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Effects of bending and shearing properties of leaf blade sections of orchardgrass on biting forces exerted by sheep

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採食時のヒツジが使うバイト強度におよぼすオーチャードグラス葉身の曲げ強度とせん断強度の影響

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Abstract

The biting force used by sheep was investigated in order to clarify the effect of bending and shearing properties of leaf blade sections of orchardgrass (*Dactylis glomerata*). Five, 10, 15, 20 or 25 leaf blade sections per loadcell from basal and middle parts were offered to sheep. The three-dimensional biting forces were digitally recorded at 0.006-second intervals using the three-dimensional loadcell. DM weight per mean biting force (benefit/cost ratio) was not significantly different among any treatments, and its grand mean was 16.7±1.1 mg-DM/N. There was a significant correlation between bending strength and shearing strength, strongly suggesting that sheep may recognize chewing ease of leaf blade sections through sensing bending strength prior to prehension and adjust leaf number per bite and biting force. This hypothesis was supported by the result that 87 % of a total of 173 bites were completed by only one peak biting force. Biting force per leaf used by sheep was 2.53±0.37 N and 1.98±0.26 N in the basal and middle sections, respectively. Shearing strength per leaf was 3.35±0.20 N and 1.93±0.19 N in the basal and middle sections, respectively. These results suggest that sheep break-down leaves principally using shearing force.

Keywords: bending, biting force, orchardgrass, shearing, sheep

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1. Introduction

Grazing animals try to gather the maximum amount of food with minimum effort (Vincent 1982; Illius et al. 1992) and to choose plant parts which can be eaten quickly with ease (Kenney et al. 1984; O'Reagain 1993; Hongo 1998). Grazing is an action to break plant organs (Vincent 1982; Wright and Vincent 1996). Grazing animals usually remove only the uppermost parts of plants because of different resistances to defoliation imposed by the physical structure of plant tissue (Illius et al. 1995). There have been a number of studies to determine how sward canopy structure, through its linkage with herbage strength, influenced the grazing behaviour or bite dimensions of grazing animals. These studies mainly looked at the effect of vertical distribution of sward components (Milne et al. 1982; Illius et al. 1992; Carrere et al. 2001). Grazing behaviour is also influenced by other sward factors such as pseudo-stem height (Wright and Illius, 1995; Woodward, 1998), sward surface height (Laca et al. 1992), stem mixture (Hongo 1998; Drescher et al. 2006), accessibility (Dumont et al. 1995; Ginane et al. 2003), and stiffness of plant units (Hodgson 1985; Laca et al. 1992; Devee et al. 2009). MacAdam and Mayland (2003) studied the relationship between leaf strength and cattle preference for eight cultivars of tall fescue and found that both tensile and shear strengths of leaves were negatively correlated with preference. However, there are few studies on physical properties at different sites along the grass leaf. We were interested to determine how animals respond to different biomechanical properties within an individual leaf blade.

The objective of this study was to clarify the effect of biomechanical properties of basal and middle sections of orchardgrass leaf blade on biting forces exerted by sheep.

2. Materials and methods

The experiments were carried out to follow the guideline of Obihiro University of Agriculture and Veterinary Medicine for proper conduct of animal experiment and related activity in academic research.

2.1. Forage

A sward of orchardgrass (*Dactylis glomerata*), sown in May 1988, was fertilized and harvested regularly. It was mown on 30th June and 9th August 2005 and after each harvest applied with a compound fertilizer (10-18-12 % of N-P2O5-K2O) equivalent to 200 kg/ha was applied. Leaves at the second harvest were used for the biting-force trials.

During the biting-force trials , fresh grass was cut in the early morning. Undamaged, mature leaf blades of vegetative tillers were cut at the ligule. The two youngest leaves were selected. Each leaf blade was clipped into two sections (basal and middle sections), to be representative of different levels of stratum in a sward, with a length of 100 mm to make different cutting treatments for comparison. Leaf blades were stored in a polyethylene bag. Five nominal leaf densities for each cutting treatment were taken by attaching 5 (5L), 10 (10L), 15 (15L), 20 (20L) or 25 (25L) leaf blades per loadcell to an iron bolt, which was coated with rubber tubing, with cotton adhesive tape and further tied fast with wire 1 mm in diameter. The bolt was then inserted into a nut on the upper end of the loadcell and fixed before each grazing trial. One clump of leaf blades was used in each biting-force trial.

