Effect of Biomechanical Properties of Herbage Grasses on Grazing Behaviour of Sheep

2009

The United Graduate School of Agricultural Sciences
Iwate University
Course of the Science of Biotic Environment
(Obihiro University of Agriculture and Veterinary Medicine)

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(イネ科牧草のバイオメカニクス的特性がヒツジの採食行動におよぼす影響)

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Effect of Biomechanical Properties of Herbage Grasses on Grazing Behaviour of Sheep

A Dessertation Submitted to
The United Graduate School of Agricultural Sciences
Iwate University

In Partial Fulfillment of the Requirements for the Degree of
Doctor of Agricultural Sciences

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March, 2009

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ABBREVIATIONS

OG	Orchardgrass (*Dactylis glomerata* L.)
TF	Tall fascue (*Festuca arundinaceae* Schreb)
PRG	Perennial ryegrass (*Lolium perenne* L.)

DM	Dry matter
GIT	Gastro-intestinal tract
SF	Safety factor

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Chapter 1

GENERAL INTRODUCTION

1.1 The biomechanical properties of herbage grasses

The principles of engineering design can be applied successfully to studies of mechanical function in organisms (Wright and Vincent, 1996). Biomechanics is the study of the mechanics of biological materials and structures (Wright and Vincent, 1996). Principles and procedures in plant biomechanics have been thoroughly discussed by Gordon (1976, 1978), Wainwright *et al.* (1976), French (1988), Lucas & Pereira (1990; 1991), Vincent (1992), Wright and Vincent (1996) and Niklas (1992).

The mechanical properties and analysis of grass are of interest for several reasons. Agronomists want to know if mechanical factors affect the choice of herbage grass by grazing animals (selective grazing); how mechanical properties affect the digestibility of grass; and how they affect processing (harvesting, hay-making etc.); whether mechanical propeties are concerned in the resistance of grass to trampling. Naturally this information is of use to the plant breeder who can then select for the important characteristics (Vincent, 1982).

1.1.1 The anatomy of grass leaf and factors conferring plant biomechanical properties

Plants are the staple source of mammallian herbivore diet. Of three main morphological organs (root, stem and leaf), leaves are the most preferred part within plant body. The main function of the leaves is the synthesis of organic compounds using light as a source of the necessary energy, a process known as photosynthesis. The external and internal structures of the leaf are correlated to its role in photosynthesis and transpiration (the loss of water as vapour). The leaf is flat and thin, thus enabling the solar rays to penetrate into all cells. The high surface to volume ratio also enables successful gas excange (Fahn, 1990).

Monocotyledons such as grasses have laminas with parallel veins and are generally linear in shape. One surface is ridged, the other smooth. The leaf is composed of four types of tissue system as follows (Fahn, 1990).

The epidermis constitutes the outermost layer of cells of the leaves, floral parts, fruits, and seeds, and of stems and roots before they undergo considerable secondary thickening. Functionally and morphologically the epidermal cells are not uniform and among them, apart from the ordinary cells, many types of hairs, stomatal guard cells, and other specialized cells are found. The epidermal cell wall differs in thickness – some cells are thin-walled while in others the outer and inner periclinal walls are thicker than the anticlinal walls. The epidermis, because of its compact structure and the strength of the cuticle, and the fact that the walls of its cells may sometimes be thick or impregnated with silica, gives support to the lamina (Fahn, 1990). The analysis of leaf structure by Greenberg *et al.* (1989) proved that epidermal cells play a major role as a load-bearing component.

Sclerenchyma is a tissue composed of cells with thickened secondary walls, lignified or not, whose principal function is support and sometimes protection. Sclerenchyma cells exhibit elastic properties. Sclerenchyma is the main fibrous tissue, most of which occurs in distinct bundles of fibres, but some of which occurs in association with the bundles of vascular tissue which transport water and nutrients along the leaf (Vincent, 1982). The amount of sclerenchyma associated with the fibres is directly related to the tensile strength of grass leaves, and the distribution of fibre and associated sclerenchyma influence the toughness of the leaves (Vincent, 1991). Vincent (1982) modeled grass leaf as a three-component composite system consisting of sclerenchyma fibres, vascular bundles and a matrix containing relatively large, thin-walled cells under turgor pressure. Experimental values of plant stiffness were presented by a Voigt model in which fibre components accounted for 90 to 95% of the longitudinal stiffness while occupying only about 8 vol % of the composite (Vincent, 1982). Fibres act as crack-stoppers, increasing the energy required to propagate a crack across the leaf. Many fibres will deflect the crack more often than few fibres, so a leaf with many small fibres will be tougher than a leaf with few large fibres (Wright, 1992). Tough leaves are difficult to chew. If, however, sclerenchyma is present in more than 15% of the volume fraction of the leaf (Vincent, 1982), cracks propagate easily, since there is so much fibrous material that the fibre is continuous across the leaf and the leaf is brittle (Wright and Vincent, 1996). A leaf can also be brittle if the sclerenchyma extends in an unbroken zone through the thickness of the leaf.

The veins seen in the leaf blade contain vascular tissues. Vascular system is composed of several vascular bundles. The veins that pass along the entire leaf may be almost of the same thickness or they may be of different thickness. In the latter case the thick and thin veins are arranged alternately. The median vein is usually the thickest. Vincent (1982) noted the importance of the midrib in the leaf strength, containing about 20% of the total volume-fraction of fibre. In monocotyledonous leaves the vascular bundles are accompanied by many fibres. In the Gramineae and in many other monocotyledons the fibres form girders on one side or both sides of the bundles, and in many leaves they continue from the bundle sheaths to epidermis, the cells of which, in such regions, may then also become fibre-like (Fahn, 1990).

It has been confirmed that C_4 plant species are stronger than C_3 plant species (Zang, 2004; Zang *et al.*, 2004). The differences between the leaf anatomy of grasses from C_3 and C_4 photosynthetic pathways are the greater number of veins, and smaller interveinal distance (Scheirs *et al.*, 2001; Wilson *et al.*, 1989), and a higher proportion of sclerenchyma (Akin and Burdick, 1975; Wilson *et al.*, 1989) in C_4 species. These structural characteristics strengthen plant tissues (Vincent, 1983). In tropical ecosystems, environmental temperature increases the rate of plant growth, which increases plant strength (Vincent, 1983), and also reduces the moisture content between the sclerenchyma fibres (Vincent, 1983), which leads to increased herbage strength (Halyk and Hurlbut, 1968; Henry *et al.*, 2000).

The relationship between mechanical and anatomical properties of plant tissues has been the subject of considerable speculation because it is evident that, aside from their physiological functions, every tissue type contributes in some way to the mechanical behaviour of organs (Schwendener, 1874; Carlquist, 1961, 1969, 1975; Wainwright *et al.*, 1976; Niklas, 1992; Speck, 1994; Spatz *et al.*, 1995).

Niklas (1992) emphasized the importance of geometry or shape of plant organs in their mechanical design. Dehydration can reduce flexural stiffness by changing geometry of cross-sectional area (Niklas, 1992).

1.1.2 Fracture mechanics of plant material

To survive, the organism must have mechanisms for resisting fracture (the initiation and propagation of cracks) in order to withstand the mechanical effects of wind, water, and gravity, to grow in such a way that bits do not fall off or split open unannounced, and to resist attack from herbivores. An organism may also cease to be able to carry the loads that it must do in order to survive, due to structural failure. This may involve fracture but also involves other forms of deformation, both elastic and plastic (Vincent, 1992).

Fracture involves the failure or cracking (not necessarily the breaking into pieces) of a material. A crack must first be initiated. Small imperfections can act as initiators, but for a given stress level these imperfections must be above a certain critical size (a Griffith crack (Gordon, 1976)). The initiation of a crack therefore depends, to some extent, on strength (Vincent, 1992) while crack propagation depends on toughness (Gordon, 1978; Atkins and Mai, 1985). There are two criteria for the initiation and propagation of cracks: sufficient force must be provided to break the chemical bonds which hold the material together and sufficient energy must be available to generate the new surfaces. This is true for all cracks passing through all materials and structures (Wright and Vincent, 1996).

Once initiated, the crack can be propagated in one of three ways: mode I crack propagation is due to tension or crack-opening. Mode II is due to edge-sliding, or in-plane shear, which is a type of deformation which the crests of the molar teeth can give. Material fails in the direction of the applied force. Mode III fracture is caused by tearing or out-of-plane shear, which is how scissors cut (Fig. 1.1). Where ruminants are concerned, mode I fracture tests best describe the harvesting of herbage grass in a predominantly vertical dimension while mode III fracture represents the mechanisms of fracture that take place when forage is crushed and ground against the molars during chewing. In the leaves of a plant such as grass where orientation of the sclerenchyma fibres imposes a marked mechanical anisotropy (Vincent, 1982), the different modes of fracture can require forces and energies differing by factors of 5 to 10 (Vincent, 1982, 1991; Wright, 1992), so it is important to distinguish the three modes.

1.1.3 Techniques for measuring fracture properties

The application of material science theory to understanding biological problems in herbivores has led to an interest in quantifying plant fracture mechanics.

Plant tissues are more complex than most engineering structures, making their mechanical properties often difficult to measure, interpret, and predict. In order to be able to measure the fracture properties of plant tissues it is necessary to use proper engineering and materials science methods. There are various methods available for measuring leaf biomechanical properties but there has been little use of these in relation to ecological questions. It is unlikely that there is one biomechanical test that gives an adequate measure of leaf properties that are relevant to all herbivore.

