Copyright is owned by the Author of the thesis. Permission is given for a copy to be downloaded by an individual for the purpose of research and private study only. The thesis may not be reproduced elsewhere without the permission of the Author.

THE EFFECTS OF LEAF SHEAR BREAKING LOAD ON THE FEEDING VALUE OF PERENNIAL RYEGRASS FOR SHEEP

A thesis presented in partial fulfilment of
the requirements for the degree of
Doctor of Philosophy
in Animal Science
at Massey University,
Palmerston North,
New Zealand

TATSUSHI INOUÉ

Preface

The contents of this thesis represent original work conducted by the author under the supervision of Dr Ian Brookes and Professor Tom Barry of Department of Animal Science, Massey University and Dr Andrew John of Applied Biotechnology Division, DSIR and Dr Warren Hunt of Grasslands Division, DSIR.

Abstract

Inoué, T., 1992. The Effects of Leaf Shear Breaking Load on the Feeding Value of Perennial Ryegrass for Sheep. 194pp.

Reducing physical resistance has been thought to be a key factor to increase efficiency of masticatory breakdown of forage, which may lead to faster rumen fractional outflow rates (FOR) and consequently to increased voluntary feed intake and hence improved feeding value (FV). Two selections of perennial ryegrass (PRG) were selected for low (LS) and high leaf shear breaking load (HS) based on the maximum load required to shear across the leaf, i.e. leaf shear breaking load (LSBL). The series of experiments were conducted to investigate the effects of LSBL on the FV of PRG for sheep.

LSBL, morphological and anatomical parameters were measured on the LS and HS PRG selections grown under the optimum climatic conditions. LSBL for the LS PRG selection was approximately 41 % lower the HS PRG selection. However, the LS selection had shorter leaf lengths, narrower leaf widths and narrower leaf cross-sectional area (CSA) than the HS selection. Therefore, in leaf shear strength (LSS), the LS selection was estimated to be approximately 27 % less resistant to shear than the HS selection per unit of CSA. The lower LSS in the LS selection is due to the lower concentration of sclerenchyma tissues in leaf CSA compared with the HS selection. However, the differences in the total shear load required to breakdown a unit dry weight of leaves to 1 x 1 mm particle size, namely, leaf index of masticatory load (IML) between the selections were influenced by the differences in morphological characteristics of leaves between the two PRG selections.

Comparisons were made between the LS and HS PRG selections in the efficiency of mastication by sheep on particle breakdown. There were no major effects of reduced LSBL in PRG on the efficiency of mastication during eating and during

rumination. Although the LS PRG selection was approximately 29 % lower in LSBL than the HS PRG selection, the difference for the two PRG selections in IML was almost nil.

Effects of LSBL in PRG on rumen fractional outflow rate (FOR) and apparent digestibilities were investigated in sheep fed at restricted feed intake levels. There were no effects of reduced LSBL on FOR, although the LS PRG selection was approximately 39 and 12 % lower than the HS PRG selection in LSBL and IML, respectively. The digestibility of the cellulose fractions was approximately 16 % lower in the LS PRG selection than the HS PRG selection. The leaf morphology in PRG may affect the efficiency of fibre digestibility.

Two field trials were conducted to test the hypothesis that LSBL in PRG improves FOR and leads to higher voluntary feed intake, and hence achieves improved live weight gain and wool production, namely FV. Although the LS PRG selection had 25-30 % lower LSBL than the HS PRG selection, live weight gain and wool production of sheep were not improved by reduced LSBL. FOR in sheep showed no indications of difference and voluntary feed intake was similar between the animals grazing the LS and HS PRG selections. The lack of difference in IML between the LS and HS PRG selection can be considered as a main reason for this. The hypothesis, that reduced LSBL in PRG would improve its FV, was therefore rejected.

In conclusion, there were no major effects of reduced LSBL in PRG on efficiency of masticatory particle breakdown, and consequently, FOR, feed intake and hence FV in sheep. This is due to the lack of selection effect of PRG in IML. IML is a determining factor for the efficiency of mastication both during eating and rumination. The selection of PRG for a lower IML will, therefore, be necessary in order to increase efficiency of masticatory particle breakdown, FOR and hence FV of PRG.

Acknowledgements

I want to express my sincere appreciation and gratefulness to my supervisors, Dr Ian Brookes, Professor Tom Barry of Department of Animal Science and Dr Andrew John and Dr Warren Hunt of DSIR for their enthusiastic guidance, preparation of this manuscript and assistance with field trials (even at two o'clock in the morning).

I want to thank Professor John Hodgson of Department of Agronomy, Dr Cam Reid of Department of Physiology and Anatomy, Veterinary Sciences and Dr Sydney Easton of DSIR for their valuable advice.

I also like to thank Dr Ian Gordon of Department of Agronomy, Dr Dorian Garrick and Mr Carlos Sosa-Ferreyra of Department of Animal Science for their excellent statistical guidance.

My special thanks are due to Professor Koji Toyokawa a visiting professor from, my home country, Japan for his help during his stay at Massey University.

My special thanks are extended to DSIR, Mr Barry Parlane of Animal Physiology Unit, Mr Tim Harvey, Mr Phil Whitehead and Mr Mike Hogan of Sheep and Beef Cattle Research Unit for providing the facilities, experimental animals and help with the experiments.

