PHYSIOLOGICAL AND MORPHOLOGICAL RESPONSES OF TALL FESCUE (*Festuca arundinacea* SCHREB.) AND PERENNIAL RYEGRASS (*Lolium perenne* L.) TO DEFOLIATION

A thesis presented
in partial fulfilment of the requirements
for the degree of Doctor of Philosophy (Ph. D.) in
Pasture Ecology and Physiology
Department of Plant Science
Massey University

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1993

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ABSTRACT

Tall fescue (*Festuca arundinacea* Schreb.) has been suggested as an alternative to perennial ryegrass, particularly in conditions of moisture limitation, but there is little comparative information on the plant characteristics influencing regrowth in the two species, particularly under continuous stocking. The objectives of this study were to :i) examine the response of tall fescue to continuous stocking in terms of tillering activity, leaf growth and competition, and ii) determine which physiological or morphological factors are important in influencing regrowth after defoliation, using perennial ryegrass as a reference standard. Experiments were undertaken in field, glasshouse and controlled environment conditions.

In the field sown swards of tall fescue (*Festuca arundinacea* Schreb. cv. 'Grassland Roa') and white clover (*Trifolium repens* L. cv. 'Grassland Tahora'), with volunteer grasses mainly consisting of perennial ryegrass (*Lolium perenne* L. cv. 'Grassland Nui') were continuously stocked with varying numbers of sheep to maintain sward surface heights 90-100 mm (Lax, L), 50-60 mm (Medium, M) and 30-40 mm (Hard, H). Measurements were made on areas with and without clover by removal of white clover with clopyralid. Tiller population density, tiller weight, and leaf growth and productivity of tall fescue were all reduced under hard grazing. Tall fescue was susceptible to competition from companion species, particularly perennial ryegrass, and tended to be replaced by other species under hard grazing.

Under glasshouse conditions individual plants of tall fescue and perennial ryegrass were defoliated to stubble heights of 100 mm (Lax, L), 60 mm (Medium, M), 30 mm (Hard1, H1) and 30 mm (Hard2, H2) 9 times with 5 day intervals over a period of 45 days. Treatments L, M, and H1 were initiated at an average of 11 tillers per plant for each species; treatment H2 commenced at 6 tillers per plant. Both species showed sensitivity to severe cutting treatments by reduction in tiller number, tiller weight, leaf growth and less shoot and root growth. Tall fescue showed lower leaf growth, tillering activity and herbage harvested per plant than perennial regress, but it produced larger tillers.

The comparative response of tall fescue and perennial ryegrass to leaf defoliation was studied under controlled environment conditions at both the vegetative and reproductive stages of growth. The oldest leaf lamina was defoliated regularly to maintain four, three, two or only one live leaf per tiller for six or seven leaf appearance intervals. In both species repeated removal of older leaves had little effect on tiller production, tiller weight, leaf growth rate and consequently total accumulated shoot and root weight, and mean shoot and root relative growth rates. Removal of all fully expanded leaves resulted in significant reduction in the above components, though leaf elongation rate was little affected. Leaves were shorter, narrower and lighter under hard defoliation, but leaf appearance rate was not affected. Hard defoliation affected tall fescue tiller weight more than perennial ryegrass. Water soluble carbohydrate concentrations in stem bases of plants decreased with increasing severity of defoliation especially for tall fescue. Leaf photosynthetic capacity per unit area was not influenced by defoliation intensity, but photosynthetic capacity per unit leaf weight increased under hard defoliation. Hard defoliation decreased the proportion of root mass to shoot mass, and increased the proportion of leaf mass to shoot mass. Plants showed relatively similar sensitivity to defoliation at vegetative and reproductive phases of growth. At both phases tall fescue again produced larger tillers with longer leaves and had a longer leaf life-span than perennial ryegrass, but it had lower leaf growth and appearance, and produced fewer tillers per plant. Photosynthetic activity per unit leaf area was similar for the two species, but tall fescue often had lower photosynthetic rate per unit leaf weight than perennial ryegrass.

In conclusion, hard defoliation intensity reduced both tiller population density and tiller weight and consequently decreased pasture regrowth through a reduction in LAI, life-span of leaf area, photosynthetic efficiency, and shortage of carbohydrate reserves. The factors that resulted in the regrowth of tall fescue being less responsive to hard defoliation than perennial ryegrass were slower leaf turnover, slower leaf appearance rate, lower tillering capacity and longer leaf life-span. These resulted in lack of plasticity in tiller population density of tall fescue in response to hard defoliation.

ACKNOWLEDGEMENTS

First of all praise to almighty God for giving me the ability to learn.

I would like to express my deepest gratitude to my chief supervisor Dr Peter David Kemp and co-supervisor Professor John Hodgson for their patience, enthusiastic encouragement, guidance and close supervision throughout the course of this study. I was provided with friendly answers at any time that I needed their help.

I am deeply indebted to Dr Cory Matthew for his generosity in time and useful advice made available to me through his "open door".

Thanks are extended to Drs I.L. Gordon and S. Ghaneshanandam for statistical advice, Drs A.C.P. Chu, I. Valentine and K. Harrington (from Department of Plant Science), Mr J. Brock and Drs D. Hume, and D.F. Chapman (from AgResearch CRI), Drs D.W. Fountain, C.A. Cornford and Professor R.G. Thomas (from Department of Plant Biology) for their helpful comments; Messrs B. Butler, for his tissue turnover programme, T. Lynch and M.A. Osborne for their technical field assistance, R. Johstone, C. Forbes, G. Russell, for assisting in the preparation of the Growth Cabinets and Glasshouse facilities, the staff of Horticulture CRI for organising the Climate room, Mrs S. Cleland for her technical assistance; and Mrs J. Cave, and especially, Ms C. McKenzie and Ms Frith Brown for their technical and organisational assistance made available to me at any time.

The friendly environment provided by my fellow graduate students in Plant Science Department is much appreciated, especially the friendship of Mr Manzoor-ul-Haque Awan which will never be forgotten.

The presence of all Iranian postgraduate students and their families in Palmerston North made my family and I feel at home. It is my pleasure to thank and wish them a happy and prosperous future.

I would like to express my sincere thanks to the Ministry of Jahad-e-Sazandegi and Ministry of Culture and Higher Education of IRAN, for awarding me the scholarship to undertake this study.

Special thanks to my wife Tayebeh for her patience, considerable encouragement and assistance in a number of ways, but especially undertaking my own duty to educate our children. The patience of my son Mosslem and my daughter Maryam and their positive responses to education provided for them made me happy and encouraged me to cope with difficulties. Finally the forbearance and encouragement of my other family members and friends is deeply appreciated.