Various techniques for accurate and appropriate measurement of plant fracture properties are suggested by Vincent (1990, 1992). These all require that certain precautions be taken. Thus, in order account for the mechanical energy budget within material, there should be no elastic strain energy remaining in the test piece after fracture has occurred, and the test machine should not store elastic strain energy. The propagation of the crack across the test piece should be stable and slow (Atkins and Mai, 1985). This allows proper energy budgeting and the calculation of the energy used in fracture by the work-area method (Gurney and Hunt, 1967), which requires that the sample is unloaded slowly after the specimen has been partially cleaved, thus allowing all elastic strain energy to be removed from the sample. The area under the force-displacement curve (representing the work done during fracture) does not then include the elastic strain energy which was stored in the specimen during fracture (i.e. energy used in deformation of the test piece) and can be related directly to the area cleaved, giving a direct estimate of the work to fracture (Wright and Vincent, 1996).

1.1.3.1 Tensile test

The simplest test morphology is the tensile test. Tensile test is commonly conducted by securing the test piece between two clamps and breaking the specimen by longitidunal pull. Forces were involved by motor or hand. The instrumentation used by Sun and Liddle (1993) was a modification of that used by Evans (1964). The apparatus consisted of a pivoting beam, with a clamp setup on one side and a bucket hung on the other side into which sand was poured until fracture of the specimen occurred. In spring-tensioned instrument used by Diaz *et al.* (2001), plant material is clamped between screw type clamps, and tension is applied to the plant material by winding up a spring-operated crank until fracture results. Translation of data by these two types of instrumentation to understanding grazing mechanics is, however, limited. The Instron testing instruments reported by Henry *et al.* (1996) and Wright & Illius (1995) offer tighter control over acceleration and greater precision in recording fracture force. Additionally, the machines are compatible with computers and/or plotters that plot the force-displacement curve for each test specimen, which provides visual reinforcement of the timing selection of fracture.

Studies of leaf tensile strength by Wilson (1965), Evans (1967b), and Nguyen *et al.* (1982) all measured maximum force (breaking load), which was then divided by the linier density of the specimen (dry weight per 5 cm length of leaf) to give 'tensile strength'. In later work, Vincent (1983, 1990, 1991) and Greenberg *et al.* (1989) re-assessed the tensile properties of grasses by including measurements defined in engineering terms such as: tensile strength (stress at point of fracture), strain, Young's modulus, and fracture toughness.

In tensile tests, a clamp that minimizes slippage while simultaneously minimizing damage from the compression force applied to the test specimen at the site of the clamp (Voisey, 1976) has been a big problem. There are various solutions to this problem, depending on the nature of the tissue. Samples that fracture due to damage by the clamp should be discarded (Voisey, 1976), because their inclusion will lead to erroneous data. Square clamps are often covered with rubber and/or emery paper (Evans, 1964). Henry *et al.* (1996) devised cylindrical clamps and argued that the clamp method eliminated stress concentration by allowing a gradual increase in the transmitted force to the specimen around the periphery of the cylinder, avoiding fracture at the clamp. The disadvantage of the cylindrical clamp is that long specimen length is needed for testing. Vincent (1982) recommended that specimens be glued to tabs of aluminum, which could then be held by clamps.

Notching has been used to control the site of fracture, involving the creation of small notch at edge of the test piece using a needle or razor blade. Many monocotyledons with their parallel venation do not transmit shear and are considered notch-insensitive (Vincent, 1983). Notch insensitivity implies that a single fiber can be broken without affecting the strength of the test specimen since the stress is distributed evenly among the remaining fibers. In spite of many advantages, the procedure has not been more widely utilized.

Shearing test

Shear occurs when two opposing parallel forces cause fracture at a 90 degree angle to the length of the leaf. Many researchers have used a Warner-Bratzler shear apparatus (Mackinnon *et al.*, 1988; Easton, 1989; Inoue *et al.*, 1989; John *et al.*, 1989; Hughes *et al.*, 2000; Griffiths *et al.*, 2003a,b) that was originally designed for measuring the shear strength of meat as a measure of meat tenderness. Strength was reported as maximum force exerted, or as maximum force divided by the linear density of the plant material.

In contrast, Lucas and Pereira (1990), Lucas *et al.* (1991), and Choong *et al.* (1992) used instrumented scissors to shear individual leaves. Their measure of shear strength was calculated as the energy required to shear the specimen, divided by the product of the length of the cut and the specimen thickness and was termed fracture toughness. Lucas and Pereira (1990) and Vincent (1992) described how scissors can be mounted on a force tester and used to shear through a section of a leaf. Vincent (1992) details the corrections that must be made in determining the force on the scissors. The distance from the hinge to the cutting point is constantly changing, so each data point must be corrected separately. The exact location of the test piece on the blades must also be recorded. As the blades close, the geometry of the cut changes and corrections must be made so that the displacement axis maps directly onto the width of the specimen. Scissors function by the elasticity of the blades, which in good quality scissors are curved across each other. As the blades close, they bend, maintaining a spring-loaded compression between the blades at the cutting point. Taking a blank run before or after the trial run and subtracting the blank curves can control for much of this effect. The second problem is that the constantly changing approach angle of the closing blades, and the changing amounts and kinds of tissue being cut at any one moment, make it difficult to discriminate between tissues being cut. Some of these problems can be resolved by using a single blade fixed to the moving platform of the force tester, and fixing another blade to the force transducer. Constant relief and rake angles, all of which affect the results, can be maintained. Unlike scissors, the same correction factor for blade approach angle can be applied to all data points, as the angle of cutting remains constant throughout the test. Because the geometry is constant, no corrections for force due to changing displacement have to be made.

Henry *et al.* (1996) showed that the force to shear a leaf directly and positively correlated with the length of cutting blade in contact with the leaf material, and consequently, the most appropriate measure of shear strength of a leaf was a property, termed intrinsic shear strength, in which the force exerted to shear the leaf was corrected for the length of cutting blade in contact with the material. This eliminated problems of changes in leaf thickness and small variations in blade angles.

Biological materials fequently transgress the assumptions required by 'proper' fracture tests, being anisotropic, or very strechy or inhomogeneous, or of an odd shape. There is a pragmatic way (work-area method) of coping with these problems. The area enclosed by the force-deformation curve which a mechanical test generates represents work (force x distance) (Gurney and Hunt, 1967). So with a little care it is possible to measure that area, hence the work, and express it in terms of the area of material cleaved (Vincent, 1982).

1.1.3.2 Bending test

Flexural tests, such as bending or torsion test, are less commonly used (Vincent 1982; Greenberg *et al.*, 1989; Wright and Illius, 1995; Henry *et al.*, 1996; Paolillo and Niklas, 1996; Sanson *et al.*, 2001). Investigations into bending strength of herbage grasses provide a deeper understanding of the mechanical design of the structure of the grass. It can also be useful for understanding of diet selection behaviour by herbivores. Herbivores might be able to get primary signal about herbage grass strength on contact.

Tests in compression are more complex than tensile tests in that the structure becomes more important. Cantilever and three- or four-point bending tests can be very useful for long thin specimen such as grass leaves.

Cantilever tests are exceedingly easy on large specimens. Specimen can be held in a retort clamp and and weights hung from the other end on a loop of string or cotton.

Three- or four-point bending tests are very easy since there is no problem with end clamps. However, the supports must be well-rounded enough to avoid bruising the specimen but not so broad as to make the point of application of the load indeterminate.

With point loads, a beam will experience both shear and tensile/compressive stresses when it is bent. If the specimen is too short, some of the resistance to bending will be due to shear along the neutral axis, rather than simple compression and tension on opposite sides of the neutral axis. This can be countered by increasing the span (or decreasing the depth) of the specimen until the calculated Young's modulus does not increase any more. Suitable span-to-depth (S/D) ratios, chosen to avoid shear, have been recommended (Roark, 1965) for various materials. The more anisotropic the specimen the greater the required S/D ratio (Vincent, 1992).

Clearly, shape alone does not define the capacity of any object to resist bending. The material moduli of an object dictate the relation between stresses and strains for any level of stress. Thus the magnitude of the bending moment must be related both to shape and to a material modulus. The product of the second moment of area *(I)* and the elastic modulus *(E)*, called flexural stiffness, measures the ability of a column to resist compression or of a beam or cantillevered column to resist bending. In biological contexts, I largely reflects morphology, while the value of E largely depends on anatomy (Niklas, 1992).

Chan *et al.* (1999) studied variation of bending moment capacity along the lamina length of a grass species (*Imperata cylindrica* var. *major*) using a simple three-point bending test. The bending moment capacity was defined as the maximum bending moment that can be sustained by the lamina while bending strength was defined as the stress at which failure occurs and corresponds to the bending moments induced by the failure load P. They suggested that the tapered beam model can be modified to a simple three-segment model to describe the bending moment capacity of grass.

Glossary of related terminologies

Bending moment is the product of a bending force and the length of the radius arm, at right angles to the direction of application of the bending force.

Bending stresses are caused by bending, of which there are three kinds: tensile (σ+), compressive (σ-), and shear bending stresses (τ). Bending tensile and compressive stresses increase in intensity toward the perimeter of cross sections; bending shear stresses increase in intensity toward the centroid axis.

Breaking load is a load that results in the mechanical failure of a structure. The strength of a structure expressed in units of weight.

Brittleness: factures at low strain, so high-carbon steel and table jelly are both brittle.

Elastic modulus (Young's modulus or modulus of elasticity), symbolized by E, is the ratio of normal stress to normal strain measured within elastic range of behaviour of a material.