I was fortunate to have excellent technical support in the field trials from Ms Jenney Wickham, Ms Catriona Jenkinson, Mr Dean Burnham and the late Mr Merv Wycherley of Department of Animal Science and Mr John Kook, Mr Peter Millner and Mr Norman Dench of DSIR.

I want to gratefully thank to laboratory staff, Ms Rosemary Watson, Mrs Barbara Purchas, Mrs Kathy Morton, Mr Dave Hamilton of Department of Animal Science and Mr David Shelton of DSIR for their excellent service and technical assistance, Mr A. Craig and Mr D. Hopcroft of DSIR for providing excellent technical assistance with microscopy, Mr Leo Bolter of Department of Engineering and Mr K. Palmer of Victoria University for the marker analysis.

My special thanks are also extended to Mr Mike Conlon of Department of Food Technology and Mrs Elizabeth Halligan and Technical Services Group of Plant Physiology Division, DSIR for providing the research facilities and technical assistance.

Thanks are also due to Mrs Barbara Purchas and Ms Margaret Scott for proof-reading the manuscript.

I want to thank all the staff and postgraduate student in the Department of Animal Science for friendship, support and understanding which made my stay in New Zealand an enjoyable and memorable one.

I want to express my appreciation to my student colleagues, Françoise, Raymundo, Christine (MacArthur), Sunan, Warren, Min and, especially, Zheng Zhong for their help.

I acknowledge the personal financial support received from the New Zealand University Grants Committee Scholarship. This project was financially supported by the C. Alma Baker Trust, the Grant-in-aid from DSIR and the Massey University Research Fund.

I am particularly grateful to my friend, Sabine, for her support and encouragement.

Finally, I also want to specially thank my parents for their continued encouragement and support throughout my life.

Table of Contents

	Page
Pre	<i>eface</i> i
Abs	stractii
Ack	knowledgementsiv
Lis	t of tablesxvi
Lis	t of figuresxxiv
Lisi	t of Abbreviations xxviii
Inti	roduction1
Cha	apter One A Review of Factors Limiting the Feeding Value of Perennial Ryegrass
1.1	Introduction
1.2	The role of perennial ryegrass in the New Zealand pasture
	1.2.1 Agronomic characteristics of perennial ryegrass
	1.2.2 Animal production response to perennial ryegrass
	1.2.2.1 Definition of feeding value
	1.2.2.2 Feeding value of perennial ryegrass
	1.2.3 Conclusion
1.3	Factors limiting the feeding value of perennial ryegrass
	1.3.1 Factors limiting nutritive value of perennial ryegrass
1	1.3.1.1 Apparent digestibility of perennial ryegrass
•	1.3.1.2 Efficiency of utilisation of perennial ryegrass
	1.3.1.3 Conclusion
	1.3.2 Factors limiting intake of perennial ryegrass
	1.3.2.1 Non-nutritional factors
	1.3.2.1.1 Sward condition and prehending behaviour

		1.3.2.2	Nutritional factors	16
		1.3	.2.2.1 Metabolic factors	16
		1.3.	2.2.2 Physical factors	17
		1.3.2.3	Conclusion	. 17
	1.3.3	Digesta	passage from the rumen	19
		1.3.3.1	Physical reduction in particle size and microbial digestion	. 19
		1.3.	3.1.1 Chewing during eating	. 19
		1.3.	3.1.2 Chewing during rumination	. 20
		1.3.	3.1.3 Role of microbial attack in the rumen	. 23
		1.3.3.2	Passage through the reticulo-omasal orifice	. 23
		1.3.3.3	Conclusion	. 24
1.4	Atte	mpts to	improve feeding value of perennial ryegrass by	
	reduc	ing phys	ical resistance to breakdown	. 24
	1.4.1	Physica	al resistance of perennial ryegrass to fracture	. 24
		1.4.1.1	Anatomy of perennial ryegrass	. 24
		1.4.1.2	Forces applied at fracture	. 28
		1.4.	1.2.1 Perennial ryegrass in tensile stress	. 31
		1.4.	1.2.2 Forces applied to the feed material during	
			mastication by ruminants	. 35
		1.4.	1.2.2.1 Masticatory movements of ruminants	. 35
		1.4.	1.2.2.2 Forces applying to the feed	
			material by teeth	. 37
		1.4.	1.2.3 Conclusion	. 37
	1.4.2	Contribu	ution of reduced leaf shear breaking load in perennial	
		ryegras	s towards improved intake and feeding value -	
		Backgro	ound studies	. 40
		1.4.2.1	Selection for low and high leaf shear breaking load	
			perennial ryegrass	. 40
ι		1.4.2.2	Rates of dry matter consumption, digestibilities and	
			liveweight gains of sheep grazing two perennial	
			ryegrass selections selected for low and high leaf	
			shear breaking load	. 43
		1.4.2.3	Conclusion	43