TABLE OF CONTENTS

ABSTRACT ii
Acknowledgments iv
Contents vi
List of Tables xi
List of Figures xvii
List of Plates xviii

CHAPTER 1: General introduction and objectives 1

CHAPTER 2: Literature review 3

- 2.1 Introduction 3
- 2.2 The morphology and growth characteristics of perennial ryegrass and tall fescue. 3
- 2.3 Performance of tall fescue 6
- 2.4 The effect of defoliation on pasture production 7
- 2.5 Effect of defoliation on persistence of plants 9
- 2.6 Cutting vs. grazing managements 11
- 2.7 Factors influencing regrowth after defoliation 13
  - 2.7.1 Residual leaf area 13
  - 2.7.2 Leaf growth 14
  - 2.7.3 Leaf carbon budget 15
  - 2.7.4 Tillering activity 18
  - 2.7.5 Meristem damage 19
  - 2.7.6 Carbohydrate reserves 21
  - 2.7.7 Stage of growth 22
  - 2.7.8 Root growth 23
  - 2.7.9 Plant competition 24
- 2.8 Effects of defoliation on plant size and structure 26
- 2.9 Summary and conclusion 28

CHAPTER 3: Regrowth and competitiveness of tall fescue under grazing management 29

3.1 Introduction 29
3.2 Materials and methods 29
    3.2.1 Experimental conditions 29
    3.2.2 Measurements 30
    3.2.3 Statistical analysis 33
3.3 Results 35
    3.3.1 Herbage mass 35
    3.3.2 Botanical composition 35
    3.3.3 Tiller population density and tiller weight 39
    3.3.4 Leaf area index and leaf area per tiller 41
    3.3.5 Leaf growth 42
    3.3.6 Leaf defoliation 45
3.4 Discussion 48
    3.4.1 Regrowth of tall fescue in response to defoliation . . 48
    3.4.2 Botanical composition 50
3.5 Summary 52

CHAPTER 4: Effect of cutting on regrowth of tall fescue and perennial ryegrass 53

4.1 Introduction 53
4.2 Material and methods 53
    4.2.1 Experimental conditions 53
    4.2.2 Measurements 54
    4.2.3 Statistical analysis 56
4.3 Results 57
    4.3.1 Herbage harvested 57
    4.3.2 Tiller number and tiller weight 60
    4.3.3 Leaf growth 64

4.3.4 Total herbage harvested and plant shoot and root mass 64
4.4 Discussion 67
4.5 Summary 70

CHAPTER 5: Response of tall fescue and perennial ryegrass to leaf defoliation 71

5.1 Introduction 71

5.2 Vegetative stage 72

5.2.1 Material and methods- experiment 1 72
5.2.1.1 Experimental conditions 72
5.2.1.2 Measurements 73
5.2.1.3 Statistical analysis 79
5.2.2 Results- experiment 1 80
5.2.2.1 Plant herbage mass components and relative growth rate 80
5.2.2.2 Tiller number and tiller weight 85
5.2.2.3 Leaf appearance and site filling 89
5.2.2.4 Leaf growth 90
5.2.2.5 Leaf characteristics 92
5.2.2.6 Leaf photosynthesis and respiration 94
5.2.2.7 Water soluble carbohydrate 94
5.2.3 Material and methods- experiment 2 97
5.2.3.1 Experimental conditions 97
5.2.3.2 Measurements 98
5.2.3.3 Statistical analysis 99
5.2.4 Results- experiment 2 100
5.2.4.1 Plant herbage mass components and relative growth rate 100

5.2.4.2 Leaf area per plant and leaf area ratio 105
5.2.4.3 Tiller number and tiller weight 105
5.2.4.4 Leaf appearance and site filling 108
5.2.4.5 Leaf growth 109
5.2.4.6 Leaf characteristics 112
5.2.4.7 Leaf photosynthesis and respiration 114
5.2.4.8 Water soluble carbohydrate 120

5.3 Reproductive stage 121

5.3.1 Material and methods- experiment 3 121
5.3.1.1 Experimental conditions 121
5.3.1.2 Measurements 122
5.3.1.3 Statistical analysis 123
5.3.2 Results- experiment 3 124
5.3.2.1 Plant herbage mass components and relative growth rate 124
5.3.2.2 Tiller number and tiller weight 128
5.3.2.3 Leaf growth 133
5.3.2.4 Leaf characteristics 133
5.3.2.5 Leaf photosynthesis 136
5.3.2.6 Water soluble carbohydrate 139
5.3.3 Material and methods- experiment 4 140
5.3.3.1 Experimental conditions 140
5.3.3.2 Measurements 140
5.3.3.3 Statistical analysis 140
5.3.4 Results- experiment 4 141
5.3.4.1 Plant herbage mass 141
5.3.4.2 Tiller number and tiller weight 141
5.3.4.3 Water soluble carbohydrate 144
5.4 Discussion 147
5.5 Summary 156

CHAPTER 6: General discussion and conclusion 157

6.1: General discussion 157
6.2 Comment and conclusion 163

REFERENCES 165

APPENDICES 185

Appendix 3.1: Summary of rainfall, temperature and sunshine . . 185
Appendix 3.2: Number of sheep in each plot over trial period. . . 186
Appendix 3.3: Analysis of variance of tall fescue herbage mass 187
Appendix 4.1: Analysis of variance of herbage harvested for the two grass species and different treatments over time. . . . 188
Appendix 4.2: Effect of cutting heights on herbage harvested per plant of perennial ryegrass and tall fescue. 189
Appendix 4.3: Effect of cutting heights on tiller number per plant of perennial ryegrass and tall fescue. 190
Appendix 5.1: PAHBAH regent. 191
Appendix 5.2: Standard curve for determination of WSC 192

LIST OF TABLES

CHAPTER 3:

Table 3.1: Effect of grazing management on leaf,pseudostem and total herbage mass of tall fescue. 36

Table 3.2: Effect of grazing management on leaf,pseudostem and total herbage mass of tall fescue grown with and without clover 36

Table 3.3: Herbage mass of tall fescue, white clover, other grasses and total biomass under different grazing management: with clover. 37

Table 3.4: Herbage mass of tall fescue, other grasses and total biomass under different grazing management: without clover. 37

Table 3.5: Effect of grazing management on tall fescue tiller population density and tiller weight 40

Table 3.6: Tiller population density and tiller weight of tall fescue grown with and without clover. 40

Table 3.7: Effect of grazing management on tall fescue leaf area index and leaf area per tiller. 41

Table 3.8: Leaf area index and leaf area per tiller of tall fescue grown with and without clover. 41

Table 3.9: Total leaf elongation, senescence and net leaf elongation rates under different grazing managements 43

Table 3.10: Tall fescue total leaf elongation, senescence and net leaf elongation rates grown with and without clover. 43

Table 3.11: Estimation of net leaf elongation rates per unit area and net leaf weight production of tall fescue under different grazing managements 44

Table 3.12: Estimation of net leaf elongation rates per unit area and net leaf weight production of tall fescue grown with and without clover. 44

Table 3.13: Comparison of leaf defoliation (%) of marked tillers between different grazing treatments. 46