Fracture force is a measure of the force required to fracture a plant organ and can be assessed from the maximum force recorded on the force-displacement curve that produces fracture.

Fracture toughness is the resistance to crack propagation and is a measure of the energy required to fracture the leaf (Wright and Vincent, 1996). The area under a stress-strain diagram provides a measure of material's toughness in terms of the energy absorbed per unit volume (Niklas, 1992).

Resistance is a plant-based term that has no underlying engineering concept, but it carries importance in the application of plant fracture mechanics to predicting grazing strategies in ruminants. It can be defined as the accumulated force required by the animal to sever all the plant organs encompassed within the bite (Griffiths, 2006).

Shear is the result of the tangential application of an external force to the surface of a material or a structure.

Shear strain, symbolized by γ, is the tangent of the rotation angle (in radians) resulting when a material is subjected to a tangentially applied force.

Shear stress, symbolized by τ, is the shear force component divided by the tangential area over which the shear force component acts.

Stiffness (resistance to deformation) has the same units as stress and, in tension, is numerically equal to the stress required to double the length of the test piece.

Strain is the imposed deformation standardized to the size of the test piece (Vincent, 1992), which in engineering is the increase in length divided by the original length.

Strain energy is the component of the total energy within an object or a structure that is stored in the form of molecular deformations. Strain energy is a form of potential energy; in elastic materials, within the proportional limits of loading, the strain energy is used to restore the material's original dimensions when the stress is removed. Within the range of elastic behaviour, the strain energy is the area measured in the stress-strain diagram.

Strength may be defined as the maximum stress at which the test piece breaks and is a measure of the resistance of a material to crack initiation (Wright and Vincent, 1996).

Stress is imposed force normalized to the size of the test piece (Vincent, 1992), and is measured by the force divided by the cross-sectional area over which the force is applied. It is a measure of the resistance of a material to crack initiation (Wright and Vincent, 1996).

1.2 Interaction on plant-animal interface

The interface between a grazing animal and a sward is relatively unexplored area of study. Grazing by ruminants is an action to break plant parts. The mechanical properties of plants determine the effort animals must expend both to harvest and digest them, and are therefore important aspects of plant resistance to herbivory (Laredo and Minson, 1973; Lees *et al.*, 1981; 1982). In turn, plant mechanical properties influence evolution of the behaviour and morphology of the animals that feed upon them (Kay, 1975; Lucas, 1979; Bernays, 1986; Janis, 1988; McArthur and Sanson, 1988).

The interactions between plants and herbivores are central issues in ecology. The grazing system, consisting of soil, plants, and animals, is a dynamic system. The plant-animal interface describes the continuum of interactions of the grazers with the sward. The plant grows and produces its tissues, ultimately for reproduction and persistence. The grazer harvests parts of the plant which provide nutrients for maintenance and production. Gain is influenced by many factors, including characteristics and stage of growth of both the plant and the animal (Coleman, 1992).

The grazed ecosystem is dynamic from both the plant and the animal standpoints.

During plant growth, new tissue provides a different architecture, different nutrient combinations, and different tissue choices from which grazer may select. At the moment of prehension and severance of a bite from the sward, the action of the grazer has changed the resulting structure and architecture, the amount and class residual tissue for carrying on plant photosynthetic and respiratory functions, and the potential for growth and reproduction. Therefore, making measurements to determine the activities in the grazed ecosystem is very difficult (Coleman, 1992).

Pasture affects grazing animals through the amount of feed available, the seasonal pattern of production and through pasture quality. Sward architecture or structure affects how and to what extent the grazer acquires its nutrient requirements. The two components of nutrient acquisition are rate of intake and composition or quality of the diet. Plant structure may limit nutrient acquisition by limiting nutrient density in the grazed horizon so that the animal cannot reasonably consume sufficient quantities within a day (Hodgson, 1982). The plant may also limit selectivity of more nutritious parts with physical barriers, thus reducing the quality of diet.

1.2.1 Animal effects on pasture

The animal drive is to fulfill its nutrient requirements. Grazing produces a complex situation where several dynamic processes interact with each other. Defoliating (Scott, 1956), treading (trampling) and excretion (dung and urine) (Edmond, 1963) by the animal influence plant growth and persistence. Each factor affects herbage production, herbage quality and botanical composition and each factor, in turn, is affected by these sward attributes so that there is no true cause and effect (Snaydon, 1981).

Various defoliation regimes affect herbage production differently at different times of the year (Brougham, 1959). These differences appear to be due partly to the effects upon leaf area index (Brown and Blaser, 1968), but other factors, such as tillering rate, are probably involved (Snaydon, 1981).

The intensity and timing of grazing have large effects on plant species composition and diversity. Natural populations of large grazers are reported to increase plant species diversity (McNaughton, 1985), but domesticated grazers at high stocking rates can decrease diversity (Hobbs and Huenneke, 1992) and abundance.

Probably the most important effect of grazing on pasture composition is the effect on grass:legume ratio. Frequent intense grazing usually increases the proportion of short and stoloniferous legumes, but decreases the proportion of erect, non-stoloniferous species (e.g. Brougham, 1960).

The effects of treading on the growth and botanical composition of pasture is frequently visible on pathways. It seems that normal levels of treading do not have a major effect on yeild, except in wet conditions. Botanical composition is rather more affected (Snaydon, 1981).

Dung or urine can have large local effects upon the yield, quality, palatability and botanical composition of pasture. However, the effects on the whole pasture are much less, because only a small area is affected (Snaydon, 1981).

1.2.2 Plant response to grazing

Different herbage grass species vary in their response to grazing. Grazing resistance describes the relative ability of plants to survive and grow in grazed communities. Grazing resistance can be divided into avoidance and tolerance components, based on the general mechanisms conferring resistance (Briske, 1986, 1991, 1996; Rosenthal and Kotanen, 1994; Briske and Richards, 1995). Grazing avoidance involves mechanisms that reduce the probability and severity of grazing, while grazing tolerance consists of mechanisms that promote growth following defoliation. Avoidance mechanisms are composed of architectural attributes, mechanical deterrants and biochemical compounds which reduce tissue accessibility and palatability. Tolerance mechanisms are composed of the availability and source of residual meristems and physiological processes capable of promoting growth following defoliation (Briske, 1996).

In order to survive, plants have developed defence mechanisms. Plants use chemical, morphological (physical), and physiological measures to cope with grazing stress. Chemicals that repel or cause a negative selection pressure include tannins, oils, phenolics, and alkaloids.

Mechanical properties of plants are widely assumed to function as deterrants to grazing by animal. The effect or potential effect of leaf structure or texture acting as antiherbivore defences has been noted in a number of study. Sanson *et al.* (2001) noted the possibility that leaves of two species could potentially have identical chemistry but differ in the way the components are arranged, which can confer different mechanical properties. Tensile strength of herbage grass has been used to explain the intake rates of sheep and cattle (Wright and Vincent, 1996). These studies indicate that plant properties such as hardness, toughness, strength and stiffness have the potential to act as antiherbivore defences.

1.2.3 Plant factors affecting intake

Many studies (e.g. Minson, *et al.*, 1964; Demarquilly *et al.*, 1966) have confirmed the general positive relationship between intake and forage digestibility.

Forages of low digestibility contain large quantities of indigestible fibre, so that quite small intakes of forage fill rumen with indigestible fibre which stays there longer. Conversely, highly digestible forages contain little indigestible fibre, so, assuming that the indigestible fibre is retained in the rumen for the same length of time, more can be eaten before the rumen is filled (Minson, 1987).

The relationship between intake and digestibility differs between plant species and cultivars (Minson, 1987).

The greater intake of the leaf material has been confirmed in some studies (Minson, 1972; Laredo and Minson, 1973), where leaf and stem fractions have been fed separately to animals. The intake of leaf was 59% greater than that of the stem at a given digestibility.

Legumes contain less fibre than grasses of similar digestibility (Minson, 1982); as a consequence, the intake of legume is much greater than that of grasses of similar digestibilty (Minson, 1987).

It is often suggested that the intake of succulent forages is depressed by their greater water content. Moreover, intake is usually depressed when feed is deficient in any essential nutrient.

Where the herbage contains toxic levels of any element or organic compound the animals become ill, intake is reduced.

When there is little herbage available, intake is restricted. One of the main reasons for reduced intake, where there is little available herbage, is that the amount that can be taken with each bite is low (Stobbs, 1973). This can partly be offset by the animal increasing the number of harvesting bites, but there is an upper limit to the total number of bites animals will take each day (Stobbs, 1973). If the distribution of forage is uneven, as occurs with forage sown in wide rows, the maximum intake is achieved at a lower herbage availability than for a uniform pasture, since there is a smaller effect on bite size (Minson, 1987).

Heterogeneity of sward can have a negative effect on animal intake rate. Pastures can be heterogeneous in terms of their leafiness, maturity, species composition, and soiling by excreta. Animals select within this variation and as a result eat more forage, and forage of a higher quality, than might be expected on the basis of the average forage on offer (Arnold and Dudzinski, 1978). Although selective grazing can have nutritional advantages, there can also be disadvantages. For example, animals may continue to search for a component that is present in small proportions, and so intake is reduced (Minson, 1987).

Similarly, when pastures contain both green and dead material, intake and liveweight gain of both sheep and cattle are more closely related to the quantity of green dry matter per unit area than to the total forage present (Willoughby, 1958; Yates *et al.*, 1964; Arnold and Dudzinski, 1966; Mannetje, 1974), since animals eat little dead material if green feed is available (Mannetje, 1974; Chacon and Stobbs, 1976; Hendricksen and Minson, 1980).