	1.4.3 Obje	ect1v	es of investigations in this thesis	46	
Chapter Two		Sh	Comparisons of Leaf Anatomy, Leaf Morphology and Leaf Shear Strength between Two Perennial Ryegrass Selections		
		36	elected for Low and High Leaf Shear Breaking Load		
2.1	Introduction	n		48	
2.2	Materials a	and	methods	48	
	2.2.1 Low	and	d high leaf shear breaking load perennial ryegrass		
	selec	ction	18	49	
	2.2.2 Expe	rim	ental design	49	
	2.2.2	2.1	Plant allocation	51	
	2.2.2	2.2	Identification and allocation of leaves	51	
	2.2.3 Colle	ectio	on of leaves	51	
	2.2.4 Mea	.sure	ements of leaf morphology	52	
	2.2.5 Dete	rmi	nation of leaf shear breaking load	52	
	2.2.5	5.1	The position of shear on the leaf	52	
	2.2.5	5.2	Shear apparatus	52	
	2.2.5	5.3	Determination of leaf shear breaking load	53	
	2.2.6 Estin	mat	ion of leaf cross-sectional area and anatomical		
	exam	nina	tion of leaf cross-section	53	
	2.2.6	5.1	Collection of leaf cross-sections	54	
	2.2.6	5.2	Preparation of specimens for microscopy	54	
	2.2.6	5.3	Microscope examination	54	
	2.2.6	.4	Determination of leaf cross-sectional area	55	
	2.2.6	.5	Mathematical estimation of leaf cross-sectional area		
t			from width	55	
1	2.2.7 Dete	rmi	nation of leaf shear strength	55	
	2.2.8 Cher	nica	ıl analyses	55	
	2.2.9 Stati	istic	al analyses	56	
2.3	Results			56	
	2.3.1 Cros	s-se	ections of the leaves of the low and high leaf shear		

	bı	eaking load perennial ryegrass selections	56
	2.3.2 M	orphology of the leaves of the low and high leaf shear	
	br	eaking load perennial ryegrass selections	58
	2.3.3 SI	near breaking loads and shear strengths of the leaves of the	
	lo	w and high leaf shear breaking load perennial ryegrass	
	se	lections	63
	2.3.4 C	oncentrations of dry matter, organic matter, lignin and cell-	
	W	all constituents in the leaves of the low and high shear	
	br	eaking load perennial ryegrass selections	66
2.4	Discuss	ion	70
	2.4.1 E	fects of selection	70
	2.4.2 Le	af anatomy	70
	2.4.3 Ef	fects of leaf emergence	71
	2.4.4 E	fects of aging	73
	2.4.5 In	teraction between leaf shear breaking load and leaf morphology.	74
2.5	Conclus	ion	77
Cha	pter Thre	Perennial Ryegrass upon Particle Breakdown du	
		Mastication in Sheep	
3.1	Introduc		
3.2		tion	78
۷.۷		tions and methods	
۷,۷	Materia		
J.L	Material	s and methods	78
J. <u>L</u>	Materia: 3.2.1 Lo	s and methodsow and high leaf shear breaking load perennial ryegrass	78 79
J.L	Material 3.2.1 Lo se 3.2.2 Ex	s and methodsow and high leaf shear breaking load perennial ryegrass lections	78 79 79
J.L	Material 3.2.1 Lo se 3.2.2 Ex 3.2.3 Ex	s and methods	78 79 79 79
J.L	Material 3.2.1 Lo se 3.2.2 Ex 3.2.3 Ex 3.3.5	s and methods	78 79 79 79 79
J.L	Material 3.2.1 Lo se 3.2.2 Ex 3.2.3 Ex 3.3.3	s and methods ow and high leaf shear breaking load perennial ryegrass lections perimental animals perimental design 2.3.1 Adjustment period	78 79 79 79 79
J. L	Material 3.2.1 Lo se 3.2.2 Ex 3.2.3 Ex 3.3.3	s and methods ow and high leaf shear breaking load perennial ryegrass lections perimental animals perimental design 2.3.1 Adjustment period 2.3.2 Voluntary feeding period	78 79 79 79 79

			3.2.3.3.2 Trial 2: Efficiency of chewing during	
			rumination upon particle breakdown	81
	3.2.4	Record	ling of jaw movements	83
	3.2.5	Particle	size analyses of rumen contents	83
	3.2.6	Determ	nination of the index of masticatory load of leaves	84
		3.2.6.1	Measurements of leaf morphology	84
		3.2.6.2	Measurement of leaf shear breaking load and	
			determination of index of masticatory load	84
	3.2.7	Chemic	al analyses	85
	3.2.8	Statisti	cal analysis	85
3.3	Resu	lts		85
	3.3.1	Leaf m	orphology, leaf shear breaking loads and indices of	
		mastica	tory load of the low and high leaf shear breaking load	
		perenni	al ryegrass selections	. 85
	3.3.2	Trial 1		. 87
		3.3.2.1	Masticatory behaviour and efficiency of chewing in	
			wethers during eating the low and high breaking load	. 87
		3.3.2.2	Particle size distributions in the rumen contents	
			recovered from the wethers immediately after	
			ingesting the low and high leaf shear breaking load	
			perennial ryegrass selections	. 90
	3.3.3	Trial 2		. 90
		3.3.3.1	Rumen pool sizes of the wethers ruminating the low	
			and high breaking load perennial ryegrass selections	. 90
		3.3.3.2	Masticatory behaviour and efficiency of chewing in	
			wethers during ruminating the low and high breaking	
			load perennial ryegrass selections	. 93
		3.3.3.3	Particle size distributions in the rumen contents	
			recovered at 10:30 and 17:30 hours from the wethers	
			ruminating the low and high leaf shear breaking load	
			perennial ryegrass selections	. 93
3.4	Disc	ussion		. 96
	3 / 1	Effect (of reduced leaf shear breaking load on the index of	