Table 3.14: Comparison of leaf defoliation (%) of marked tillers of tall fescue grown with and without clover. 47

CHAPTER 4:

Table 4.1: Comparison between herbage harvested per plant of perennial ryegrass and tall fescue. 58

Table 4.2: Effect of cutting treatments on herbage harvested per plant. 58

Table 4.3: Herbage harvested per tiller of the two grass species. 59

Table 4.4: Effect of cutting treatments on mean herbage harvested per tiller. 59

Table 4.5: Tillering rates of perennial ryegrass and tall fescue; mean of treatments L and M. 63

Table 4.6: The effect of cutting treatments on tillering rates. 63

Table 4.7: Tiller weight of perennial ryegrass and tall fescue under different cutting treatments at final harvest. 63

Table 4.8: Comparison of total herbage harvested, total plant shoot mass and root mass of perennial ryegrass and tall fescue. 66

Table 4.9: Effect of cutting treatments on total herbage harvested, total plant shoot mass and root mass. 66

CHAPTER 5 (Vegetative stage- experiment 1)

Table 5.1: Accumulated dry mass of leaf, pseudostem, total shoot, and mean shoot relative growth rates of perennial ryegrass and tall fescue. 81

Table 5.2: Effect of defoliation on accumulated dry mass of leaf, pseudostem, total shoot, and mean shoot relative growth rates. 82

Table 5.3: Tiller number per plant of perennial ryegrass and tall fescue (unadjusted mean). 86

Table 5.4: Effect of defoliation on tiller number per plant of pooled perennial ryegrass and tall fescue (unadjusted mean). 86

Table 5.5: Tiller number per plant of perennial ryegrass and tall fescue (adjusted mean). 87

Table 5.6: Effect of defoliation on tiller number per plant of pooled perennial ryegrass and tall fescue (adjusted mean). 87

Table 5.7: Tillering rates of perennial ryegrass and tall fescue. 88

Table 5.8: Effect of defoliation treatments on mean tillering rates of perennial ryegrass and tall fescue. 88

Table 5.9: Effect of defoliation on tiller weight 88

Table 5.10: Leaf number, leaf appearance rates and site filling of perennial ryegrass and tall fescue. 89

Table 5.11: Leaf number, leaf appearance rates and site filling of the two species under different defoliation treatments.. 89

Table 5.12: Leaf elongation rates of the two grass species. 90

Table 5.13: Effect of defoliation on leaf elongation rates 91

Table 5.14: Leaf lamina growth rates of perennial ryegrass and tall fescue. 91

Table 5.15: Effect of defoliation on leaf lamina growth rates. 91

Table 5.16: Individual leaf characteristics of perennial ryegrass and tall fescue 93

Table 5.17: Individual leaf characteristics of the two grass species under different defoliation treatments. 93

Table 5.18: Leaf photosynthetic and dark respiration rates of the uppermost fully expanded leaf of the two grass species 95

Table 5.19: Effect of defoliation on leaf photosynthetic and dark respiration rates of the uppermost fully expanded leaf 96

Table 5.20: Effect of defoliation on water soluble carbohydrate concentrations in the stem bases of the two grass species. 96

CHAPTER 5 (Vegetative stage- experiment 2)

Table 5.21: The accumulated dry mass of leaf, pseudostem, shoot mass, root mass and total biomass, and mean shoot and root relative growth rates of perennial ryegrass and tall fescue. 101

Table 5.22: Effect of defoliation on accumulated dry mass of leaf, pseudostem, shoot, root and total biomass, and mean shoot and root relative growth rates 102

Table 5.23: Leaf area per plant, leaf area ratio per shoot mass and per biomass of the two grass species under different defoliation treatments. 105

Table 5.24: Tiller number per plant of the two grass species. 106

Table 5.25: Effect of defoliation on tiller number per plant: mean of perennial ryegrass and tall fescue data. 106

Table 5.26: Tillering rates of perennial ryegrass and tall fescue. 107

Table 5.27: Effect of defoliation on tillering rates 107

Table 5.28: Effect of defoliation on tiller weight. 107

Table 5.29: The mean leaf number per tiller, leaf appearance rates and site filling of perennial ryegrass and tall fescue. 109

Table 5.30: Leaf number, leaf appearance rates and site filling of the two species under different defoliation treatments. 109

Table 5.31: Leaf elongation rates of the two grass species. 110

Table 5.32: Effect of leaf defoliation on mean leaf elongation rates 111

Table 5.33: Leaf lamina growth rates of the two grass species.. 111

Table 5.34: Effect of defoliation on leaf lamina growth rates. 111

Table 5.35: Individual leaf characteristics of the two grass species. . . . 113

Table 5.36: Individual leaf characteristics of perennial ryegrass and tall fescue plants under different defoliation treatments. 113

Table 5.37: The leaf photosynthetic rates of control plants. 115

Table 5.38: Photosynthetic rates of leaves in different position in a tiller of control plants 116

Table 5.39: Leaf photosynthetic rates of the two grass species. 117

Table 5.40: Effect of defoliation on leaf photosynthetic rates. 118

Table 5.41: Water soluble carbohydrate concentrations in stem bases of the two grass species under different defoliation treatments. 120

CHAPTER 5 (Reproductive stage- experiment 3)

Table 5.42: Accumulated dry mass of leaf, pseudostem, seed head, total shoot, and mean shoot relative growth of the two grass species. . 125

Table 5.43: Effect of defoliation on accumulated dry mass of leaf, pseudostem, seed head, total shoot, and mean shoot relative growth rates. 126

Table 5.44: Tiller number per plant of the two grass species (unadjusted mean). 129

Table 5.45: Effect of defoliation on mean tiller number per plant of the two grass species (unadjusted mean). 129

Table 5.46: Tiller number per plant of perennial ryegrass and tall fescue (adjusted mean). 130

Table 5.47: Effect of defoliation on mean tiller number per plant of perennial ryegrass and tall fescue (adjusted mean). 130

Table 5.48: Tillering rates of perennial ryegrass and tall fescue. 130

Table 5.49: Effect of defoliation on tillering rates. 131

Table 5.50: Percentage of tillers with seed heads under different defoliation treatments. 132

Table 5.51: Effect of defoliation on tiller weight. 132

Table 5.52: Leaf elongation rates of the two grass species. 134

Table 5.53: Effect of defoliation on mean leaf elongation rates of perennial ryegrass and tall fescue. 134

Table 5.54: Leaf lamina growth rates of the two grass species. 134

Table 5.55: Effect of defoliation on mean leaf lamina growth rates of perennial ryegrass and tall fescue. 134

Table 5.56: Individual leaf characteristics of the two grass species 135

Table 5.57: Individual leaf characteristics of perennial ryegrass and tall fescue under different leaf defoliation treatments. 135

Table 5.58: Photosynthetic rates of the uppermost fully expanded leaf of perennial ryegrass and tall fescue. 136