2.2. Artificial sward board

The same sward board previously described by Hongo et al. (2007) was used for artificial construction of swards. The three-dimensional biting forces were digitally recorded at 0.006-second intervals using the three-dimensional loadcell (Figure 1).

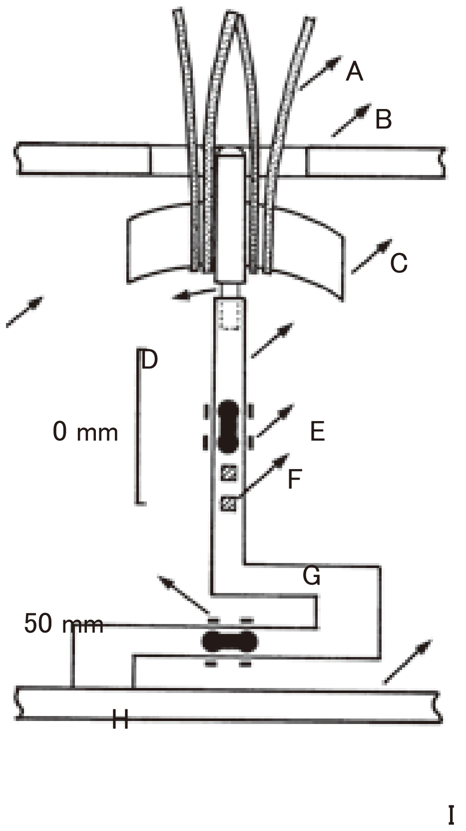

Figure 1　An outline of three-dimensional loadcell used in an artificial sward board. (A) Leaf blade sections, (B) Wooden board with a hole 50 mm in diameter, (C) Cotton adhesive tape, (D) Iron bolt (6 mm in diameter) coated with rubber, (E) Aluminum square bar 12 mm in width, (F) Strain gauge for sideward force, (G) Strain gauge for backward or forward force, (H) Strain gauge for vertical force, and (I) Iron plate.

2.3. Biting-force trials

Biting-force trials were carried out using two Suffolk wethers (mean live weight of 71 kg) aged 2 years, from 1st to 4th August, 2005, at the Obihiro University of Agriculture and Veterinary Medicine in Hokkaido, Japan. Sheep were fed fresh leaves of orchardgrass and hay of timothy at maintenance level. Two days before the commencement of g biting-force trials , sheep were trained to be led with a halter and rope, and became accustomed to the hand-constructed sward. Two animals which were more comfortable using the apparatus were selected.

At a biting-force trial, sheep were led with a halter and rope to the sward board. The duration of time in building the swards for each biting-force trial was less than 5 min. During this period, animals were constrained with a rope.

The clump weight of leaf blades including an iron bolt was separately measured before and after each biting-force trial. Leaf blades protruded 60 mm above the upper wooden board of the sward board. When most of the leaf blade material was eaten, the animals were removed. Animals received three replicated clumps from each nominal leaf blade density and from both the basal and the middle leaf blade sections for three days, which made 90 trials in total (3 days x 3 replications x 5 nominal leaf blade densities x 2 sections of leaf blade). After each biting-force trial, the clump of leaf blades was removed from the loadcell. Residual lengths of all leaf blade sections were individually measured, and bite depth, the average depth of insertion of the mouth into the sward canopy, was calculated from the original length of 100 mm. Sub-samples of about 100 g fresh leaf blades were dried in an oven at 70 ℃ for dry matter (DM) determination. From these results, herbage DM intake was determined. Water loss from the plant surface by evapotranspiration was ignored because of the short time on biting-force trial.

2.4. Mean biting force

Three-dimensional biting forces were vectors and crossed at right angles each other. By the composition of two forces, the resultant force was obtained by the vector addition method. At first, horizontal force was calculated from the composition of backward/forward and rightward/leftward forces, and total biting force from the composition of horizontal and vertical forces. The duration time of each biting force was equal to the duration of vertical force, since horizontal forces were used in collecting and handling grass leaves during prehension (Hongo et al.

2007). From this total biting force/time curve, mean biting force was calculated.

2.5. Leaf blade measurements

After grazing trials, similar leaf blade samples were collected. Total length of leaf blades was measured and averaged about 600 mm. Then, a leaf blade was cut into four segments (basal 100 mm, intermediate, middle 100 mm and residual apical length). After absorbing water from a paper towel, fresh weight of each was determined. Leaf blade samples of basal and middle sections 100 mm in length were immersed in distilled water for at least 5 minutes to maintain a saturated condition, so that full turgor could be achieved before a measurement of biomechanical properties. The remaining sections of leaf blades were then dried to obtain DM content.