	m	asticat	ory load of leaves	96
	3.4.2 Ef	fects	of reduced leaf shear breaking load on particle size	
	di	stribut	tion in the rumen contents	96
	3.4.3 In	fluenc	e of index of masticatory load on masticatory efficiency	, 97
	3.4.4 Pa	rticle	breakdown during rumination	98
3.5	Conclus	sion		100
	_	-		
Cha	pter Fou		he Effects of Reduced Leaf Shear Breaking I	
			erennial Ryegrass upon Rumen Digesta Outflow R	ate and
		\mathbf{A}	pparent Digestibility in Sheep	
4.1	Introduc	rtion		101
4.2			Methods	
7.2			d high leaf shear breaking load perennial ryegrass	101
			ns	102
			nental animals	
			nental design	
		•	Adjustment period	
			Voluntary feeding period	
			Trial period	
	т.		3.3.1 Determination of rumen digesta outflow rate	
			3.3.2 Determination of apparent digestibilities	
	424 D		ination of the index of masticatory load of leaves	
			Measurements of leaf morphology	
			Measurement of leaf shear breaking load of leaf	
			al analyses	
			cal analyses	
4.3				
			orphology, leaf shear breaking load, index of	
			tory load and chemical composition of the low and	
			ear breaking load perennial ryegrass selections	107
		•	pool size, rumen digesta fractional outflow rates.	

		rumen	digesta retention times and particle size distribution in	
		rumen	contents in wethers fed on the low and high leaf shear	
		breakin	g load perennial ryegrass selections	110
	4.3.3	Appare	nt digestibilities, concentrations of VFA and NH ₃ -N in	
		rumen	contents in wethers fed on the low and high shear	
		breakin	g load perennial ryegrass selections	110
4.4	Disci	ussion		117
4.5	Conc	clusion		118
Cha	pter F	ive T	he Effects of Reduced Leaf Breaking Load in Per	ennial
		F	Ryegrass upon Rumen Digesta Outflow Rates, Volu	ıntary
		F	eed Intake, Liveweight Gain and Wool Product	ion in
		(Grazing Sheep	
5.1	Introd	duction .		119
5.2	Mate	rials and	Methods	119
	5.2.1	Pasture		120
	5.2.2	Trial 1		120
		5.2.2.1	Determination of rumen digesta fractional outflow rates	120
		5.2.2.2	Measurements of live weight gain and wool	
			production in autumn-born lambs	121
		5.2	.2.2.1 Live weight gain	
			2.2.2 Wool production	
	5.2.3		<u>-</u>	
			Determination of rumen digesta fractional outflow rates	
			Measurements of live weight gain in ewe-hoggets	
			Measurement of voluntary organic matter intake in	
			ewe-hoggets and rumen-fistulated wethers	123
	5.2.4	Herbag	e analysis	
			Pasture mass	
			In vitro digestibility of herbage	
			Composition and in vitro digestibility of material	

		ingested by the sheep	128
	5.2.4	4 Determination of leaf shear breaking load and index	
		of masticatory load	128
	5.2.5 Chen	nical analyses	129
	5.2.5	1 Rumen contents	129
	5.2.5	2 Faeces	129
	5.2.5	.3 Herbage and oesophageal extrusa	130
	5.2.6 Stati	stical analyses	130
5.3	Results		130
	5.3.1 Trial	1	130
	5.3.1	.1 Pasture	130
	5.3.1	2 Live weight gain and wool production in autumn-	
		born lambs grazing the low and high leaf shear	
		breaking load perennial ryegrass selections	135
	5.3.1	3 Rumen pool size, digesta fractional outflow rates,	
		digesta mean retention times and particle size	
		distributions in rumen contents in wethers grazing	
		the low and high leaf shear breaking load perennial	
		ryegrass selections	135
	5.3.2 Trial	2	143
	5.3.2	.1 Pasture	143
	5.3.2	2 Live weight gain and voluntary organic matter intake	
		in ewe-hoggets grazing the low and high leaf shear	
		breaking load perennial ryegrass selections	143
	5.3.2	3 Rumen pool size, digesta fractional outflow rates,	
		digesta mean retention times and particle size	
		distributions in rumen contents in wethers grazing	
		the low and high leaf shear breaking load perennial	
١		ryegrass selections	152
5.4	Discussion		156
5.5	Conclusion		158