1.3 Grazing behaviour

1.3.1 Grazing animals

Ruminants are the hoofed animals, belonging to suborder of Artiodactyla. The success of herbivorous animals in evolutionary terms, and eventually their value as farm animals, depends upon their ability to derive an adequate intake of nutrients from a food resource which is often fibrous in nature and of low nutrient concentration, and which, because of the structure of the sward canopy, could be difficult to harvest. There are two important adaptations which make effective harvesting of grass possible: at first, the modifications of the jaws and teeth which improve the efficiency of the harvesting process, and, secondly the development of a digestive tract in which symbiotic cellulolytic bacteria are responsible for breaking down by fermentation of the refractory plant fiber and cell walls which would otherwise be largely unaffected by normal mammalian digestion (Hodgson, 1990).

1.3.1.1 The nature of digestive system of ruminants

The principal function of the gastro-intestinal tract (GIT) of animals is to provide for the digestion and absorption of nutrients and excretion of certain waste products. Since herbivorous animals apparently cannot produce cellulolytic enzymes (enzymes that are capable of hydrolyzing cellulose to cellobiose and glucose) themselves, they have developed a variety of ways to utilize cellulose and related plant polysaccharides indirectly by playing host to symbiotic microorganisms. The ruminant stomach represents one modification of the GIT which allows the animals to utilize large amounts of cellulose (Church, 1979). It has developed into an organ that provides for extensive pregastric microbial fermentation. As a result, the most significant anatomical difference between ruminants and other mammals is the four-chambered (rumen, reticulum, omasum, and abomasums) digestive system that allows ruminants to derive 60% of their energy requirements from the microbial fermentation in the rumen-reticulum of the constituents of plant cell walls.

The stomach of ruminant species is very large in proportion to body size and occupies nearly 3/4 of the abdominal cavity (Church, 1979). Food passes first into the rumen and reticulum, where it is held for several hours for microbial fermentation. Enzymic digestion starts in the abomasum or true stomach, and continues in the small intestine. The act of rumination, the regurgitation and remastication of partly digested food from the rumen, aids this process by reducing food particles to a smaller size. Nutrients are absorbed from the small intestine into the bloodstream. Water is also absorbed from the residues of digestion in the caesum and colon, and some limited fermentation occurs before the residues are expelled as faeces (Hodgson,1990).

The digestibility of the diet, the proportion of the food consumed which disappears in passage through the alimentary tract, is used as a measure of the efficiency of the digestive process and frequently as an expression of the nutritive value of the diet. The digestibility of plant tissue can range from between 80 and 90 percent in immature leaves and sheaths down to between 40 and 50 percent in mature flowering stems, and to even lower levels in woody tissue (Hodgson, 1990).

1.3.1.2 Harvesting apparatus

The ingestion of food by ruminants under pasture and range conditions often occupies a third or more of their time, thus it is an important aspect of digestive physiology (Church, 1979).

The term prehension means the seizing and conveying of food to the mouth. In ruminant species the lips, teeth, and tongue are the principal prehensile organs. However, their relative importance varies with the species of animal, its age and the type of food being eaten (Church, 1979).

Physically, the harvesting apparatus is housed within an elongated and bluntly pointed skull. The jaws are the housing to which teeth and muscles are attached. The upper jaw bone, called the maxilla is fused to skull. The lower jawbone, termed the mandible, is hinged at each side to the bones of the temple by legaments.

Common to all ruminants are the four-paired anterior teeth consisting of true incisors and incisiform canines set on the lower jaw, believed to have evolved for harvesting of plant material. One peculiarity of ruminant animals is that they do not have incisor teeth on the upper jawbone. Rather, the upper incisors are replaced with a tough and thick pad of connective tissues (dental pad), which provides a surface against which the lower incisors can put pressure. Toward the back of the mouth ruminants have sets of molars and premolars that are flat and lined with sharp ridges of enamel. Because tooth shape governs functionality, these posterior teeth generally do not make contact with bulk of the grasped forage during prehension, and their pivotal role lies in chewing the severed bite contents. The young ruminant is born with a set of incisor and premolar teeth, and these juvenile (milk) teeth are replaced by a full set of adult teeth by 3-4 years of age in both sheep and cattle (Hodgson, 1990)

In bovines, the chief prehensile organ is the tongue. The tongue, a long mobile organ, is used to pull grass or other herbage into the mouth where it can be clipped off with the incisor teeth and dental pad. Near the tip of the tongue, there are number of filiform papillae which are stiff and project in a caudal direction. These papillae aid in collecting small particles of food (Church, 1979).

The large gap between the incisors and molars provides room for tongue movements associated with the collection and manipulation of plant leaves and stems (Hodgson, 1990).

The lips, which are relatively immobile in bovines, become more important as prehensile organs when the animal is cropping short, lush, young grass. Sheep and numerous other species have an upper lip, often partially cleft, which is much more mobile than that of bovines. This type of a lip permits very close grazing, although the incisor teeth and tongue are considered to be principal prehensile structures. The tongue is not protruded as much in grazing as it is in cattle. This type of prehensile lip, which is facilitated by the manner in which the tongue is used, allows many species to be very selective when consuming grass, mixed herbage, browse or forbs (Church, 1979).

Smaller animals have a smaller harvesting apparatus in absolute terms and can remove smaller bites. But relative to body mass, smaller animals require a diet of higher nutritional quality compared with larger animals to meet higher metabolic requirements per unit of body weight. It is believed that small animals have, therefore, evolved a jaw configuration that is narrower relative to larger-bodied animals and additionally supported by prehensile and mobile lips that permit the selection of leaves. By contrast, larger-bodied animals have wide jaw configuration, and irrespective of whether these species can perceptually discriminate between leaf and stem, they are constrained by the inability to selectively remove leaf from stem because of the constraints of the wide muzzle (Griffiths, 2006).

Mastication or chewing is the mechanical reduction of food to a smaller size. In herbivores, well-developed lateral movements greatly facilitate the grinding action which is required to reduce fibrous plant material to a size or shape that may be swallowed. Due to lateral movements of the jaw, the molar teeth develop a chisel-shaped grinding surface (Church, 1979).

The number of jaw movements during mastication would appear to be on the order of 15,000 to 20,000 in cattle and 10,000 to 45,000 in sheep with approximately an additional 25,000 and 40,000 during rumination in cattle and sheep, respectively. The total daily mastications would, therefore, be on the order of 50,000-85,000 for sheep and 40,000-45,000 for cattle. Mastication appears to increase the solubility of some nutrients. The rate of mastication varies with hunger and nature of the feed (Church, 1979).

The harvesting apparatus and body mass of animals account for much of the variation that exists in selection strategies between species (Griffiths, 2006).

1.3.2 Grazing process

Grazing system research seeks to improve the understanding of the determinants of the grazing process as they influence herbage intake and diet quality. Grazing ruminants vary their bite dimensions, bite rate and grazing time in response to changes in sward conditions (Hodgson, 1981; Milne *et al.*, 1982a; Penning *et al.*, 1991; Gibb *et al.*, 1997). However, the mechanism through which sward characteristics and animal factors influence bite dimensions and therefore herbage intake is not fully understood. Mouth size of the animal (Taylor *et al.*, 1987; Illius, 1989; Laca *et al.*, 1992b), proximity of the bite to the ground (Hughes *et al.*, 1991), and the effort required to break a bite (Hughes, *et al.*, 1991) may all influence bite dimensions of grazing ruminants.

The food-gathering process is a demanding one for grazing animals. For example, a cow has an incisor only 8-9 cm wide (distance across the incisor teeth) and even though she uses her tongue to increase the effective area grazed, the weight of herbage obtained at a single bite is likely to be only 0.2-1.0 g of herbage DM in most circumstances. Thus, in order to achieve a daily herbage DM intake of 12-16 g she will have to take between 20,000 and 40,000 individual bites over periods of grazing activity occupying, in total, between 6 and 12 hours, depending upon sward conditions. In that time, she will have walked 3-4 km. Sheep have smaller appetites and smaller mouths in absolute terms, though not relative to body size, but their total grazing effort, measured in terms of the number of grazing bites and the distance traveled, is similar. In addition to the work involved in grazing, ruminating activity is likely to occupy between 6 to 8 hours daily, and a further 15,000-20,000 jaw movements (Hodgson, 1990).

Cattle and sheep normally divide their working day into alternating periods of grazing, rumination and rest. There are usually between three to five periods of grazing during the day, the longest and most intensive being after dawn and before dusk. Most grazing activity occurs during daylight hours in temperate climates, though short periods of night grazing are not uncommon. There is usually period of ruminating activity after each grazing period, but much of the rumination occurs at night.

The behavioural components associated with taking a bite are searching and handling. Searching includes the movement of the animal through its grazing environment, and all cognitive and sensory processes entailed in the decision to take a bite at a specific spot in the sward. Handling comprises biting (manipulative movements of head and mouth parts to gather herbage into the mouth, and severance of the herbage), chewing and swallowing. Not all the above behavioural components are mutually exclusive (Ungar, 1996).

