in penetration depth for broad-leaved and fine-leaved species, with the ratio between pseudostem height and grazed height changing little across the sward species [42]. It, therefore, seems likely that the avoidance of a lower stratum may be unrelated to the greater effort required by the animal to detach plant organs relative to bite reward. Rather, it may reflect the fact that encompassing pseudostem within the bite slows down bite formation, and would require additional jaw movements to chew the more fibrous material. Therefore, the animal strikes a balance between severance and chewing constraints, as discussed in the model of Spalinger and Hobbs [65] and further evaluated by Shipley and Spalinger [63]. The relationship between bite mass and chewing behaviour has also been ascribed to the need to strike a balance in the maintenance of a grazing momentum [49]. However, the importance attached to striking a balance between severance and processing may be over-emphasised since cattle are able to prehend, and manipulate the contents of existing bites, within the same jaw movement [49], effects that were assumed to be mutually exclusive in Spalinger and Hobbs' model [65]. The overlap between prehension and chewing can be, however, incorporated into models, as shown by Farnsworth and Illius [24].

6.3. Marginal revenue

Delving deeper into the application of economic principles, a study by Illius et al. [42] marked a further attempt to understand the conceptual basis of bite depth. These authors demonstrated, using goats and a group of fine- and broad-leaved grasses, that depth of penetration into a sward could be predicted when account was taken of the marginal revenue i.e. the differential increase in bite force relative to the differential increase in energy intake rate. Despite the variation in the predicted bite forces (by indirect measures) and contrasting grazing depths, the goats grazed to a common marginal revenue, although the value of marginal revenue differed between the fine- and broad-leaved species. This hypothesis is both puzzling and plausible. Among the three fine-leaved species, there was a clear linkage between the mass of material removed and the force involved in severing those bites, but the reason for differing common marginal revenue between the fine- and broad-leaved species remains unclear. It is worth noting that had these authors examined only one plant species from each of the fine- and broad-leaved categories, an approach that would have been reasonable, their conclusion would not have held, emphasising that the marginal revenue hypothesis may not explain penetration responses across swards of greater structural complexity. Critical evaluation of the hypothesis across swards of contrasting structure and animals of different body size awaits.

To summarise, the evidence to support the three current hypotheses is weak and new initiatives are required to shed light on the determinants of bite mechanics.

7. EFFORT VS. FORCE

Increasingly it has become obvious that there is no conclusive evidence to support

any of the three key hypotheses that have been put forward as mechanisms for observed bite depth penetration responses. It may not be that we need to put forward new hypotheses, rather we need to discover new approaches of thinking the problem. Central to our understanding of biting force has been the assumption that the force applied in severance will be proportional to the strength of individual plant components, although Illius et al. [42] argued that the structural arrangement of the plant components has the greater bearing on the force exerted. Nevertheless, the implication is that severance occurs as a result of muscle moving against a fixed anchor of body mass, and the costs of severance for a given force are then lower for species of greater body mass, owing to the allometric scaling of force with body mass ($W^{0.67}$ [58]; $W^{0.69}$ [42] using the assumption that the force generated by muscle is proportional to muscular cross-sectional area [14]). Leaf tensile strength has been found to be of greater importance in determining plant acceptability for sheep than for cattle [54], a finding that more likely reflects the constraints imposed on the smaller body mass and thus smaller potential muscular effort, rather than the suggested shorter retention time and lower digestive ability of small ruminants [54]. An intra-specific allometric relationship between body mass and grazing depth ($M^{-0.15}$) has been reported [31, 42], although the relationship was only present on the tall swards in the study by Gordon et al. [31]. By contrast Canigano et al. [15] did not find evidence for an intra-specific relationship between body mass and grazing depth in cattle, despite a wide contrast in body mass (256–608 kg). Furthermore, there has been consistency in bite depth for inter-species variation in body mass; cattle vs. sheep [55], sheep vs. guanacos (*Lama guanicoe*) [6]. Given these inconsistencies in the literature on intra- and inter-specific species depth of penetration responses we are left wondering about the real costs involved in grazing [42]. It

might then be helpful to begin by thinking of the act of severing plant material as a two-step process; (i) ‘head’ resistance, which is the force required to accelerate the mass of the head in a steady momentum and (ii) ‘herbage’ resistance, the strength and architectural arrangement of the plant organs in 3D-space, with the summation of these two resistances shaping the biting effort ([53], J. Hodgson personal communication). This provides a clear distinction between biting effort and biting force.