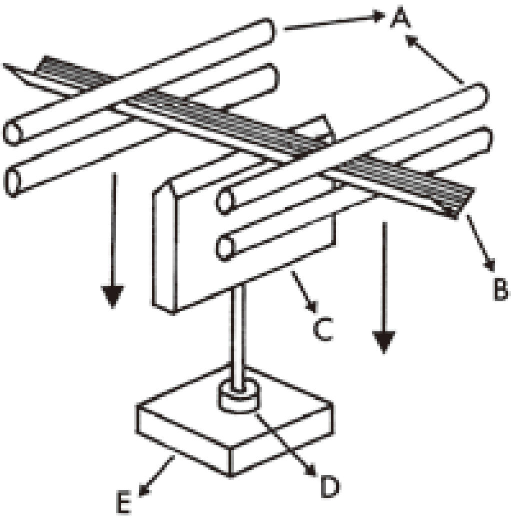

Figure 2 Diagram of bending test machine. A leaf blade section was supported between two stainless steel rods 3 mm in diameter, which were inlaid into a plastic frame (not shown), and moved downward at a rate of 10 mm/min. The span of specimen was 40 mm and the maximum bending depth was 10 mm.
A: Stainless steel rods, B: Leaf blade section, C: Acrylic resin plate with stainless steel rod, D: 2 N loadcell, E: Fixed base plate.

In order to measure bending strength, a bending test machine was constructed (Figure 2). A leaf blade sample and an aluminum frame (not shown in Figure 2), in which four stainless steel rods 3 mm in diameter were fixed, were moved downward together at a rate of 10 mm/min. The centre of a leaf blade segment made contact with a stainless steel rod on the upper side of the acrylic resin plate, which was connected to a 2 N loadcell fixed on a base plate. The length of the specimen between two rods was 40 mm and the span/depth ratio was 4. Bending force was measured up to the maximum bending depth of 10 mm. Downward movement of the aluminum frame was monitored using 50-mm displacement transducer (NEC San-ei; 9E08). Electrical signals of a loadcell detecting a force and a displacement transducer detecting a length were sent to a dynamic strain amplifier (Teac Co.; SA-30A). Each amplified signal was digitally recorded as strain-time data using a recorder (Hioki Co.; 8808 Type). After measurement of bending force, leaf blade samples were again immersed in distilled water.

Usually, the bending moment capacity is defined as the maximum bending moment that can be sustained by the lamina. The internal moment under a three-point bending test is proportional to the applied load (Roark and Young 1975). Force versus deflection length was calculated. Bending strength (S) is given by the expression (Goodman and Ennos 1997):

$$S = F_{max} L / 4$$

where Fmax is the maximum bending force and L is the span distance between two supports.

Tensile strength of each leaf blade section was measured using a 200 N loadcell, which was fixed to a breaking test machine (Aikoh Engineering Co.; Model 2257). Both ends of a leaf blade section were seized with clamps. One clamp was fixed and connected with a loadcell and the other clamp was moved downward at 10 mm/min for a low rate of deformation (Vincent 1992). The initial length between two clamps in the test machine was 27 mm. Tensile strength was recorded using the same amplifier and recorder as a measurement of bending strength.

Shear strength was measured using a pair of scissors (Plus Co., No.135) with sharp stainless blades. The principle structure was the same as in previous reports (Pereira et al. 1997; Lucas and Pereira 1990). Scissors were attached by their handles to a shaft hanger fitted with ball-bearings (Vincent 1992) and mounted on a test machine (Aikoh Engineering Co.; Model 2257). One handle of the scissors was attached to the moving cross-head while the other was fixed to a support. A leaf blade length of about 50 mm was used in the test. Before each measurement, the surface of blades was rubbed with a swab including a lubricant oil to reduce friction (Vincent 1992). The travel rate of the intersection point of the two blades was 20 mm/min.