Table 5.59: Effect of defoliation on photosynthetic rates of the uppermost fully expanded leaf 137

Table 5.60: Water soluble carbohydrate in stem bases of perennial ryegrass and tall fescue under different defoliation treatments. 139

CHAPTER 5 (Reproductive stage- experiment 4)

Table 5.61: Total accumulated shoot mass of the two grass species . . 142

Table 5.62: Total accumulated shoot mass of perennial ryegrass and tall fescue under different defoliation treatments. 142

Table 5.63: Tiller number per plant of the two grass species (adjusted mean). 143

Table 5.64: Effect of defoliation treatments on mean tiller number per plant of perennial ryegrass and tall fescue (adjusted mean). 143

Table 5.65: Tiller number per plant for perennial ryegrass and tall fescue (unadjusted mean). 143

Table 5.66: Effect of defoliation treatments on mean tiller number per plant of perennial ryegrass and tall fescue (unadjusted mean). 144

Table 5.67: Tiller weight of perennial ryegrass and tall fescue. 145

Table 5.68: Effect of defoliation on tiller weight of perennial ryegrass and tall fescue. 145

Table 5.69: Water soluble carbohydrate in the stem bases of perennial ryegrass and tall fescue. 146

Table 5.70: Water soluble carbohydrate in stem bases of perennial ryegrass and tall fescue under different defoliation treatments. 146

LIST OF FIGURES

CHAPTER 3:

Figure 3.1: Botanical composition of pastures grown with clover. 38

Figure 3.1: Botanical composition of pastures grown without clover. . . . 38

CHAPTER 4:

Figure 4.1: Tiller number per plant of the two grass species 61

Figure 4.2: Effects of cutting heights on tiller number 62

Figure 4.3: Leaf elongation rates of the two grass species 65

Figure 4.4: Effect of defoliation on leaf elongation rates 65

CHAPTER 5: (Vegetative stage- experiment 1)

Figure 5.1: Leaf defoliation treatments 74

Figure 5.2: Effect of defoliation on proportion of leaf to shoot mass . . . 84

CHAPTER 5: (Vegetative stage- experiment 2)

Figure 5.3: Effect of defoliation on proportion of leaf to shoot mass . . . 104

Figure 5.4: Effect of defoliation on proportion of root to shoot mass . . . 104

Figure 5.5: Effect of leaf age on photosynthetic efficiency 119

Figure 5.6: Effect of leaf age on respiratory activity 119

CHAPTER 5: (Reproductive stage- experiment 3)

Figure 5.7: Effect of defoliation on proportion of leaf to shoot mass . . . 127

Figure 5.8: Effect of leaf age on photosynthetic efficiency 138

CHAPTER 6:

Figure 6.1: Relationship between tiller weight and population density of tall fescue. 161

Figure 6.2: Relationship between tiller weight and population density of three grass species. 161

LIST OF PLATES

Plate 3.1: General views of the grazing experiment 31
Plate 4.1: A general view of cutting experiment 55
Plate 5.1: Measurement of Leaf carbon exchange by 77
Plate 5.2: A general view of individual plants of 83
Plate 5.3: Accumulation of root mass 103

CHAPTER 1: General introduction and objectives

The most common pastures in New Zealand are based on ryegrass (*Lolium perenne* L.) and white clover (*Trifolium repens* L.) but these have failed to generate high growth rates in areas of low rainfall and high soil temperature in summer, and are also susceptible to grass grub (*Costelytra zealandica*) attack (MacFarlane, 1990). Tall fescue (*Festuca arundinacea* Schreb.) has recently been considered as an alternative pastoral plant in drier areas, and in regions prone to grass grub attack (Brock, 1983).

There has not been widespread acceptance of tall fescue by farmers (Brock, 1983; Lancashire & Brock, 1983; Prestidge *et al.*, 1989). The possible reasons are slow establishment (Anderson, 1982), low tolerance of hard grazing and poor persistence (Allo & Southon, 1967; Brock, 1983; Lancashire and Brock, 1983; Miller, 1984), low palatability and fear of animal health problems (Miller, 1984), and the high cost of seed for establishment (Pottinger *et al.*, 1987).

The general consensus about tall fescue is that for achieving yield potential, it should not be managed similarly to a perennial ryegrass pasture but needs lax and infrequent defoliation management (Allo & Southon, 1967; Levy, 1970; Brock, 1983; Lancashire & Brock 1983; Kerrisk & Thomson, 1990). The available information on the management of tall fescue is mostly related to intermittent defoliation, but there is little information on its performance under continuous stocking. The objectives of this study were;

i) to examine the response of tall fescue to continuous stocking in terms of tillering activity and leaf growth.

ii) to examine the outcome of competition between tall fescue and companion species as change in botanical composition.

iii) to determine which physiological or morphological factors are important in influencing regrowth after defoliation in tall fescue, using perennial ryegrass as standard for reference.

Studies on tall fescue were carried out under field, glasshouse and controlled environment conditions, with particular reference to physiological factors influencing growth tolerance of defoliation.

CHAPTER 2: Literature review

2.1 Introduction

The main goal in pasture management is to maximize herbage production and animal performance, without inducing pasture deterioration. Regrowth of plants after defoliation can be influenced by residual photosynthetic tissue, carbohydrate and other reserves, the rate of recovery of root growth and nutrient and water uptake, and the quantity and activity of meristems remaining. The relative importance of these influences is determined by environmental limits to growth in any particular situation and the adaptive characteristics of the species present which enable them to recover from defoliation (Harris, 1978). Thus, it is important to identify the factors limiting plant regrowth after defoliation, and to establish the relative importance of these factors for alternative forage plant species.

Recently some workers (e.g. Davies, 1988; Briske, 1991; Vallentine, 1991; Chapman & Lemaire, 1993; Richards, 1993) have reviewed the response of plants to defoliation. In this review the effect of defoliation in terms of frequency and intensity on regrowth will be considered mainly for tall fescue and perennial ryegrass. Examples from other plants are used where necessary. The morphology and growth characteristics of tall fescue, using perennial ryegrass as a reference, will be described first. Also, attention will be given to the performance of tall fescue, mainly in New Zealand. Then the effects of defoliation on the production and persistence of forage plants, responses of pasture species to defoliation, and the effects of defoliation on plant growth and growth characteristics will be reviewed in detail.

2.2 The morphology and growth characteristics of perennial ryegrass and tall fescue.

The reaction of a pasture species to defoliation is affected by its morphology and growth characteristics. In order to evaluate the potential of pastoral plants it is necessary to understand both the basic structure of the plant and how the functional organs are affected by the stresses imposed in a pasture environment. In this section a brief description of the morphology and growth characteristics of perennial ryegrass and tall fescue is presented with attention to the comparison of the two species.

Perennial ryegrass (*Lolium perenne* L.)