Chapter Six General Discussion and Conclusion

6.1	Introduction	on	160
6.2	Relations	hips between leaf shear breaking load and index of	
	masticator	ry load of leaf in perennial ryegrass	160
6.3	Limitation	of reducing leaf shear breaking load in perennial ryegrass	
	on improv	ring feeding value to sheep	162
6.4	Influence	of index of masticatory load on particle breakdown and	
	masticator	y behaviour in sheep	166
6.5	Direction	of further studies	167
6.6	Conclusio	on	168
	endix 2.1	Newcastle State University Phytotron Nutrient Solution	169
App	endix 2.2	Movements of the blade and position of the slot of a	
		Warner-Bratzler meat shear apparatus in shearing action	170
App	endix 2.3	An example of table of analysis of variance for fresh	
		weight of the leaves of the low and high shear breaking	
		load perennial ryegrass selections	171
App	endix 2.4	Concentrations of organic matter, lignin and cell-wall	
		constituents of the second-emerged, fourth-emerged	
		and sixth-emerged leaves of the low and high leaf shear	
		breaking load perennial ryegrass selections at	
		maturation, 10 days and 20 days after the maturation	172
App	endix 3.1	An example of a table of analysis of variance for the	
		proportion of particles larger than 1 mm in rumen	
		contents recovered from wethers immediately after	
		ingesting the low and high shear breaking load	
i		perennial ryegrass selections	173
App	endix 5.1	Portable marker infusion backpack set	174
		Portable marker infusion set in operation	175
App	endix 5.2	Diurnal pattern of total rumen pool and dry matter	
		rumen pool of rumen-fistulated wethers grazing	

	perennial ryegrass	176
Appendix 5.3	Preparation of Co(III)-EDTA	177
Appendix 5.4	Estimation of Cr release rate	178
References		179

List of Tables

	Page
Table 1.1	The relative feeding value of New Zealand pasture species
	under grazing conditions for young sheep (Ulyatt, 1970)6
Table 1.2	Composition, decline in apparent in vivo digestibility and
	utilisation of metabolisable energy (ME) of dried S23
	perennial ryegrass harvested at 4 stages of maturity and fed
	to sheep at maintenance level of intake (adapted from
	Waghorn <i>et al.</i> , 1987)8
Table 1.3	Data on the digestion of Ruanui perennial ryegrass and Huia
	white clover by sheep (Ulyatt, 1981)10
Table 1.4	The effect of chewing during eating (C.EAT) on feeding
	behaviour and particle size reduction in sheep (n=6) fed
	three fresh herbages and two chaffed hays (adapted from
	Ulyatt <i>et al.</i> , 1986)21
Table 1.5	Effect of chewing during rumination (C.RUM) on particle
	size distributions in sheep (n=6) fed three fresh herbages and
	two chaffed hays (adapted from Ulyatt et al., 1986)22
Table 1.6	Mean leaf strengths, sclerenchyma wall percentages and
	cellulose percentages of perennial, Ariki, Italian and Short-
	rotation ryegrass and mean liveweight gain of sheep
1	(adapted from Evans, 1964a, and Rae et al., 1964)32
Table 1.7	Young's modulus of tensile strength and volume-fraction of
	leaf of perennial ryegrass (adapted from Vincent 1982 and
	Betteridge <i>et al.</i> , 1986)34

Table 1.8	Mean leaf shear breaking load (LSBL) of parent plants (n=6)	
	selected for low (LS) and high (HS) leaf shear breaking load	
	at the time of selection (1984) and in January 1986, and of	
	the original population (adapted from MacKinnon et al.,	
	1988)	41
Table 1.9	Mean leaf shear breaking load (LSBL) of the progeny	
	population for low (LS) and high (HS) leaf shear breaking	
	load perennial ryegrass selections in December 1985	
	(n=120) and March 1986 (n=240) (adapted from Mackinnon	
	et al., 1988)	42
m 10 440		
Table 1.10	Means of rate of dry matter (DM) eaten and disappearance	
	in the rumen of sheep (n=6), of vegetative perennial ryegrass	
	(PRG) selected for low (LS) and high (HS) leaf shear	
	breaking load, and of white clover (adapted from	
	MacKinnon et al., 1988)	44
Table 1.11	Live weight gains of 8-month-old lambs grazing low (LS)	
	and high (HS) leaf shear breaking load perennial ryegrass	
	selections and means of leaf shear breaking load (LSBL) of	
	the two selections during the trial (adapted from Kolver, 1989)	15
	1909)	43
Гable 2.1	Means of anatomical measurements and proportions of	
	sclerenchyma and vascular tissue in the cross-sectional area	
	at the midway point along the leaves (n=11) of the low (LS)	
	and high (HS) leaf shear breaking load perennial ryegrass	
	selections	59
	/f	
Γable 2.2	Relationships between width and cross-sectional area at the	
	midway point along the leaves (n=11) of low (LS) and high	•
	(HS) leaf shear breaking load perennial ryegrass selections	60