When grazing intensively, a cow or a sheep will walk forward with its head held low and swinging from side to side in order to prospect a strip of sward 1-2 m wide, biting off mouthfuls of herbage at the rate of between 1 and 2 bites per second. The direction of travel is erratic but collection and ingestion of herbage are almost continuous. This pattern of behaviour is typical of the main grazing periods on uniform, leafy swards. On more heterogeneous swards or towards the end of a grazing period even on highly nutritious swards, animals tend to move faster, to hold their heads higher, and to snatch single bites or groups in passing. The rate of biting will be much slower, probably more than thirty to forty bites per minute. In some cases they may walk purposefully from one patch of herbage to another, but in other cases they appear to take intermittent mouthfuls of herbage in the course of an essentially random pattern of movement (Hodgson, 1990).

1.3.2.1 Intake and bite formation

Intake is a major determinant of animal production and, through its effect on sward structure, of plant production (Ungar, 1996). Better knowledge and understanding of intake should facilitate better management. The rate of intake and the quality of herbage selected by grazing animals are the key variables that the study of intake seeks to understand. They are both notoriously difficult to measure.

The bite is the fundamental unit of intake. Biting, or the taking of a bite, is defined here as the series of head and mouth-part movements that precede and include the severance and bringing into the mouth of herbage. The bite is the herbage thus ingested. A bite can be viewed as having an effective volume. This is not the volume of the buccal cavity but rather the equivalent volume of sward in its natural spatial arrangement that is occupied by the herbage ingested in a bite (Ungar, 1996). Bite weight is the product of the bite volume and the bulk density of herbage where the bite was removed (Hodgson, 1985).

The dimensions of a bite can be summarized in terms of bite area and bite depth, even though the true shape of the sward volume swept or actually removed in the course of a bite may be more complex. Bite area is the total area of plant structural units grazed to any extent divided by the number of bites taken. Bite depth is the difference between the initial and mean residual height of the same plant structural units (Ungar, 1996).

Bite depth is primarily a function of sward height, but there is a negative interaction with bulk density (Ungar, 1996). Wade *et al.* (1989) found that bite depth of cattle operated on a constant fraction basis, averaging 0.34 of initial extended tiller height over the height range 12-39 cm. A decline in bite depth with increasing bulk density was found for sheep in the microsward study of Black and Kenney (1984). In the microsward study of Burlison *et al.* (1991) linear regression of bite depth on initial sward height (of range 6 to 55 cm) showed that sheep removed 37% of sward height above 2.7 cm. Bite area ranged from 9 to 36 cm^2, but variance in bite area was not explained well by measured features of the sward. Maximum bite weight was 326 mg DM. In the microsward study of Illius *et al.* (1992) on pure ryegrass swards, sheep removed 71% of sward height above 2.9 cm, assuming minimal depletion. In a field experiment, Milne *et al.* (1982a) determined the relationship between initial sward height and grazing depth in sheep. Based on their regression equation, sheep removed a constant one-third of the sward height above 2.4 cm. Data given by Curll and Wilkins (1982) in a study of the frequency and severity of defoliation of grass and clover plant units by sheep yields a curvilinear relationship between sward height and grazing depth, and a proportion removed that declined from 60 to 45% with increasing sward height.

Intake can be defined as the product of mean bite weight, the mean rate of biting during active grazing bouts and the active grazing time (Spedding *et al.*, 1966; Allden and Whittaker, 1970; Chacon, *et al.*, 1976). Intake rate is the ratio of bite weight to the time required to take a bite (Ungar, 1996). Bite size has the greatest influence on intake, with rate of biting and grazing time being compensatory variables (Forbes, 1988). Structure of the sward canopy is expected to influence bite size and potentially rate of biting directly (Hodgson, 1982).

1.3.3 Application of plant fracture mechanics to grazing strategy

There is very little work being conducted on biomechanical properties from the herbivore's viewpoint.

During prehension of grasses, tensile strength is important (Evans, 1967a; Henry *et al.*, 1996; Vincent 1990), whereas shear strength may be important during chewing (Mackinnon *et al.*, 1988; Hongo *et al.*, 2007).

The interest in relating the tensile properties of plants to aspects of grazing behaviour, particularly prehension, becomes popular (Illius *et al.*, 1995; Tharmaraj, 2000; Wright and Illius, 1995), 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 (chew) in the mouth (Griffiths and Gordon, 2003).

While herbage biomechanical properties may integrate many sward canopy characteristics in influencing the grazing process of animals, information on the effect of biomechanical properties of swards on the prehensile process and the resultant intake and diet quality of grazing ruminants is deficient.

The force that grazing animals exert in procuring a bite has received little attention despite the clear linkages with herbage intake. This probably reflects the difficulties associated with quantification of bite force.

A number of different studies have shown inverse correlation between the strength of grass and 'palatability' (e.g. Theron and Booysen, 1966) so that the weaker grass is, the more the animal will eat.

Summit force hypothesis

Grazing animals must expend energy in order to sever and chew herbage. The amount of energy expended is a function of the mechanical properties of the plant material, which vary considerably between plant parts and species (Wright and Illius, 1995). It has been suggested that the force required to sever a bite may be a factor determining bite weight (Hodgson, 1985). This force would be expected to be related to the cross-sectional area of herbage material along the line of bite severance and hence to bite area. Bite depth *per se* would not be expected to influence the force required to sever a bite, although it may have an indirect effect if there is sward structural differentiation in the vertical plane. Hendricksen and Minson (1980) found that the shear load required breaking stems of *Lablab purpureus* increased greatly with distance from the shoot apex. According to the summit force hypothesis, there is a limit to the force animals exert to sever the herbage encompassed within the bite area. Once this limit is reached, animals should respond to further increases in sward density or strength of the herbage by reducing bite area to maintain a constant maximum force of severance. The microsward study of Hughes *et al.* (1991) with sheep was the first attempt to measure the force exerted by a grazing ruminant directly. It did not yield supporting evidence for the above hypothesis. Illius *et al.* (1995) also suggested that the biomechanical properties of plants determine the effort animals expend to harvest and digest herbage particularly in relation to chewing process. In the microsward study of Laca *et al.* (1992a) with cattle, which used a force plate, it was found that bite area decreases with sward bulk density, as discussed earlier, but the force exerted in bite severance did not appear to reach maximum or constant value. However, in an experiment designed specifically to test the summit force hypothesis, bite area was lower on the species with higher tensile strength of leaf blades at a given bulk density (Laca *et al.*, 1993). A study by Benvenutti *et al.* (2008) confirmed that the summit bite force hypothesis applied for tropical swards that have greater grazing resistance than temperate swards.

1.3.3.1 Newton's laws of motion

The first law. In the absense of external forces (animal exertion etc.) when viewed from an inertial reference frame, a plant body at rest remains at rest and a plant body in motion continues in motion with a constant velocity. In simpler terms, we can say that when no force acts on a plant body, the acceleration of the plant body is zero.

The second law. When viewed from an inertial reference frame, the acceleration of an object is directly proportional to the net force acting on it and inversely proportional to its mass.

The third law. If two objects (animal and plant) interact, the force F_{12} exerted by object 1 (an animal) on object 2 (plant body) is equal in magnitude and opposite in direction to the force F_{21} exerted by object 2 on object 1. $F_{12} = -F_{21}$. Newton's third law is equivalent to stating that forces always occur in pairs, or that a single isolated force cannot exist. The force that an animal exerts on plant body can be called the action force and the force of a plant body on animal the reaction force. In reality, either forces can be labeled the action or reaction force. The action force is equal in magnitude to the reaction force and opposite in direction. In all cases, the action and reaction forces act on different objects and must be of the same type (Serway, 1982).

1.3.3.2 Biting impulse

During the grazing, the biting force exerted by animal is not constant but changing with time. Therefore, maximum biting force or a biting force at a certain time point is not appropriate to understand biting effort or biting energy spent by animal. It can also be expected that bites of a longer duration would utilize more muscular effort than those bites that result in rapid fracture (Griffiths, 2006).

Study of biting impulse is an important new approach in grazing study. A measure of the degree to which an external force changes the momentum of an object is called impulse. Therefore, it is necessary to know only the momentum change, which is determined by the impulse. The relation between momentum and impulse has the advantage of eliminating the need for a detailed knowledge of how the forces change with time (Serway, 1982). In her review, Griffiths (2006) termed the same concept as "bite effort" suggesting to use the integral of force over time to measure.

The concept of impulse is generally most useful when the forces are large but act only for a short period.

1.3.4 Selective grazing

Grazing ruminants face complex decisions in searching for and harvesting adequate forage to meet their energy requirements for survival, growth, and reproduction. They exploit the heterogeneity of feed resources through selective grazing, often choosing a diet that is of better quality than the average vegtation on offer (Jamieson and Hodgson, 1979; Prache *et al.*, 1997).

The grazer seeks to consume nutrients by selecting a community within the grazing landscape, and ultimately within various tissues of the individual plant (Coleman *et al.*, 1989). The composition of diet is often very different from that on offer. Selection is most intense when food is abundant and varied (Leigh and Mulham, 1966a, b), and may only be slight when swards are simple (Davis, 1964; Arnold *et al.*, 1966; Milne *et al.*, 1982a)

Generally, selectivity is divided into two parts: the desire or drive to select, and the opportunity or ability to select under field conditions (Hodgson, 1979). Diet selection is a stimulus response behaviour (Booth, 1990) of the grazing animal that is the result of three factors: (1) animal preference, (2) forage palatability and (3) forage availability. It is evident that differences in selectivity occur, both among various types of vegetation and among grazer species. For instance, diets of grazing animals almost always contain a higher leaf-to-stem ratio and a higher live-to-dead ratio than the average of the vegetation on offer (Chacon and Stobbs, 1976; Arnold, 1981). The selected material usually contains more nitrogen, phosphate and gross energy, but less "fibre" (Arnold, 1987). It is recognized that whatever the basis, selective grazing almost invariably results in some improvement in nutrient content of the diet (Arnold, 1964).