Perennial ryegrass is a long-lived perennial capable of forming many leafy tillers and thus a dense sward. It has a shallow root system. It is a hairless plant with flattened tillers bearing dark green leaves which are ribbed above and very shiny below. The auricles are very small and often not easily distinguished and the ligule is short and inconspicuous. The inflorescence is a spike with the spiklets containing 3-10 fertile florets. Perennial ryegrass is an outcrossing species (Walton, 1983; Langer, 1990; Langer & Hill, 1991).

Leaf laminae are up to 30 cm long and up to 7 mm wide (Lamp *et al.*, 1990). In vegetative swards the number of green leaves per tiller increases up to three, and thereafter leaf appearance is balanced by death (Robson, 1973). Robson (1973) also observed that under constant controlled environment conditions the final size of successive leaves on ryegrass tillers increased up to leaf 9-10. At Palmerston North, tillers of perennial ryegrass 'Grasslands Nui' produced a new leaf every 5-10 days in October-January when swards are well fertilised and irrigated (Korte *et al.*, 1985). In another experiment Barker *et al.* (1985) recorded a leaf appearance interval of 8 days.

To persist and produce well perennial ryegrass requires fertile soil of heavy texture, plus adequate rainfall or irrigation (Lamp *et al.*, 1990). The optimum temperature for the growth of ryegrass is 18-20°C and growth occurs between 5 and 30°C (Mitchell, 1956).

Perennial ryegrass is easy to establish. In general, the plant can stand up to hard grazing due to its vigorous tillering and rapid leaf production. It has the plasticity of rapid adjustment of tiller population in relation to grazing management (Bircham & Hodgson, 1983).

Tall fescue (*Festuca arundinacea* Schreb.)

Tall fescue is a robust perennial, with rounded tillers bearing large dark green leaves which are distinctly ribbed on the upper surface. The auricles at the base of laminae are permanent and bear minute hairs, but the ligule is not conspicuous. Tall fescue has a deep root system. The inflorescence is an open panicle, each spikelet containing 3-10 florets which separate at maturity. Tall fescue is a cross-pollinating plant (Miller, 1984; Langer, 1990).

Leaf laminae are up to 60 cm in length, and between 3-15 mm wide (Lamp *et al.*, 1990). Robson (1967) observed less than three live leaves per tiller in S.170 and AH tall fescue under outdoor conditions, whereas indoor plants had up to 4.6 live leaves per tiller.

Tall fescue is adapted to a wide range of soils including dry, wet, poorly drained areas and can grow in both acid (pH 4.7) and alkaline (pH 9.5) soil. The optimum growing temperature is 20-25°C, but it will grow in the temperature range from 5-29°C. It is reasonably drought tolerant and will also withstand waterlogging. Tall fescue requires high fertility for optimum growth (Miller, 1984; Langer, 1990).

Tall fescue is slower to establish than perennial ryegrass, so careful management is needed during establishment. It has shown good persistence but under laxer grazing than perennial ryegrass (Levy, 1970; Brock, 1983; Bell, 1985).

2.3 Performance of tall fescue

Tall fescue is an important forage species in U.S.A. and considered as predominant cool-season perennial grass especially in the Eastern States (Buckner & Bush, 1979) whereas in New Zealand its potential is due to good summer growth (Brock, 1982, 1983). Good liveweight gains have been achieved by beef animals over summer compared with other grasses in a number of trials (Buckner & Bush, 1979). In a study in North Carolina (Burns *et al.*, 1973) with tall fescue alone, tall fescue and ladino white clover, and tall fescue rotated with a bermuda grass mid-summer, the tall fescue- white clover gave the best results. Calves grazing tall fescue alone and calves grazing the tall fescue- white clover had an average weight of 169 and 197 kg respectively (Buckner & Bush, 1979).

In New Zealand, tall fescue often has the ability to produce more herbage than ryegrass in dry conditions. For example, in Canterbury with an average annual rainfall of 725 mm and 1106 mm evapotranspiration potential, tall fescue produced 12% more dry matter than perennial ryegrass over three years (Watkin, 1975). In South Taranaki, in a grass grub prone, summer-dry environment annual production of tall fescue was 20% more than that of old ryegrass pasture (Judd *et al.*, 1990). Over the months January to March, in trials in Waikato, Roa tall fescue produced 20% more dry matter than ryegrasses and was growing at a rate in excess of 60 kg dry matter ha^{-1} day^{-1} ,and resulted in 10% greater liveweight gains of steers (Goold & Van der Elst, 1980).

Tall fescue appears to outproduce perennial ryegrass only under stress. For example, in Waikato the annual production of tall fescue and perennial ryegrass was similar under irrigation. Brock (1982), comparing the frequency and intensity of defoliation of Roa and S170 tall fescue with Ruanui ryegrass showed greater herbage yield for tall fescue over the dry period summer-autumn, equal yield in winter and lower yield in spring than for perennial ryegrass. At the moister Ballantrae and Fairplace sites, Nui ryegrass was the best species in terms of dry matter accumulation, whereas at Taupo Roa tall fescue showed better performance than perennial ryegrass (Barker *et al.*, 1993).

The performance of animals grazing on tall fescue and ryegrass swards has been compared in several experiments. On a Massey University Dairy Unit, Wilson (1975) reported similar milk production by cows grazing either Roa tall fescue or Nui ryegrass. In another experiment, tall fescue produced about 17-20% more dry matter than ryegrass, but the total milk fat production was similar for both pastures (Thomson *et al.*, 1988).

Animal performance trials in the Southern Hawkes Bay, at the MAF Takapau Research Area, demonstrated liveweight gains and carcass weights of weaned lambs and hoggets were similar on Roa tall fescue and Nui perennial ryegrass based pastures (Wright et al., 1985). Recently, MacFarlane (1990) reported animal growth rates of 155, 225 and 266 g per day for high and non endophyte ryegrass and Roa tall fescue respectively.

2.4 The effect of defoliation on pasture production

Evidence from several studies indicates that herbage yield is depressed under close and frequent defoliation managements. For example, the yield of tall fescue populations was studied under four cutting intervals (2, 4 ,8 and 16 weeks) for two years by Schiller and Lazenby (1975); results showed that total dry matter yield was reduced as the cutting interval decreased. Kerrisk and Thomson (1990) also noted that over all seasons, pasture growth rates were increased under lax defoliation, and the frequency of defoliation was critical for growth under close defoliation but not under lax defoliation. Zarrough *et al.* (1983a) suggested that raising cutting height from 5 cm to 10 cm resulted in increased yield per tiller and increased total herbage yield for the season in tall fescue genotypes, while tiller density remained constant. In a mixed sward the contribution of tall fescue to accumulated yield was least at 21-day defoliation frequency and greatest at 63-day defoliation frequency (Bell, 1985).