Table 2.3	Least square means of length, widths at 1/4 (0.25L), 1/2
	(0.50L) and 3/4 (0.75L) of the leaf length from the position
	of the ligule to the apex of the leaf, and fresh weight of the
	leaves of the low (LS) (n=991) and high (HS) (n=998) leaf
	shear breaking load perennial ryegrass selections61
Table 2.4	Least square means of length, widths at 1/4 (0.25L), 1/2
	(0.50L) and 3/4 (0.75L) of the leaf length from the fresh
	weight (mg) position of the ligule to the apex of the leaf, and
	fresh weight of the second-emerged (2nd), fourth-emerged
	(4th) and sixth emerged (6th) leaves of the low (LS) (n=991)
	and high (HS) (n=998) leaf shear breaking load perennial
	ryegrass selections62
Table 2.5	Least square means of estimated cross-sectional area, shear
	breaking load and shear strength at the midway along the
	leaves of the low (LS) (n=117) and high (HS) (n=120) leaf
	shear breaking load perennial ryegrass selections64
Table 2.6	Least square means of estimated cross-sectional area, shear
	breaking load and shear strength at midway along the second
	emerged (2nd), fourth-emerged (4th) and sixth-emerged
	(6th) leaves of the low (LS) (n=117) and high (HS) (n=120)
	leaf shear breaking load perennial ryegrass selections65
Table 2.7	Concentrations (fresh %) of dry matter, organic matter,
	lignin, cellulose and hemi-cellulose in the leaves (n=12) of
	the low (LS) and high (HS) leaf shear breaking load
1	perennial ryegrass selections67
Table 2.8	Concentrations (fresh %) of dry matter, organic matter,
	lignin, cellulose and hemi-cellulose in the second-emerged
	(2nd), fourth- emerged (4th) and sixth-emerged (6th) leaves

	(n=12) of the low (LS) and high (HS) leaf shear breaking
	load perennial ryegrass selections68
Table 2.9	Concentrations (fresh %) of dry matter, organic matter,
	lignin, cellulose and hemi-cellulose in the second-emerged
	(2nd), fourth- emerged (4th) and sixth-emerged (6th) leaves
	(n=12) of the low (LS) and high (HS) leaf shear breaking
	load perennial ryegrass selections at maturation (M00) and
	at 10 days after the maturation69
Table 2.10	Length:dry weight ratio, and index of masticatory load
	(IML) of the leaves of the low (LS) (n=117) and high
	(n=120) leaf shear breaking load perennial ryegrass
	selections76
Table 3.1	Means of morphology, shear breaking load, index of
	masticatory load (IML), in vitro dry matter digestibility
	(IVDMD) and concentration of total nitrogen (N) of the
	leaves of the low (LS) and high (HS) leaf shear breaking
	load perennial ryegrass selections86
Table 3.2	Masticatory behaviour and index of efficiency of chewing
	(<c.eat>) in wethers (n=8) during eating the low (LS) and</c.eat>
	high (HS) shear breaking load perennial ryegrass for a
	period of 30 minutes88
Table 3.3	Rumen pool sizes at 10:30 and 17:30 hours and rate of dry
	matter disappearance in the wethers (n=8) ruminating low
1	(LS) and high (HS) leaf shear breaking load perennial
	ryegrass and their in vitro dry matter digestibilities
	(IVDMD) and concentrations of total nitrogen (N)92

Table 3.4	Masticatory behaviour and index of efficiency of chewing (<c.rum>) in wethers (n=8) during ruminating the low (LS) and high (HS) shear breaking load perennial ryegrass</c.rum>	
	for a period of 7 hours	94
Table 4.1	Means of morphology, shear breaking load and index of	
	masticatory load (IML) of the leaves of the low (LS) and	
	high (HS) leaf shear breaking load perennial ryegrass selections	108
T. 1.1. 4.2		
Table 4.2	Concentrations of dry matter, organic matter, total nitrogen	
	and cell-wall constituents of the low (LS) and high (HS) leaf	
	shear breaking load perennial ryegrass offered to the	100
	animals	109
Table 4.3	Total and dry matter rumen pool sizes in wethers (n=8) fed	
	on the low (LS) and high (HS) leaf shear breaking load	
	perennial ryegrass selections	112
Table 4.4	Rumen digesta fractional outflow rates (FOR) and rumen	
	digesta mean retention times (MRT) for liquid-phase and	
	particulate-phase in wethers (n=8) fed on the low (LS) and	
	high (HS) leaf shear breaking load perennial ryegrass	
	selections	113
Table 4.5	Apparent digestibilities (%) of dry matter, organic matter,	
	total nitrogen and cell-wall constituents in wethers (n=8) fed	
1	on the low (LS) and high (HS) leaf shear breaking load	
	perennial ryegrass selections	115
Table 4.6	Concentrations and proportions of volatile fatty acids (VFA)	
	and concentration of NH ₃ -N in the rumen fluid in	
	wethers (n=8) fed on the low (LS) and high (HS) leaf shear	

	breaking load perennial ryegrass selections
Table 5.1	The schematic presentation of the experimental design of Trial 1
Table 5.2	The schematic presentation of the experimental design of Trial 2
Table 5.3	Mean values of pasture mass (n=6), in vitro organic matter digestibility (IVOMD) (n=4), leaf shear breaking load (n=3), leaf length:dry weight ratio (n=3) and index of masticatory load of leaf (n=3) of low (LS) and high (HS) leaf shear breaking load perennial ryegrass selections on offer during Trial 1
Table 5.4	Mean values of composition and in vitro organic matter digestibility (IVOMD) of the oesophageal extrusa (n=7) of animals grazing the low (LS) and high (HS) leaf shear breaking load perennial ryegrass selections during Trial 1
Table 5.5	Mean values of live weight gain and total fleece wool growth of lambs (n=23) grazing the low (LS)and high (HS) leaf shear breaking load perennial ryegrass selections during Trial 1
Table 5.6	Rumen pool size, rumen digesta fractional outflow rate (FOR) and rumen digesta mean retention time (MRT) for liquid-phase and particulate-phase in wethers (n=11) grazing the low (LS) and high (HS) leaf shear breaking load perennial ryegrass selections
Table 5.7	Mean values of pasture mass (n=8), in vitro organic