After measuring biomechanical strengths of leaf blades, the fractions of leaf blades were immediately stored in water for further investigation. For a measurement of cross-sectional area, leaf blades were sliced 3 mm lengths using a razor blade and were vertically kept in touch with a side wall of a plastic block. Cross sections of leaf blades were photographed under a stereo-microscope and the pictures were digitally recorded. Each picture was projected onto a monitor screen at a magnification of about 50X. The contour line of the cross-section was delineated with a cursor on a monitor screen using commercial computer graphics software (Photo studio, Arcsoft Japan). The area inside this contour line was calculated using commercial software (Lia32, Nagoya University).

2.6 Statistical analysis

In the statistical analysis, experimental days and two sheep were treated as replicates. Variables of bite characteristics were analyzed using a paired t-test and an analysis of variance (Snedecor and Cochran 1980). Regression analysis was applied for testing the relationship between bending strength and shearing energy of fracture.

3. Results

3.1. Two patterns of biting force

Two patterns of biting forces were identified (Figure 3A). In Case 1 with only one peak, sheep broke leaf blades in one bite. In Case 2 with two peaks, sheep tried to break leaf blades with horizontally backward force, but could not severed leaf blades at this first attempt. Then, sheep changed horizontal force, resulted in successful break in leaf blades. In these cases, peak force was 56.8 N in Case 1 versus 64.6 N in Case 2, and mean force was 24.3 N versus 25.5 N (Figure 3B). In this study, a total of 173 bites were observed and only 22 bites (12.7 %) included more than 2 peak forces during one bite. Figure 3C shows the trace of vectors of total biting forces at an interval of 0.006 sec.

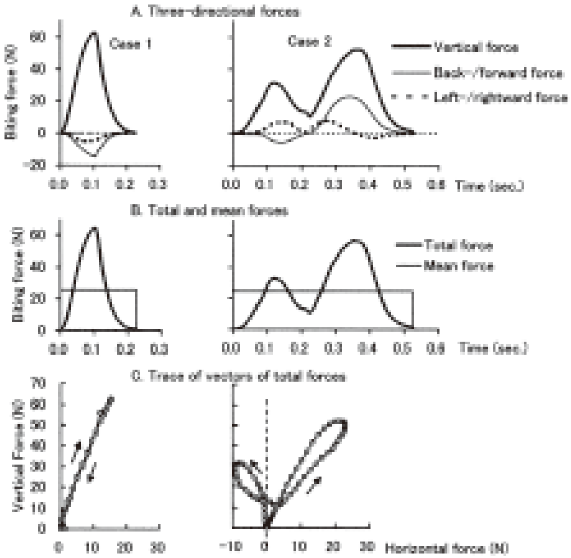

Figure 3 Two patterns of biting forces. Case 1 had one peak and Case 2 had two peaks. (A) Three-dimensional forces, (B) Total and mean forces. Mean force was obtained from averaging total forces observed. (C) Trace of vectors of total biting forces at an interval of 0.006 sec.

3.2. Biting parameters

The number of bites per point was not significantly different between the basal and middle leaf blade sections, but significantly different ($p<0.001$) between