Selection may occur because animals prefer certain material or merely because that material is more easily grazed. It is therefore important to examine the basis of selection. Similarly, it is important to know whether the selected diet is nutritionally more valuable and whether animals exhibit "nutritional wisdom" in diet selection (Arnold, 1987).

Grazing animals use the senses of sight, touch (lips and mouth), taste, and smell in selecting their diet. Sight is used primarily to orient the grazing animal to other animals and to its environment. Sheep and cattle can recognize conspicuous food plants by sight but use sight very little in selection of grazing (Arnold, 1966a).

Both Arnold (1966b) and Krueger *et al.* (1974) have shown that touch, taste and smell are used in selective grazing, but that taste is the most important sense. Smell is less important. For example, Milne *et al.* (1982b) found that only in one of five cases did anosmic sheep select a diet different from that chosen by normal sheep.

There are differences in both preference and degree of selection among animal species (Arnold, 1981). A typical example is that sheep select diets higher in digestibility than cattle from similar swards (Jamieson and Hodgson, 1979). The reason may be attributed to differences in size and shape of the mouth and placement of the teeth, which give sheep a more precise prehending ability.

Grazing animals also exhibit selective patterns of spatial use about the landscape. In some environments, where necessary resources (water, shade, forage, minerals, escape topography or cover) are scarce, areas of use will be focused about these limiting elements. Many of the herding ungulates, however, repeatedly regraze certain areas and avoid other equally suitable portions of the landscape (Vavra and Ganskopp, 1998). It has been arguably demonstrated that with repeated use of specific areas, these animals maintain their forages in an earlier (softer) and more nutritious stage of phenology throughout the grazing season (McNaughton, 1984; Westoby, 1986).

1.4 The objective of the study

In grazing ruminants, animal performance depends on the daily nutrient intake which is a function of the time they spend grazing and the rate of nutrient intake (Gordon and Lascano, 1993). Grazing animals can compensate for a decreasing rate of nutrient intake by increasing grazing time, however, this occurs only up to a certain limit and once this limit is reached the rate of nutrient intake constrains daily nutrient intake thus animal performance. The rate of nutrient intake is the result of both diet quality and instantaneous intake rate which is a function of the time the animals spend per bite and bite mass (Allden and Whittaker, 1970). Plant biomechanical properties in the sward may interfere with the process of bite formation and affect bite dimensions and selectivity.

Animals try to gather the maximum amount of food with minimum effort (Vincent, 1982). Grazing animals tend to make a grazing choice, which maximizes the intake rate (Illius *et al.*, 1992), and they tend to choose plant parts, which can be eaten quickly and with ease (Kenney *et al.*, 1984; Hongo, 1998; O'Reagain, 1993). Herbivores typically remove only the uppermost parts of plants, which seems to be related to the different resistances of plant tissues to defoliation, imposed by their physical structure (Illius *et al*, 1995). Because grazing by ruminants is an action where break plant organs (Vincent, 1982; Wright and Vincent, 1996), it is important to involve plant fracture mechanics in studies of herbivory. Characteristics like though, strong or brittle leaves, which may be difficult for an herbivore to harvest, are often seen as defensive (Lucas *et al.*, 1991). Together, intake rate and digestibility provide a measurement of the 'quality' of the forage, in terms of animal productivity (Moore and Mott, 1973). Grasses, which are difficult to harvest, have low intake rates (Theron and Booysen, 1966; Martens and Booysen, 1968; Evans, 1967a; Nguyen *et al.*, 1982).

There are plenty of works that studied how sward canopy structure, through its linkage with herbage strength, influences the grazing behaviour and/or bite dimensions by grazers. Those studies mainly looked at the effect of vertical distribution of sward components such as leaf, pseudo-stem, and dead material etc. 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 strength of leaf were negatively correlated with preference.

Despite the advances that have been made in understanding forage intake, mechanistic explanations for diet choice and observed behaviour remain scarce. The mechanistic relationships between animal and plant mechanical properties, particularly of contrasting body size, are not well understood. The force that grazing animals exert in taking a bite has been studied little despite the clear linkages with herbage intake. This probably reflects the difficulties associated with quantification of bite force.

The objective of this study is to clarify special feature of biomechanical properties of herbage grasses and their influence on animal grazing behaviour and analyze the three-directional biting forces and biting impulse associated. We hypothesized that the higher intake by animal would be positively related to the ease of harvest grass leaves or to lower leaf strength.

Two parts of experimentation were carried out. In experimentation part one, biomechanical properties of herbage grasses were examined, while in experimentation part two, grazing trials were conducted to measure biting force and intake parameters by animal. We aimed to answer following questions:

In experimentation part one: How do biomechanical properties of leaves vary across plant species? Is there seasonal variation in plant physical properties? What does contribute plant biomechanical properties?

In experimentation part two: How do grazers behave in response to the variation in grass physical properties? Do animals use grazing strategy to overcome physical constraints? What are these strategies?

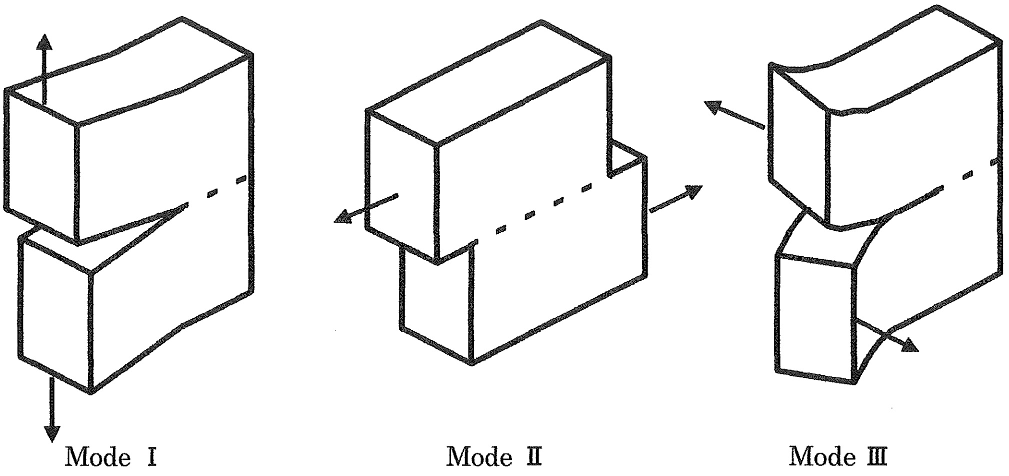

Fig. 1.1 The three modes of fracture (Vincent, 1990). Mode Ⅰ. Tension; Mode Ⅱ. Edge-sliding, or in-plane shear; Mode Ⅲ. Tearing, or out-of-plane shear (scissors cut).

Chapter 2

GENERAL METHODOLOGY

2.1 Measurements of plant biomechanical properties

Bending, tensile and shearing tests were conducted for determination of biomechanical properties of plant materials. In order to account for the mechanical energy budget within the material, there should be no elastic strain energy remaining in the test piece after fracture has occurred, and the test machine should not store elastic strain energy. The propagation of the crack across the test piece should be stable and slow (Atkins & Mai, 1985). This allows proper energy budgeting and the calculation of the energy used in fracture by the work-area method (Gurney & Hunt, 1967).

Bending test

The micro load of bending strength was detected with a scale in 0.1 gram using the original bending test machine (Fig. 2.1). A segment of plant material, which was supported between two stainless steel rods at both sides of an aluminum frame (Fig. 2.2), was moved downward in a horizontal position at a rate of 10 mm/min. The centre of the specimen made contact with the upper end of acrylic resin plate, which was connected with 0.5 N loadcell fixed on a base plate. The length of specimen 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 monitored using 50-mm displacement transducer (NEC San-ei; 9E08-D3). 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 force-time data in the memory card using the memory hicorder (Hioki Co.; 8808 Type) at a rate of 6.25 ms interval.

Usually, the bending moment capacity is defined as the maximum bending moment that can be sustained by the lamina. The internal moment under three-point bending is proportional to the applied load (Roark and Young, 1975). The maximum bending stress is usually obtained to divide the bending moment capacity by the sectional modulus. From the saved data in a computer, a graph of force versus deflection length was drawn. Bending moment *(S)* was given by the expression (Goodman and Ennos, 1997):

$S = F_{max} L 4^{-1}$

where F_{max} is the maximum bending force and L is the span distance between two supports.

The engineering theory of bending is based on the following assumptions (Roark, 1965): the beam is of homogeneous material, the beam is straight, and the cross section is uniform. However, the morphology of cross section in the grass leaf is very variable as shown in Fig. 3.1.1. In this study, the maximum bending stress was obtained by dividing the maximum bending moment by the cross-sectional area.

The extent to which the load capability exceeds the actual (working) load is called the factor of safety (Niklas *et al.*, 1999). The factor of safety for leaves was calculated as the breaking load (in g) divided by the leaf distal (dorsal) fresh weight (in g). Distal fresh matter weight is total weight from a point measuring bending strength to the tip of leaf blade (Fig. 2.3).

Tensile test

The breaking force of plant material segments in tension 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 were seized with original jaw clamps (Fig. 2.4). The upper clamp was fixed and connected with a loadcell and the lower clamp was moved downward at 10 mm/min for a low rate of deformation (Vincent, 1992). The initial length of samples between the two clamps in the test machine was 27 mm. The tensile force was recorded using the same amplifier and recorder as for the bending force. A graph of applied force versus deflection was produced from the saved data. The tensile stress is the breaking strength normalized with respect to the cross-sectional area.