Reduced plant dry weight and lateral stem formation was observed (Krans & Beard, 1985) in Kentucky bluegrass (*Poa pratensis*) when cut to 2.5 cm height with frequent clipping (twice weekly) relative to a 6.2 cm cutting height and infrequent clipping (biweekly). The reduced growth and vigour associated with close and frequent clipping of Kentucky bluegrass was attributed to loss of leaf area. Similar results were reported by Madison (1960, 1962) for creeping bentgrass (*Agrostis palustris*).

In contrast, some studies indicate that moderate defoliation may result in more production than lax defoliation. For example, higher dry matter yield was obtained for perennial ryegrass under a 5 cm grazing height than a 8 cm height (Ollerenshaw & Hodgson, 1977). Over 5 years (Reid, 1962) a ryegrass mixture consistently gave greater dry matter and crude protein yields of herbage when cut to 2.5 cm than cut to 5-6.5 cm from ground level; the mean dry matter difference was 34%. Bircham and Hodgson (1983) reported that when ryegrass-white clover pasture was maintained at an LAI between 1.9-4.5, dead matter build-up and reduction in herbage mass accumulation was low. At lower LAI the production of pasture decreased due to lower tissue growth and tiller population. At a high LAI accumulation of dead material and the shading of green leaf tissue and tiller bases resulted in low tillering activity and also reduced light-use-efficiency. All of these effects resulted in reduced net herbage production.

Plants respond differently to defoliation in terms of dry matter production, and production is influenced by the growth habits of pasture species. For erect species such as *Panicum maximum* (McIvor, 1978) and *Bromus inermis* (Xia, 1991) increased yields have been observed with a decrease in cutting interval or less intensive defoliation. For *Brachiaria* *decumbens* (Signal grass) which is a prostrate plant, McIvor (1978) found that yield was higher with more frequent defoliation. Motazedin and Sharrow (1986) clipped the sward of ryegrass-subclover (*Trifolium subterraneum*) to three stubble heights (40, 55 and 70 mm) with four defoliation intervals (7, 21, 35 and 49 days). In the first year when pasture was dominated by erect growing ryegrass more dry matter was produced when 70 mm of stubble remained after defoliation; but when the more prostrate subclover dominated in the second year the pasture yielded more with a 40 mm stubble. An increase in the interval between defoliations produced more dry matter at both cutting heights.

2.5 Effect of defoliation on persistence of plants

The ability of a pasture plant to survive and maintain its abundance and productivity within a plant community subjected to herbivory is dependent upon both avoidance and tolerance components to grazing (Briske, 1986). In general, plants with characteristics such as prostrate habit (Harris, 1978), lower position of apical meristems in the vegetative stage (Hyder & Sneva, 1963; Hyder, 1972), high rate of shoot replacement (Briske, 1991) and phenotypic plasticity (Chapman & Lemaire, 1993) can survive better under severe grazing.

Hodgkinson *et al.* (1989) studied two Savanna grasses, *Themeda triandra* and *Cenchrus ciliaris*, which are erect bunchgrasses (the latter is weakly rhizomatous). *C. ciliaris* was maintained better under frequent defoliation than *T. triandra* due to the ability to change its morphology in response to frequent defoliation; this species also produced horizontally oriented tillers, allowing it to maintain greater leaf area below defoliation height compared to similarly treated *T. triandra* plants. In another study (Xia, 1991) perennial ryegrass was relatively insensitive to hard and lax grazing due to adaptive changes in the balance between tiller population and tiller size and to rapid leaf turnover, but prairie grass (*Bromus wildenowii*) showed little adaptive response in increased tiller population density when tiller size declined, and had less leaf turnover. Among the four accessions of the semi-arid shrub legume *Psoralea erianta* that were evaluated under 3, 6 and 9 week cutting regimes for 72 weeks in pots in a glasshouse (Gutteridge & Whiteman, 1975), the erect accession had the highest mortality under the frequent defoliation. The other accessions suffered little mortality.

The survival of plants is affected by the frequency and intensity of defoliation and differs among species. For example, perennial ryegrass withstands defoliation above 2 cm under continuous stocking, but under severe defoliation to below 2 cm uprooting and death of tillers creates gaps in the canopy that are replaced progressively by *Poa annua* (Grant *et al.*, 1983; Bircham & Hodgson, 1983). The persistence and tiller density of 'Grassland Matua' prairie grass decreased under hard grazing (residual of 1000 kg DM ha^{-1}) relative to lax grazing (at 2000 kg DM ha^{-1}) (Black & Chu, 1989). But delaying hard grazing improved sward persistence and pasture utilisation. Matches (1966) reported that tall fescue plants cut to 25 mm every 10 days died after the fourth defoliation was imposed, but plants cut to leave 100 mm of stubble were able to recover sufficiently and to survive the same interval between cuts. Vartha (1978) found that tall fescue did not persist under dry conditions in Canterbury when duration of grazing was 2-3 weeks with 6-weekly intervals. In mixed swards of tall fescue, perennial ryegrass and some other species, poor persistency has also been reported for tall fescue under continuous stocking management relative to perennial ryegrass (Lancashire & Brock, 1983).

The production and persistence of 'Grassland Nui' ryegrass, 'Grassland Wana' cocksfoot, 'Grassland Maru' phalaris, 'Grassland Matua' prairie grass, 'Grassland Roa' tall fescue and resident pasture were measured between 1979 and 1986 at six New Zealand sites under several fertilizer and summer grazing (rotational and continuous) treatments by Barker *et al.* (1993) and Moloney *et al.* (1993). Grass species varied in production and persistence.

Wana and Nui were the most persistence grasses at most sites, whereas Maru and resident pasture were intermediate in terms of persistency, and both Matua and Roa were only persistent at one site.

2.6 Cutting vs. grazing managements

The effects of defoliation observed in cutting experiments have not been consistently reflected in studies of grazed pasture (Watkin & Clements, 1978). Yet much research work on herbage production has involved cutting because of shortages of land, labour and finance for grazing trials, or in some cases because of the requirement to create pasture conditions difficult to prepare by grazing.

In cutting experiments, herbage above cutting height is instantly and uniformly removed, whereas animals trample pasture, return dung and urine to the pasture, and disperse seeds. They also graze selectively by removing leaf rather than stem, and younger, more accessible leaves rather than older leaves, and by preference for some species to others (Hodgson, 1966, 1982, 1985; Watkin & Clements, 1978; Parsons *et al.*, 1991). Taller tillers are preferred to shorter ones (Hodgson & Ollerenshaw, 1969). Selectivity of grazing is a function of stocking rate. A tiller or plant may be defoliated several times during a grazing period, while others may not be grazed at all. As grazing pressure is increased, selectivity between species will be reduced, but in the extreme, animals may prefer to starve rather than eat a really disliked species (Watkin & Clements, 1978). Both the botanical composition and the herbage production of grazed pasture often differ from values in a cut sward (Korte, 1981).