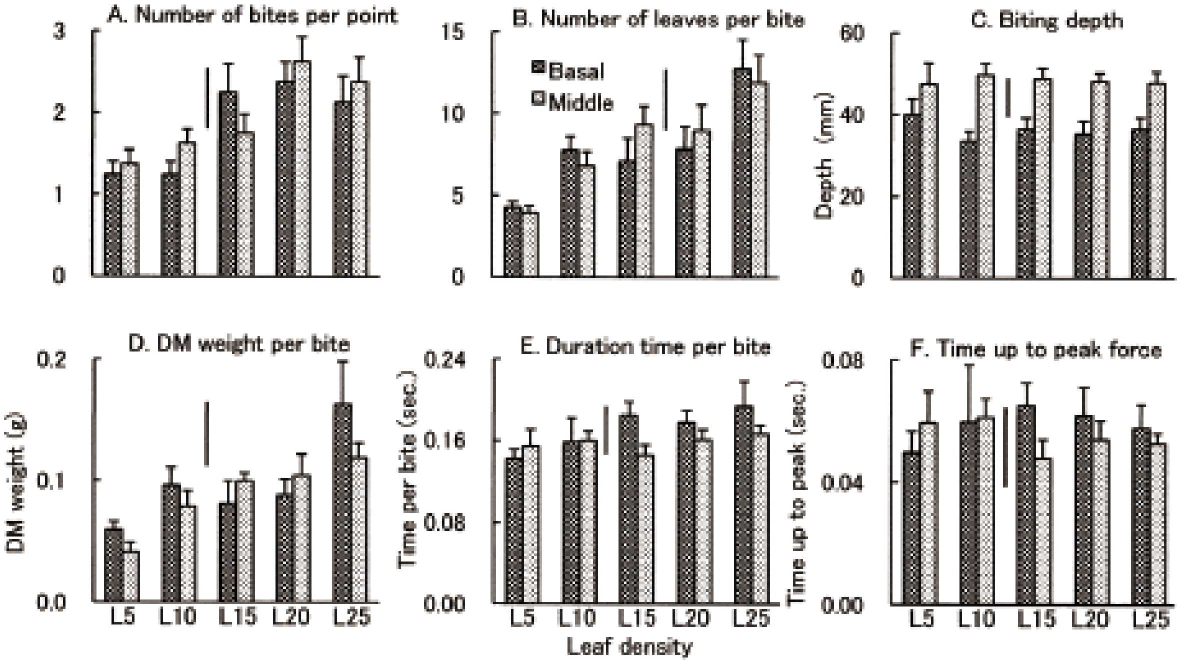

Figure 4 Number of bites per point and grazed leaves, biting depth, DM weight per bite and biting time in grazing basal and middle sections of orchardgrass leaf blades. Attached lines on bars show s.e. of mean and vertical lines show s.e.d. of the mean differences.

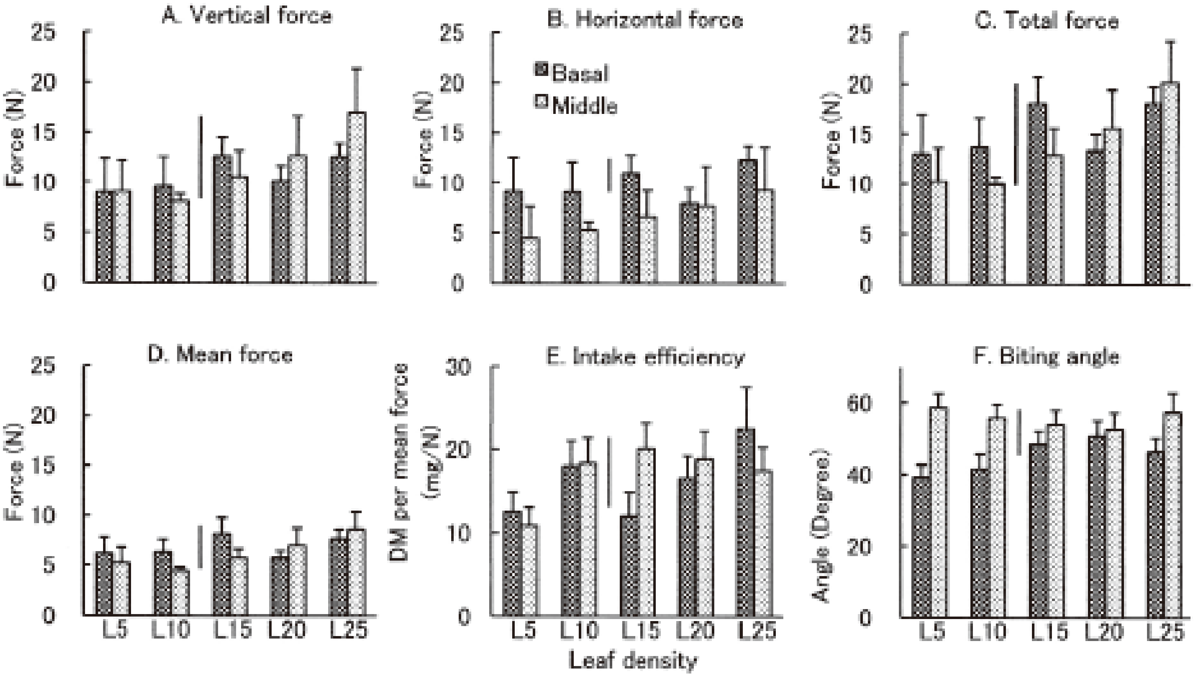

Figure 5 Vertical, horizontal, total and mean biting forces, and intake efficiency (DM intake weight per mean force), and biting angle in grazing basal and middle sections of orchardgrass leaf blades. Attached lines on bars show s.e. of mean and vertical lines show s.e.d. of the mean differences.

the 5 leaf blade densities (Figure 4A). A similar tendency was observed in the number of leaves per bite (Figure 4B), DM weight per bite (Figure 4D). However, biting depth (Figure 4C), duration time per bite (Figure 4E) and time up to peak force (Figure 4F) were not significantly different among any treatments.