Shearing test

Shearing breakdown occurs when two opposing parallel forces cause fracture at 90-degree angle to the length of material. Shearing strength was measured using a pair of the scissors with sharp stainless blades (Plus Co., No.135). The principle structure was the same as the previous reports (Pereira *et al.*, 1997; Lucas and Pereira, 1990; Vincent, 1992). 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 attached to the affixed support and connected to with a 10 N loadcell (Fig. 2.5). A leaf blade length about 50 mm in length was used in the test. Before each measurement, the surface of blades was rubbed with a swab including a lubricant oil to reduce the friction (Vincent, 1992). The travel rate of the intersection point of the two blades was 20 mm/min.

In a force/displacement curve of shearing strength, mean shearing strength was obtained by averaging of all shearing data. The area under the force-displacement curve was calculated, which represents the specific energy of fracture or toughness of the material (Atkins and Mai, 1985). In each test, two measurements were carried out: cutting of the specimen and an empty pass. The work done in the empty pass was deducted from the work done in the sample pass to give the net energy needed to cut the specimen (Pereira *et al.*, 1997). Shearing toughness was derived by dividing the total energy to fracture by the cross-sectional area of a leaf blade.

Measurement of cross-sectional areas of plant material

After measuring biomechanical properties of leaves, the fractions of leaf blades were immediately stored in water for further investigation. For a measurement of cross-sectional area, leaf blades were sliced 3mm length using a razor blade and were vertically kept in touch with a side wall of a plastic block. Cross section of the leaf segment was photographed under a stereo-microscope (Nikon; SMZ-U) and the pictures were digitally saved in a memory card (smart media). Each picture was projected onto a monitor screen at a magnification of about 50X. The contour line of cross-section was delineated with a cursor on a monitor screen using commercial software of computer graphics (Photo studio, Arcsoft Japan). The area inside the contour line was calculated using commercial software (Lia32, Nagoya University). Plant density was calculated by dividing DM weight of leaf blade of 10cm in length by volume (cross-sectional area x 10 cm in length).

2.2 Artificial sward board

The same sward board previously used by Hongo *et al.* (2004) was used for artificial construction of swards. The arrangement of the artificial sward board and three-directional loadcell were illustrated in Fig. 2.6. When sheep grazed grass leaves, loadcell responded to the prehension of bites. Electrical signals from loadcell were sent to a dynamic strain-gauge amplifier. Each amplified signal of the three-directional forces from loadcell was digitally recorded in a memory card (smart media) at 0.006-second interval as strain-time data using memory hicorder (HiokiCo.; 8860 Type) with 16 channels. One bite was distinguished on the trace by zero force for at least 0.2 sec between adjacent peaks. This definition was decided from the observation of the foraging behaviour of animals. Sequent peaks less than 0.2 sec apart were included into one bite. The number of bites was measured from discrete peaks.

2.3 Grazing trials

At a grazing trial (Fig. 2.7), animals were led with a halter and rope up to the sward board. The duration of time in building the swards for each grazing trial was about less than 5 min. During this period, animals were constrained with a rope.

When most of the leaves were eaten, the animals were removed. After each grazing trial, a clump of leaves was removed from a loadcell. The clump weight of leaves including an iron bolt was separately measured before and after each grazing trial. Residual lengths of all leaves were individually measured, and bite depth, the average depth of insertion of the mouth into sward canopy, was calculated from the original length of 10 cm. Sub-samples of about 100 g fresh leaves were dried in an oven at 70^{0}C 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 grazing time.

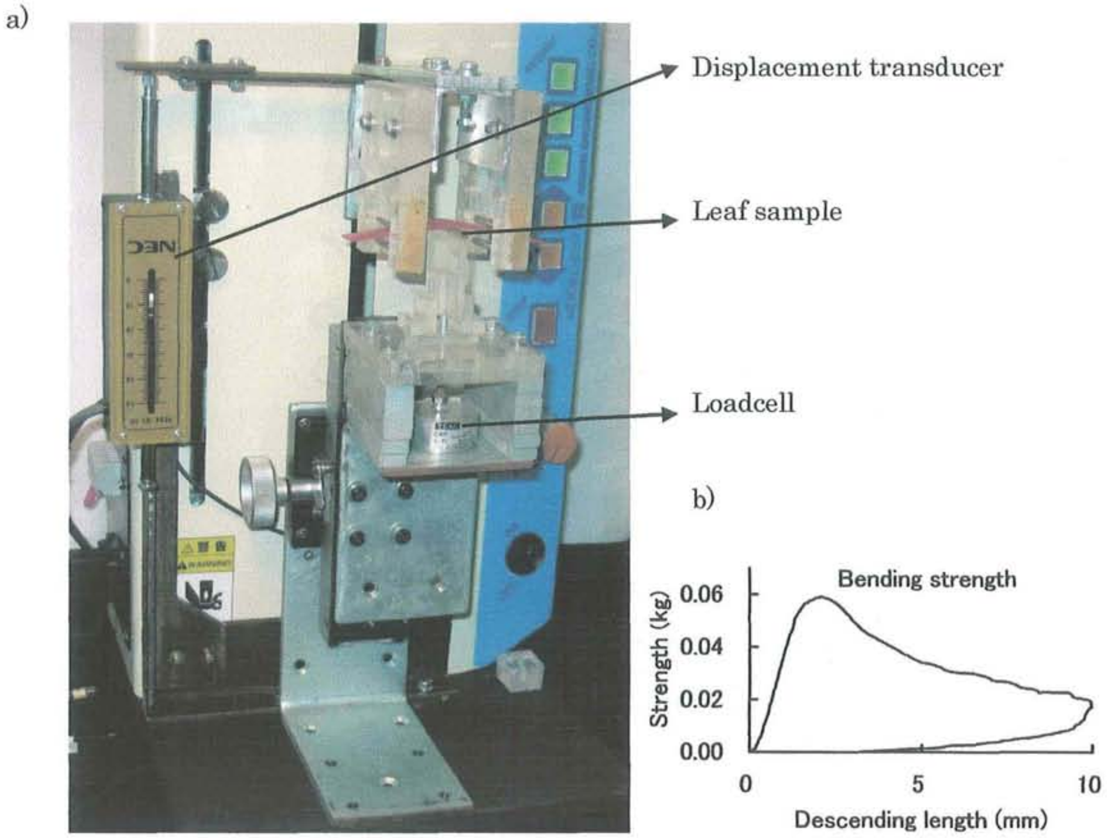

Fig. 2.1 The morphology of three-point bending test. Outline of a) bending test machine and b) obtained result. The leaf sample was supported at both sides between two stainless steel pipes, which got down. The load was applied in the centre of the span.

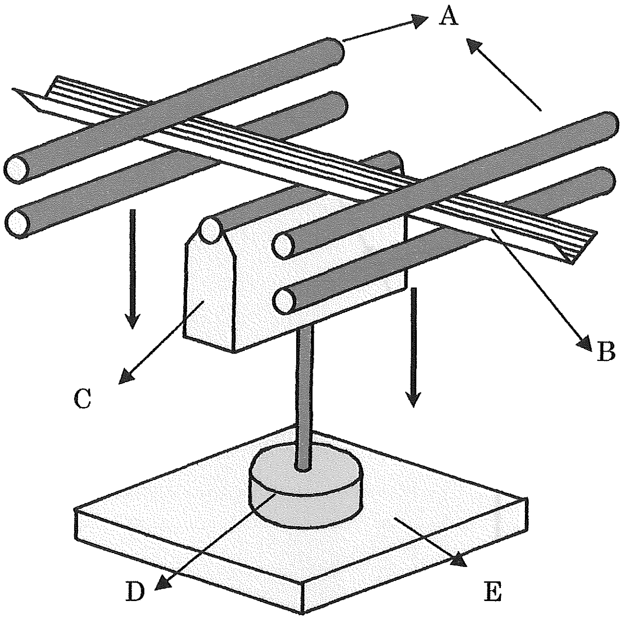

Fig. 2.2 Diagram of bending test machine. A grass leaf was supported at both sides between two stainless steel pipes in 3 mm diameter, which were inserted into a plastic frame (not shown), and was lowered at a rate of 10 mm/min. The span of specimen was 40 mm and the maximum deflection was 10 mm. A: Stainless steel pipes, B: Leaf sample, C: Iron probe of 1mm thickness connected with stainless steel pipe, D: 0.5 N loadcell, and E: Base plate.