In a study on a mixture of lucerne (*Medicago sativa*), bromegrass (*Bromus inermis*) and creeping red fescue (*Festuca rubra*) under different defoliation systems (Walton, 1983), the proportion by weight of lucerne increased under cutting at the flowering stage, remained constant under rotational grazing, but decreased under continuous stocking because it was preferentially and repeatedly grazed, resulting in depletion of reserves in the root. The proportion by weight of creeping fescue increased under continuous stocking due to escape from grazing, yet declined under both rotational grazing and cutting because of shading by the other species. The proportion of bromegrass remained constant under rotational and continuous stocking, and decreased under cutting defoliation because the late cut took place after seed head formation when the level of carbohydrate reserve was low.

In swards of Roa tall fescue- white clover (Moloney *et al.*, 1993), Roa contributed 56% to annual herbage accumulation under summer rotational grazing compared to 37% under continuous summer stocking. In contrast Nui perennial ryegrass- white clover, Nui contributed 26% more to annual herbage accumulation under continuous summer stocking than under rotational grazing.

Many studies have compared pasture and animal production under cutting or grazing managements. For example, Frame (1966) found with perennial ryegrass-white clover swards that plants grazed by sheep out-yielded cut plants in both accumulated dry matter and digestible organic matter. Bryant and Blaser (1968) on the other hand found that clipped swards consistently out-yielded cattle grazed swards of both white clover and lucerne cocksfoot pastures. Richards *et al.* (1976) quantified the difference between defoliation by cutting and defoliation by sheep for well-fertilized grass pastures. They found that swards producing less than 10000 kg herbage per ha produced more under grazing whereas in swards with yields greater than 12500 kg per ha cutting outproduced grazing. They suggested that grazing resulted in excessive wastage at high herbage availabilities.

The results of the above experiments indicate that both cutting and grazing experiments are necessary for evaluation of pasture species.

2.7 Factors influencing regrowth after defoliation

2.7.1 Residual leaf area

Leaf area is of great importance in pasture growth because it plays the principal role in intercepting light for photosynthesis. Watson (1947) found a positive correlation between crop growth rate (CGR) and leaf area index (LAI). Brougham (1956) examined the influence of residual leaf area on light interception and recovery after defoliation in a ryegrass sward containing some red and white clover. The pasture was defoliated to 2.5, 7.6 and 12.7 cm and regrowth rate was found to increase as the residual LAI increased. Bircham and Hodgson (1983) reported that when pastures of ryegrass-white clover were maintained below a LAI of 1.9, the growth and net production of pasture decreased.

The contribution of residual leaf area to regrowth after defoliation of pasture plants has been considered in many other studies. For instance, Booysen and Nelson (1975) found that both residual leaf area and carbohydrate reserves contribute energy to regrowth of tall fescue. However, residual leaf area contributed more to regrowth than carbohydrate reserves. Hart (1987) reported that severe defoliation of white clover (leaf area reduced to 17%) reduced the rate of regrowth and final leaf size more than lenient defoliation (leaf area reduced to 44%). When cocksfoot tillers were cut to leave two leaf laminae, the plants produced more dry matter during the regrowth period than when all leaves were removed from the tillers (Ward & Blaser, 1961).

Davies (1966, 1974) suggested that regrowth in vegetative plants related to stubble weight rather than to leaf area, and conducted an experiment to determine the importance of the proportion of leaf tissue in the stubble to regrowth after defoliation. She found that the removal of older laminae had less effect on growth rate than the removal of younger laminae. However, removal of two or all laminae resulted in a subsequent reduction in tiller production, relative growth rate and leaf appearance. Gold and Caldwell (1989) have also suggested that loss of old leaves usually has much less effect on plant recovery than loss of the same amount of young leaf.

The optimum height of defoliation varies among species and is influenced by plant growth habit. Haynes (1980) suggested that in cutting or grazing a relatively greater proportion of each tiller or stem from an upright plant is defoliated in comparison with a plant of prostrate growth habit, and hence in the latter case relatively more green leaf, stem, and sheath is left after defoliation to facilitate regrowth. For example, Davies (1960) found excessively hard grazing of cocksfoot reduced plant vigour but, with too lenient grazing, plants was apt to grow luxuriant and gain dominance within the sward. Among ryegrasses, the more prostrate cv. Ruanui is higher producing under close continuous stocking than the more upright cv. Manawa (Smetham, 1990). Recently Butler and Hodgson (1993) suggested optimum sward heights of 5.5, 5.5-10 and 10 cm for Yorkshire Fog (*Holcus lanatus*), perennial ryegrass and tall fescue respectively under continuous stocking.

2.7.2 Leaf growth

The rate of leaf growth after defoliation is important, because leaves are the primary photosynthetic organs, and an increase in LAI will increase light interception and sward growth rate (Nelson & Sleper, 1990). Horst *et al.* (1978) suggested leaf elongation rates as an acceptable criterion for estimating regrowth vigour and herbage yield potential of tall fescue. Leaf width was associated positively with leaf elongation rate (Nelson & SLeper, 1990), and both measurements have been related to leaf area expansion (Nelson & Sleper, 1990). However, Penning de Vries *et al.* (1979) indicated that leaf elongation rate was not a good indicator for yield in perennial ryegrass. Tallowin *et al.* (1989) measured leaf elongation and leaf growth rates as criteria for evaluating regrowth of perennial ryegrass under different grazing managements.

Rate of leaf expansion depends on tiller size and is inversely related to the severity of defoliation. Higher leaf expansion rates have been reported for larger (Nelson et al., 1977; Chapman *et al.*, 1983; Tallowin *et al.*, 1989), and older (Agyare & Watkin, 1967) tillers with larger lamina area (Grant *et al.*, 1981a). Also, less severe defoliation increases the rate of leaf expansion (Arosteguy, 1982; Wilman & Shrestha, 1985; Tallowin *et al.*, 1989). Lamina elongation rate per tiller increases linearly with an increase in sward surface height and herbage mass (Grant *et al.*, 1983; Bircham & Hodgson, 1983). However, such responses have not been observed in spaced plants indoors (Davidson & Milthorpe, 1966a) or when the lamina was removed and leaf sheath left intact (Davies, 1974), although Davidson & Milthorpe (1966a) suggested that extreme defoliation (all young leaves removed) reduced leaf growth rate.

The effect of harvest frequency (2 & 6 weeks) and amount of N fertilization (24 & 336 kg ha as NH_4NO_3) on leaf elongation rate of two tall fescue genotypes showed that the leaf elongation rate of plants harvested infrequently was 30% greater than that of plants harvested frequently. Also, the leaf elongation rate of a genotype with a high yield per tiller was 40% higher when harvested at 6 week intervals than at 2 week intervals, whereas the leaf elongation rate of a low yield per tiller genotype was only 16% greater. Plants receiving high rates of N had 89% higher leaf elongation rate than plants receiving low N (Volenec & Nelson, 1983). The effect of defoliation on leaf appearance and leaf size are considered in Section 2.8.