	(n=3), leaf length: dry weight ratio (n=3) and index of	
	masticatory load of leaf (n=3) of the low (LS) and high (HS)	
	leaf shear breaking load perennial ryegrass selections on	
	offer during Trial 2	147
Table 5.8	Mean values of composition and in vitro organic matter	
	digestibility (IVOMD) of the oesophageal extrusa (n=4) of	
	the animals grazing the low (LS) and high (HS) leaf shear	
	breaking load perennial ryegrass selections during Trial 2	149
Table 5.9	Mean values of live weight gain and voluntary organic	
	matter intake (VOMI) of ewe-hoggets grazing the low (LS)	
	and high (HS) leaf shear breaking load perennial ryegrass	
	selections during Trial 2	151
Table 5.10	Rumen pool size, rumen digesta fractional outflow rate	
	(FOR) and rumen digesta mean retention time (MRT) for	
	liquid-phase and particulate-phase in wethers (n=8) grazing	
	the low (LS) and high (HS) leaf shear breaking load	
	perennial ryegrass selections	153
Table 5.11	Voluntary organic matter intake (VOMI) estimated	
	based the Cr faecal marker and Ru-Co dual-phase ruminal	
	marker of wethers (n=8) grazing the low (LS) and high (HS)	
	leaf shear breaking load perennial ryegrass selections	154
Table 5.12	Feeding value in live weight gain (LWG) and leaf shear	
	breaking load (LSBL) for low (LS) and high (HS) perennial	
l	ryegrass selections in previous studies and in the present	
	study	157
Table 6.1	Leaf shear breaking load (LSBL), index of masticatory	
	load (IMI) of leaf and leaf length-width ratio (I WR) of the	

	low leaf shear breaking load perennial ryegrass selection	
	expressed relative to the high leaf shear breaking load	
	perennial ryegrass selection (as 100) in the present	
	investigation	163
Table 6.2	Summary of effect of the reduced leaf shear breaking load	
	(LSBL) in perennial ryegrass on masticatory behaviour	
	during eating in sheep	164
Table 6.3	Summary of effect of reduced leaf shear breaking load	
	(LSBL) on rumen pool sizes, fractional outflow rates (FOR),	
	voluntary organic matter intake (VOMI) and feeding values	
	in sheep	165

List of Figures

		Pag
Figure 1.1	The relationship of pasture intake to various pasture	
	characteristics and methods of pasture allocation (Poppi et	
	al., 1987)	12
Figure 1.2	The influence of sward height on the components of	
	ingestive behaviour (Penning, 1985)	14
Figure 1 2	The influence of pasture mass on the liveweight gain of	
rigui e 1.5	ewes offered pasture at various levels of pasture allowance	
	(Rattray et al., 1984)	15
	(Rathay et at., 1904)	13
Figure 1.4	Relationship between the voluntary intake of digestible	
Bar e	organic matter (DOMI) and the apparent retention time of	
	organic matter in the rumen (RTOM) for temperate (from	
	Ulyatt, 1971) and tropical pasture species (Thornton <i>et al.</i> ,	
	1973)	18
	1973)	10
Figure 1.5	Young plant of perennial ryegrass (x 1.75 Soper et al.,	
Bar e	1956)	25
		25
Figure 1.6	Transections of the blade of the mature leaf of perennial	
J	ryegrass (after Soper et al., 1956)	27
Figure 1.7	Types of force to apply to the material	29
1		
Figure 1.8	Hooke's elasticity in (a) tension, (b) shear and (c)	
_	compression	30
	-	
Figure 1.9	Masticatory musculature of sheep (Turnbull, 1970)	36

Figure 1.10	The movements of the lower jaw in a "typical" chewing	
	cycle in goat, in opossum and in cat (adapted from Hiiemae,	
	1978)	38
Figure 1.1	1Relationship of feed material in lateral masticatory	
	movements of opposing occlusal surfaces	39
Figure 2.1	Schematic representation of the plant and leaf allocation for the	
	controlled atmosphere trial	50
Figure 3.1	Decline of mean chewing rate of the wethers (n=8) during	
	eating the low (LS) and high (HS) shear breaking load	
	perennial ryegrass selections over a period of 30 minutes	89
Figure 3.2	Particle size distributions in the rumen contents recovered	
J	from the wethers (n=8) immediately after ingesting the low	
	(LS) and high (HS) leaf shear breaking load perennial	
	ryegrass selections	91
Figure 3.3	Particle size distributions in the rumen contents recovered at	
	10:30 and 17:30 hours from the wethers (n=8) ruminating	
	the low (LS) and high (HS) leaf shear breaking load	
	perennial ryegrass selections	95
Figure 3.4	A model of a relationship between efficiency of particle	
	breakdown and index of masticatory load (IML) of perennial	
	ryegrass	99
Figure 4.1	Particle size distributions in rumen contents in wethers	
1	(n=8) fed on the low (LS) and high (HS) leaf shear breaking	
	load perennial ryegrass selections	114
Figure 5.1	Changes in pasture mass and in vitro organic matter	
	digestibility (IVOMD) of the low (LS) and high (HS) leaf	