Vertical force (Figure 5A), total force (Figure 5C) and mean force (Figure 5D) were not significantly different among any treatments. However, horizontal force (Figure 5B) was significantly different between the basal and middle sections (p<0.001) and among the 5 leaf blade densities (p<0.039). Biting angle was significantly higher (p<0.001) at the middle sections than at the basal sections, because of the lower values of horizontal force at the middle sections.

To assess the benefit/cost ratio in biting behaviour, DM weight per mean force was calculated (Figure 5E). The ratio was not significantly different between the two sections and among the 5 leaf blade densities. Biting angles were not significantly different among any treatments (Figure 5F).

3.3 Fracture patterns of leaf blades

The patterns of fractures in both basal and middle leaf blade sections are shown in Figure 6 with pictures of cross-sections. These results were obtained from the same test specimen. The fracturing pattern in the shearing test included numerous small peaks and the highest peak at the central position corresponded to the midrib of the transverse section (Figure 6B). In a tensile strength test, there was one peak in the force/displacement curves (Figure 6A). In a bending test, the notable peak was observed at about 2 mm descending length in the basal section. This maximum force was created at the moment when an angled leaf blade as shown in the cross-section (Figure 6C) flattened. The inner angle between two central points along leaf blade and inner cross point was 85 degrees and maximum bending strength was 0.193 N in the basal section. In contrast, the inner angle was 158 degrees and maximum bending strength was 0.035 N in the middle section.

3.4. Biomechanical properties of leaf blades

Total leaf blade length was 571±26 mm. There was no significant difference between the basal and middle leaf blade sections with respect to leaf width and density (Table 1). However, cross-sectional area was 44 % higher in the basal section than in the middle section.

All values of biomechanical properties were significantly higher in the basal section than in the middle section (Table 1). Bending, tensile and shearing strengths were 8.3, 2.4 and 1.7 times higher, respectively, in the

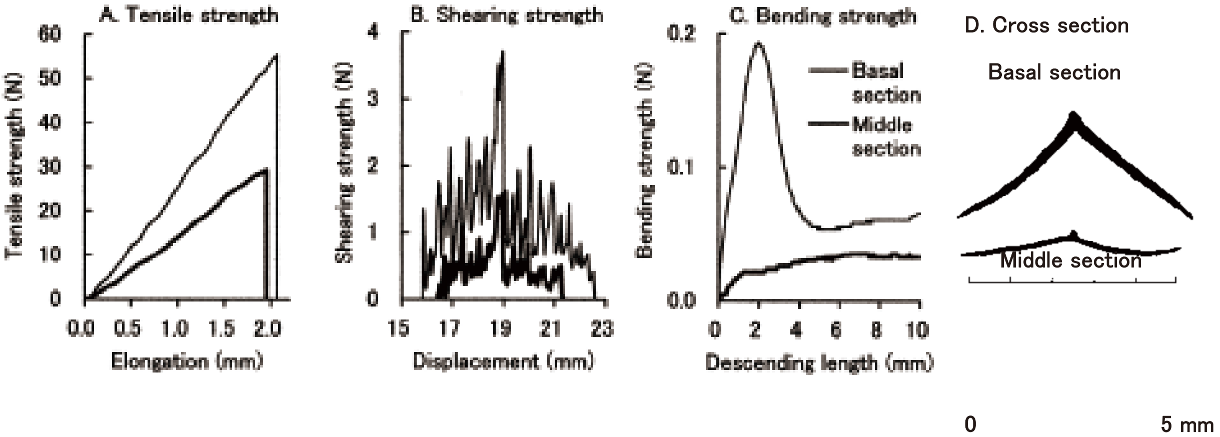

Figure 6 Tensile, shearing and bending strengths, and cross sections at basal and middle sections of orchardgrass leaf blade. Each parameter was measured in the same leaf section.