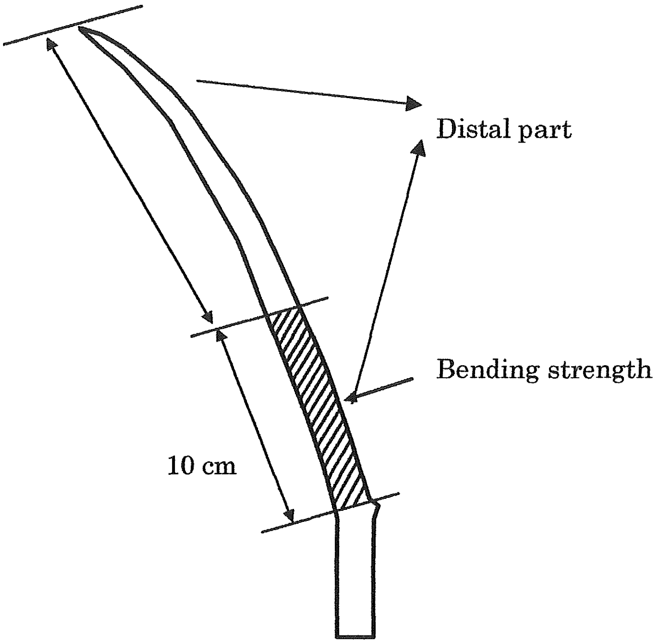

Fig. 2.3 A sampling site within a grass shoot for calculation of safety factor (SF):
Safety factor = Bending strength (g) /Dorsal fresh weight (g)

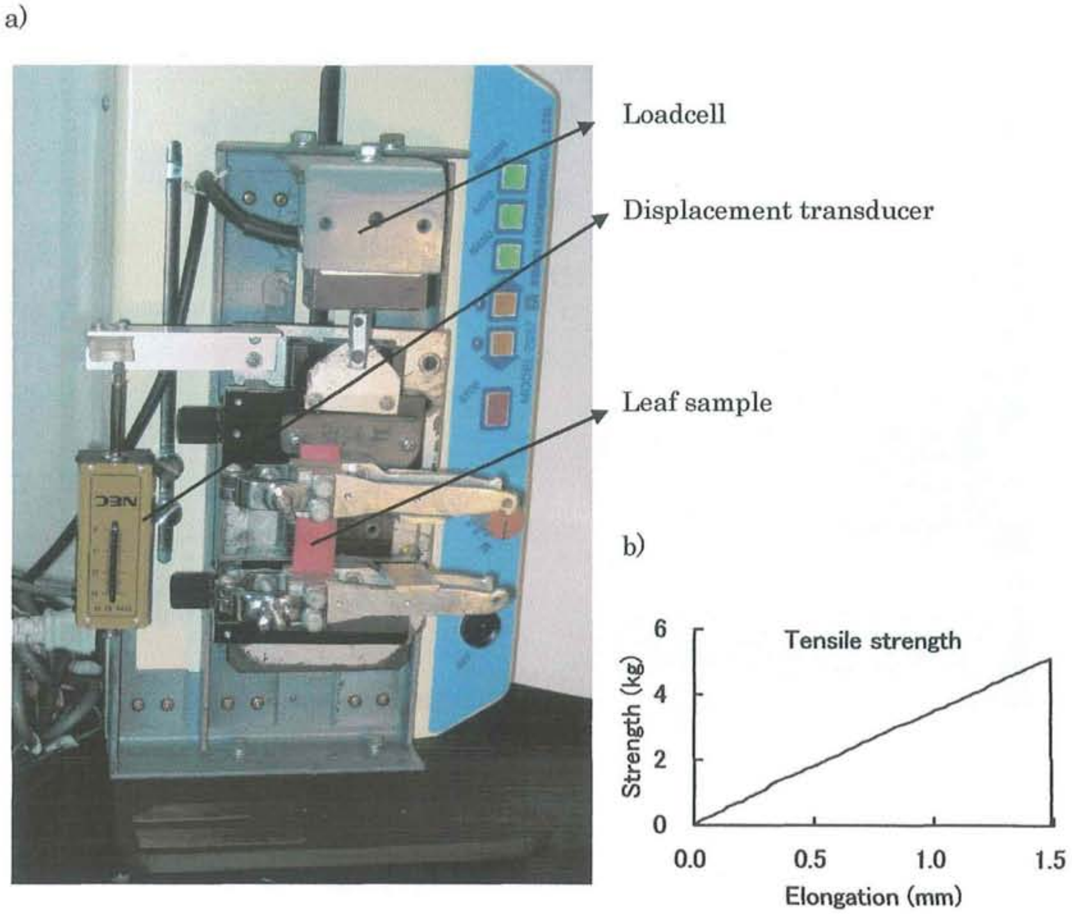

Fig. 2.4 The morphology of tensile test. Outline of a) tensile test machine and b) obtained result. Both ends of a leaf were seized with the original jaw clamps. One clamp was connected with a loadcell and the other clamp was moved downward.

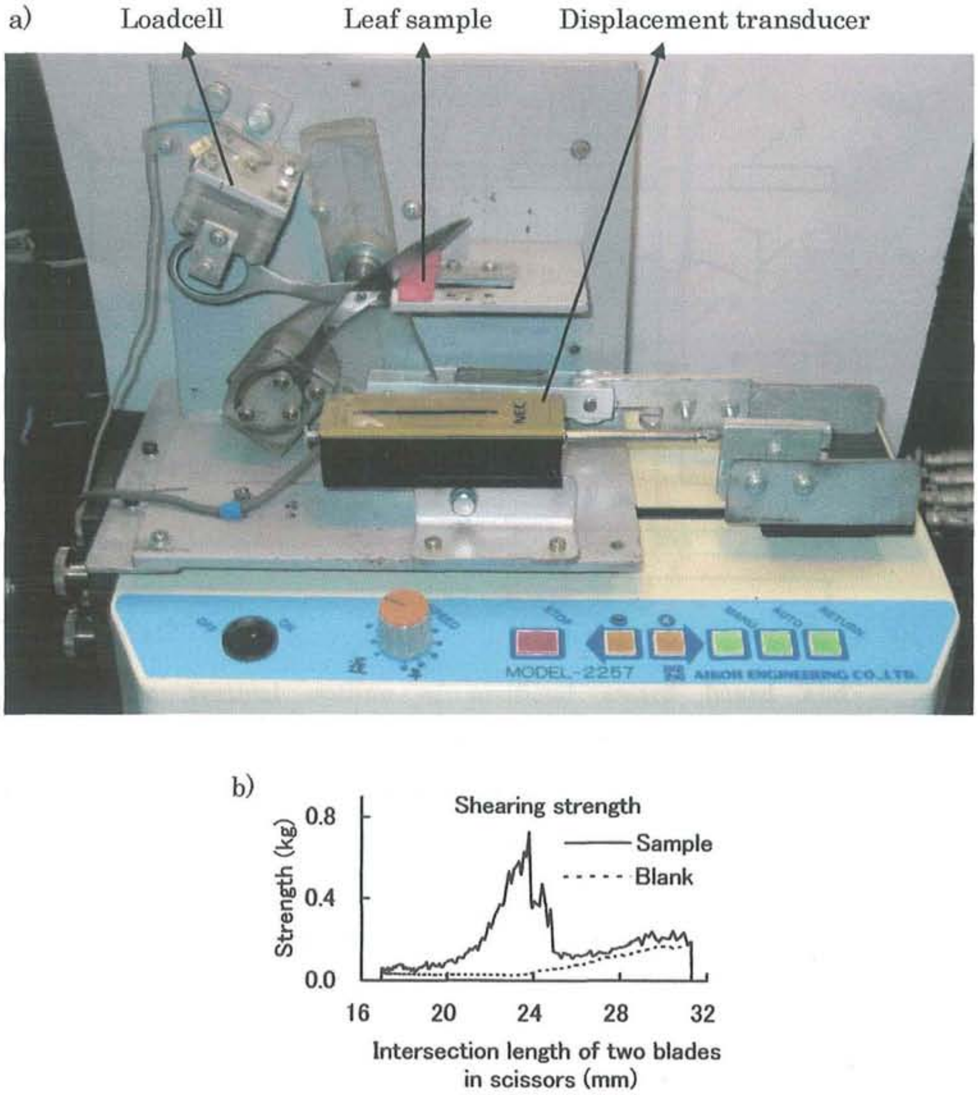

Fig. 2.5 The morphology of shearing test. Outline of a) shearing test machine and b) obtained result. The leaf sample was supported on an iron plate. The upper blade of a scissors got down and the lower blade created a load. In each test, two passes were made; cutting of a leaf sample following by an empty pass.

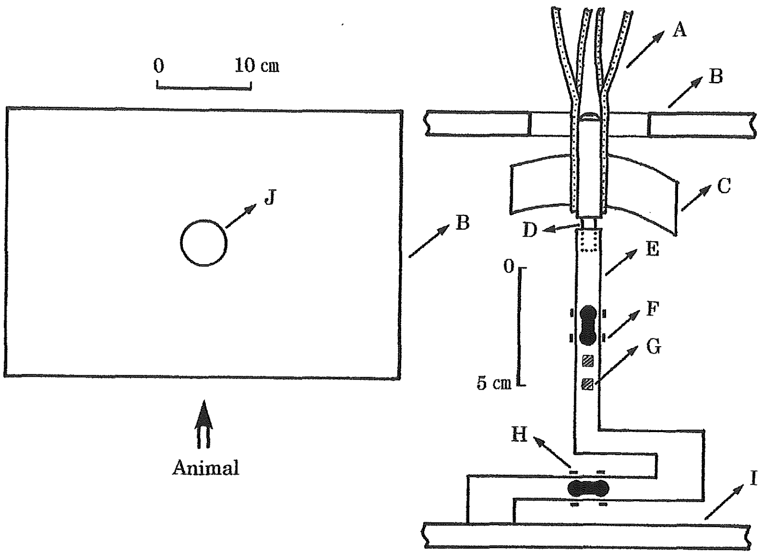

Fig. 2.6 The vertical outline of artificial sward board and three-directional loadcell. A – Grass leaves; B – Wooden board; C – Cotton adhesive tape; D – 6-mm iron bolt coated with rubber; E – Aluminum square bar of 12 mm width; F – Strain gauge for sideward force; G – Strain gauge for backward/forward force; H - Strain gauge for vertical force; I – Iron plate; J – Hole of 5 cm in diameter.

Fig. 2.7 A grazing trial.