	Shear breaking load perennial ryegrass selections during Trial 1	131
Figure 5.2	Changes in leaf shear breaking load (LSBL) and leaf length:dry weight ratio (LWR) of low (LS) and high (HS) leaf shear breaking load perennial ryegrass selections during Trial 1	132
Figure 5.3	Changes in index of masticatory load (IML) of low (LS) and high (HS) leaf shear breaking load perennial ryegrass selections during Trial 1	133
Figure 5.4	Changes in composition and in vitro organic matter digestibility (IVOMD) of the oesophageal extrusa of the animals grazing the low (LS) and high (HS) leaf shear breaking load perennial ryegrass selections during Trial 1	137
Figure 5.5	Changes in live weight of the lambs (n=23) grazing the low (LS) and high (HS) leaf shear breaking load perennial ryegrass selections during Trial 1	139
Figure 5.6	Particle size distribution of rumen contents of wethers (n=11) grazing the low (LS) and high (HS) leaf shear breaking load perennial ryegrass selections	142
Figure 5.7	Changes in pasture mass and in vitro organic matter digestibility (IVOMD) of the low (LS) and high (HS) leaf shear breaking load perennial ryegrass selections during Trial 2	144
Figure 5.8	Changes in leaf shear breaking load (LSBL) and leaf length:dry weight ratio (LWR) of the low (LS) and high (HS) leaf shear breaking load perennial ryegrass selections	

	during Trial 2145
Figure 5.9	Changes in index of masticatory load (IML) of the low (LS)
	and high (HS) leaf shear breaking load perennial ryegrass
	selections during Trial 2146
Figure 5.10	Changes in composition and in vitro organic matter
	digestibility (IVOMD) of the oesophageal extrusa of the
	animals grazing the low (LS) and high (HS) leaf shear
	breaking load perennial ryegrass selections during Trial 2148
Figure 5.11	Changes in live weight, 24-hour fasted weight and voluntary
	organic matter intake (VOMI) of the ewe-hoggets grazing
	the low (LS) and high (HS) leaf shear breaking load
	perennial ryegrass selections during Trial 2150
Figure 5.12	Particle size distribution of rumen contents of wethers (n=8)
	grazing the low (LS) and high (HS) leaf shear breaking load
	perennial ryegrass selections
Figure 6.1	Changes in leaf shear breaking load (LSBL) of low leaf
	shear breaking load (LS) and high leaf shear breaking load
	(HS) perennial ryegrass selections in the field during a year
	(April 1989 - March 1990)161

List of Abbreviations

General

ADF acid detergent fibre

CAC controlled atmosphere cabinet

<C.EAT> efficiency of chewing during eating in reducing particles to

< 1.0 mm

Co cobalt

Co(III)-EDTA cobalt ethylenediaminetetraacetic acid

Cr chromium

<C.RUM> efficiency of chewing during rumination in reducing

particles to < 1.0 mm

Cr₂O₃ chromium sesquioxide

Cr-EDTA chromium ethylenediaminetetraacetic acid

CSA cross-sectional area

d day

DM dry matter

DOMI voluntary intake of digestible organic matter

DSIR Department of Scientific and Industrial Research

ep epidermis

EPM Ellinbank pasture meter

Fig. figure

FOR fractional outflow rate

FV feeding value

GLM general linear model

HS high leaf shear breaking load

IML index of masticatory load

IVDMD in vitro dry matter digestibility

IVOMD in vitro organic matter digestibility

L. Linnaeus

LS low leaf shear breaking load

LSBL leaf shear breaking load

LSS leaf shear strength

LWG live weight gain

LWR leaf length:dry weight ratio

M. MusculiM00 maturation

M10 10 days after full maturation

M20 20 days after full maturation

ms mesophyll

N nitrogen

na not available

NDF neutral detergent fibre

NH₃-N ammonia

NV nutritive valueOM organic matter

OE oesophageal extrusa

PRG perennial ryegrass

RTOM apparent retention time of organic matter in the rumen

Ru ruthenium

Ru-Phen ruthenium tris (1,10-phenanthroline) ruthenium (II)

chloride

sc sclerenchyma

<TEC> theoretical efficiency of chewing

TSL total shear load

VFA volatile fatty acid

VOMI voluntary organic matter intake

vs vascular bundle

v/v volume by volume

WB Warner-Bratzler

WC white clover

Units

are a c centidegree centigrade \mathbf{C}° gram g G Newtonian constant of gravitation h hectohr hour in inch J joule kilok 1 litre millim m metre M mega-M mole microμ min. minute % per cent W watt

Statistical

df	degrees of freedom
n	number of observations
r	correlation
RSE	root square of error
s.e.	standard error
S.E.D.	standard error of difference
ns	not significant
*	significant at p<0.05

**	significant at p<0.01
***	significant at p<0.001
I	indicating ranges of standard error in figures