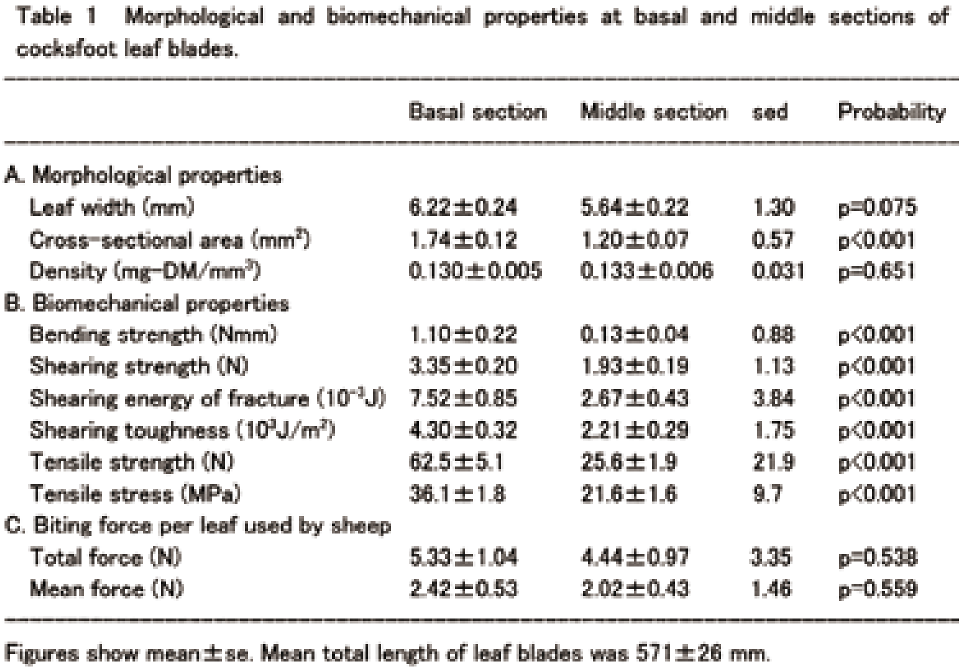

Table 1 Morphological and biomechanical properties at basal and middle sections of cocksfoot leaf blades.

	Basal section	Middle section	sed	Probability
A. Morphological properties				
Leaf width (mm)	6.22±0.24	5.64±0.22	1.30	p=0.075
Cross-sectional area (mm^2)	1.74±0.12	1.20±0.07	0.57	$p<0.001$
Density (mg-DM/mm^3)	0.130±0.005	0.133±0.006	0.031	p=0.651
B. Biomechanical properties				
Bending strength (Nmm)	1.10±0.22	0.13±0.04	0.88	$p<0.001$
Shearing strength (N)	3.35±0.20	1.93±0.19	1.13	$p<0.001$
Shearing energy of fracture (10^{-3}J)	7.52±0.85	2.67±0.43	3.84	$p<0.001$
Shearing toughness (10^3J/m^2)	4.30±0.32	2.21±0.29	1.75	$p<0.001$
Tensile strength (N)	62.5±5.1	25.6±1.9	21.9	$p<0.001$
Tensile stress (MPa)	36.1±1.8	21.6±1.6	9.7	$p<0.001$
C. Biting force per leaf used by sheep				
Total force (N)	5.33±1.04	4.44±0.97	3.35	p=0.538
Mean force (N)	2.42±0.53	2.02±0.43	1.46	p=0.559

Figures show mean±se. Mean total length of leaf blades was 571±26 mm.

basal section than in the middle section. Correspondingly, tensile stress and shearing toughness were also 1.7 and 1.9 times higher, respectively, in the basal section than in the middle section. There was a significant correlation between bending strength and shearing strength (Figure 7).

4. Discussion

4.1. Benefit/cost ratio

The benefit/cost ratio is an important parameter closely related with DM intake and growth rate (Phillips 1993). The benefit factor is usually expressed as DM weight, energy or nutrient contents (Illius et al. 1995), but there is no suitable parameter concerning the grazing cost to grazing animals. In this study, grazing cost was estimated as mean biting force. The DM weight per mean biting force was not affected by any treatments, and its grand mean was 16.7±1.1 mg-DM/N.