Further, the laws of motion state that for a given force, the rate of acceleration will be greater for a small object than for a large object. Chambers et al. [16] reported the rate of head acceleration as some 65% greater for sheep than for cattle grazing the same sward. There is little quantification of the effort and associated costs incurred in upholding the tension in the muscles of the neck to maintain the head momentum, although Illius et al. [42] comment that it must be considerable. The contribution of the ‘head’ resistance to maintain a cyclic momentum for the applied effort can be predicted to be of some significance. This is despite the relatively small energy cost associated with bite severance as a result of the small displacement, although the displacement will increase with increasing number, and height, of tillers captured within the bite. If tiller length is viewed as a moment arm, the distance and angle perpendicular to the tiller, from the tiller’s rooted position to that at severance will increase with sward height and/or tensile strength, implying that displacement and acceleration are important components of biting effort. In support, Chambers et al. [16] found that the rate of head acceleration of sheep decreased with increasing sward height. However, these authors did not observe a similar pattern for cattle.

The allometric relationship between force and body mass would provide the generality that researchers seek, but as biologists and ecologists we need to recognise

the existence of many exceptions. In the only known evaluation of biting force across species body mass, Hughes [39] showed that goats (23.5 kg W) did not fully utilise their body mass ($W^{0.37}$, estimated from Tab. 5.12 and text from p. 82 [39]) to sever bites from 15 cm perennial ryegrass swards, with bite depth substantially smaller than that recorded for sheep (64 kg W) ($W^{0.64}$, estimated from Tab. 5.12 and text from p. 82 [39]). Other studies have also observed goats to exhibit a shallow penetration depth on vegetative swards [26], suggesting that goats may not exploit the force stored in their muscles for prehension. This suggests that constraints imposed by mandibular length may be a further critical parameter that needs to be corrected for in assessing biting effort. There is ample evidence that incisor breadth scales with body mass [e.g. 29, 31], and that total masseter weight, which reflects masseter tissue size, is correlated with body mass [4]. However, whilst mandibular length does scale with body mass, there appears to be no compensation between mandibular length and masseter muscle mass in ruminants, unlike in some carnivores [44]. By inference a lack of correlation between mandibular length and masseter muscle mass implies a weaker gripping force at the incisors (see also [64]) leading to increased tiller slippage during initial clamping of herbage as well as during the jerking motion of the head. This implies that, irrespective of body mass, animals with longer mandibles are likely to incur substantially reduced bite masses for the applied bite effort with increasing canopy depth. Placing this into perspective, goats have a higher mandibular length:body mass ratio than sheep (F.J. Pérez-Barbería and I.J. Gordon, unpublished data), and this may account for the observed responses by goats in the study by Hughes [39]. These additional animal-based constraints strengthen the argument that it is biting effort rather than biting force that needs to be evaluated, and therefore

providing a 'real' measure of the constraints in handling forages rather than just a measure of the force required to fracture a given plant organ.

8. CONCLUSION

Given the importance of bite depth as a contributor to bite volume and intake rate, there remains considerable scope for understanding the mechanistic basis for bite depth regulation. Increasing evidence points towards responses in bite depth to the vertical positioning, and maturation, of the morphological organs within the sward canopy. Assessment of biting effort would represent a more holistic approach to understanding the animal's response to sward structural complexity, and might explain why the adjustments in bite geometry have been of a smaller magnitude than the change in herbage resistance. More explicit arguments have been hampered by the limited available bite force data, much of which has been collected from swards exhibiting relatively limited variation in structural strength, and from comparisons across plant species where other physical and chemical characteristics may also vary [40, 42, 46, 68]. Despite the obvious technological difficulties in quantifying the various components of biting effort that have been described in this paper, progress on this front will remain essential to aid the development of predictive foraging models.

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