4.2. Bending and shearing strengths of leaf blades

The vertical organs of terrestrial plants must mechanically sustain their own weight against the influence of gravity (Niklas 1993). They also must be sufficiently stiff and strong to resist bending and avoid breaking when subjected to large externally applied mechanical forces. In addition, terrestrial plants support and supply a maximal photosynthetic surface area with a minimal metabolic investment in nonproductive support tissue (Chazdon

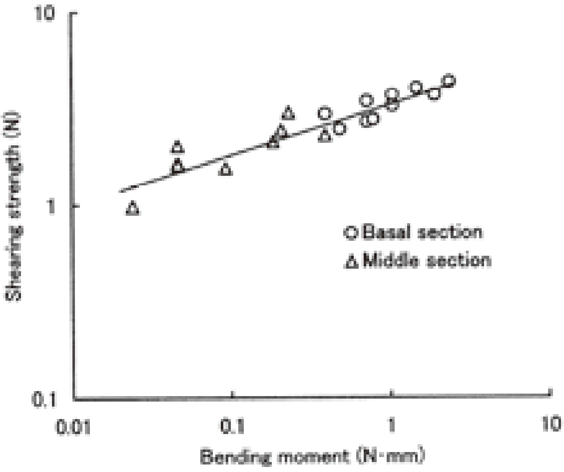

Figure 7 Relationship between bending moment and shearing strength at basal and middle sections of orchardgrass leaf blades. Correlation equation was as follows:
$\mathrm{Log}\,10\ Y = 0.253\ \mathrm{Log}\,10\ X + 0.528$
($r = 0.93$, $df = 18$, $p<0.001$).

1986). In this study, high bending resistance at the basal section was supported by greater leaf thickness, an acute inner angle and well developed midrib (Figure 6D). A thick midrib may play an important role in supporting the acute inner angle and high bending resistance.

There was a significantly positive correlation between bending strength and shearing strength (Figure 7). It has been suggested that the shearing property may be important during the chewing of leaves (Mackinnon et al. 1988). It strongly suggests that sheep may recognize chewing ease of leaves through sensing bending strength prior to prehending a bite, and adjust leaf number per bite and biting force accordingly. This hypothesis was supported by the result that 87 % of a total of 173 bites were completed by only one peak biting force.

4.3. Break-down of leaf blades by shearing force

In this study, mean biting force for one leaf blade used by sheep was 2.42±0.53 N and 2.02±0.43 N in the basal and middle sections, respectively. Tensile strength of one leaf blade was 13-25 times higher than these calculated values (Table 1). Shearing strength of one leaf blade was 1.93-3.35 N, suggesting that sheep could break-down leaf blades mainly by shearing force. Incisors may initiate a crack on leaf blades which can then be propagated with little effort (Vincent 1990). The grand mean of remaining leaf blade length after grazing trials was 17.7±0.5 mm. Sheep grazing at this low level of breaking position may be able to use shearing force by increasing involvement of incisors in biting. In the musculoskeletal lever systems, the joint between the atlas and the skull act as fulcra (Dyce et al. 1987: Devee et al. 2009). It is suggested that biting strategy of sheep may be shearing break-down by the application of the principle of the lever in order to break plant organs by lower biting force and lower cost. It has usually been suggested that the tensile property may be important during prehension of leaves (Henry et al. 1996; Vincent 1990), but this suggestion is not supported by experimental evidence.

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和文摘要

オーチャードグラス葉身の曲げ強度とせん断強度が採食時のヒツジが使うバイト強度におよぼす影響を明らかにするために実験を行った。葉身の基部と中間部を5、10、15、20、25枚づつ１個のロードセルに取り付け、ヒツジに採食させた。３方向のバイト強度を0.006秒間隔でデジタルで記録した。平均バイト強度あたりのDM重を、利潤 / 投資比率として計算すると、各処理間で有意な差はなく、全体の平均値は16.7±1.1 mg-DM/ Nであった。葉身の曲げ強度とせん断強度との間には有意な正の相関があった。この結果は、ヒツジは採食の直前に曲げ強度を感知することで葉身の破断のしやすさを判別しており、口の中に入れる葉の枚数と、そのあとの破断に使う力を決めていることを示唆している。このような仮説は、全体の173バイトのうち87% のバイトでは１回の試みですべての葉身を破断していた結果からも支持された。ヒツジが使用したバイト強度を、その時食べた葉身の枚数で割り、葉身１枚あたりのバイト強度を求めると、基部の葉身で2.53±0.37 N、中間の葉身で1.98±0.26 Nであった。葉身１枚のせん断強度は基部の葉身で3.35±0.20 Nであり、中間の葉身で1.93±0.19 Nであった。このような結果から、ヒツジは下顎の切歯の鋭さを有効に使って、せん断する方法で牧草を採食しているものと推察された。

キーワード： 曲げ、バイト強度、オーチャードグラス、せん断、ヒツジ