2.7.3 Leaf carbon budget

Approximately 90% of the plant dry weight results directly from photosynthetic assimilation of carbon. Respiration provides energy for synthesis and maintenance of live tissue by using about half of the CO_2 fixed in photosynthesis (Robson *et al.*, 1988). The efficiency by which a crop canopy converts solar energy to usable organic form through photosynthesis has an important role in plant breeding and pasture management (Nelson & Sleper, 1990).

Genetic variation for leaf photosynthetic rate per unit area and unit weight was found in tall fescue (Wilhelm & Nelson, 1985). Lambers and Poorter (1992) suggested that fast-growing species tend to have a higher rate of photosynthesis than slow-growing species, at least when photosynthesis is expressed per unit leaf weight. The high yielding genotypes of tall fescue and perennial ryegrass showed higher rates of photosynthesis and respiration than low-yielding ones at optimum temperature (20-25°C), but these rates were greatly depressed at high and low temperature (Burkert, 1992).

In contrast, some researchers such as Rhodes (1973) and Parsons *et al.* (1983b) for ryegrass, and Nelson (1988), and Nelson *et al.* (1975) for tall fescue, have shown little relationship between photosynthetic rate and forage yield. Nelson and Sleper (1990) and Mendrano (1992) pointed out that several factors including mesophyll cell size, environmental stress, sink to source ratio, canopy architecture and genotype by environment interaction can all affect the relationship between photosynthetic rate and plant production.

In grasses Woledge (1971) reported that the rate of photosynthesis and respiration fell as the leaf aged. Parsons *et al.* (1983a,b) found that growing leaves and fully expanded leaves together contributed some 75% of the total photosynthesis of the canopy whereas leaf sheaths and clover stolon contributed less than 5% to gross photosynthesis. Therefore, the proportion of leaves of different ages (Woledge & Leafe 1976; Davidson *et al.*, 1981) and also the position of these within the canopy (Sheehy & Peacock, 1977) are important in terms of photosynthetic output.

One of the major effects of defoliation on production is to reduce photosynthesis by reducing total leaf area (Briske, 1991) and life-span of leaf area, but it has also been suggested that different patterns of defoliation may affect photosynthesis by altering leaf age structure in the canopy (Parsons *et al.*, 1988). Woledge (1978) suggested that defoliation exposes to higher light intensities older leaves and leaves that developed at lower light intensities, and this may change the rate of canopy photosynthesis of plants subjected to defoliation. Reproductive swards have a greater photosynthetic potential than vegetative swards (Parsons & Robson 1981, 1982) due to stem elongation and better penetration of light into the canopy (Woledge, 1978, 1979).

The photosynthetic activity of plants after defoliation has been considered in several studies. Richards (1993) described two distinct phases; the first is a transient period of one to a few days after defoliation when the photosynthetic activity of plants decreases, and the second is a compensatory phase when plants show higher photosynthetic capacity on remaining and regrowing leaves relative to undefoliated plants. Painter and Detling (1981) reported that net photosynthesis of undamaged *Agropyron smithii* tillers declined 6-7% within 30 minutes after all other attached tillers were removed. In *Agropyron desertorum* Nowak and Caldwell (1984) observed a temporary period of reduced (up to 30%) photosynthesis compared with equivalent leaves on undefoliated plants after each of three sequential clippings. Compensatory photosynthesis has been observed in a number of species such as *Agropyron desertorum* (Caldwell *et al.*, 1981; Nowak & Caldwell, 1984), *Festuca ovina* (Atkinson, 1986), *Lolium multiflorum* (Gifford & Marshall, 1973) and *Lolium perenne* (Woledge, 1977). Increase in carboxylase activity and leaf conductance to carbon dioxide, and a decrease in feed-back inhibition resulting from a greater demand for carbon following defoliation (i.e. greater sink strength), have been suggested as potential mechanisms contributing to compensatory photosynthesis (Briske, 1991).

In *Lolium perenne* the compensatory photosynthesis of developing leaves on defoliated plants was inhibited when they were maintained in a shaded environment (Woledge, 1977). It was suggested that compensatory photosynthesis in *Lolium perenne* was light dependent, rather than being determined only by source-sink or hormonal changes in the plant (Woledge, 1977).

In contrast, in uniculm barley (Ryle & Powell, 1975), and in *Juncus squarrosus* and *Deschampsia flexuous* (Atkinson, 1986) photosynthetic rates of leaves of defoliated plants were lower than undefoliated plants. The different net photosynthetic response between these studies and those reporting compensatory photosynthesis has not been adequately explained, although substantial physical damage or repeated defoliation seem to be common precursors to these observations (Richards, 1993).

2.7.4 Tillering activity

Grass tillers have two important functions in terms of establishment of seedlings and the regeneration of the sward following the removal of terminal meristems by cutting or grazing (Jewiss, 1972). Low tillering rates may result in poor perenniality (Cooper & Saeed, 1949). Davies (1977) suggested that to persist a sward must maintain an effective tiller population evenly distributed over the pasture area. Tiller density influences the development of leaf area index under frequent defoliation (Hill *et al.*, 1985), and thereby affects the efficiency of light interception and consequently herbage yield. In annual ryegrass (*Lolium rigidum*) the rate of regrowth in terms of an increase in LAI after defoliation increased with the number of tillers up to about 10,000 tillers per m^2, after which it remained constant (Cocks, 1974). Davies (1966) reported that regrowth of S24 perennial ryegrass was related to tiller density between 5,400 and 8,700 tillers per m^2.

Under spaced-plant conditions, Nelson *et al.*, (1977) showed that the rate of tillering of tall fescue was about 1.5 times more important than weight per tiller in determining yield per plant. Under sward conditions, however, Hart *et al.* (1971) found that tiller density of tall fescue tended to stabilize for a given management system and remained nearly constant during the vegetative growth period. When tiller density is stable, yield is determined largely by weight per tiller. Hodgson *et al.* (1981) have shown that tiller numbers and tiller weights in vegetative swards maintained at different herbage masses by continuous grazing were related to each other through the self-thinning law (-3/2) established by Yoda *et al.* (1963). When the swards were maintained at low herbage mass, tiller numbers increased at the expense of tiller size, and vice versa. Under rotational grazing tiller numbers were reduced relative to the control (sward maintained at 3.5 cm height by continuous stocking), but the reduction was compensated for by an increase in tiller size (Grant *et al.*, 1988).

In a comparative study, both results from the sward of perennial ryegrass maintained between 700 and 2800 kg ha^{-1} herbage mass, and values from hand-planted perennial ryegrass followed the pattern of tiller activity according to the self-thinning law (Grant *et al.*, 1981b). However, the latter results have been restricted to experiments in which swards had attained a closed canopy and tiller numbers had either reached a maximum or were declining. An increase in the cutting height of transplanted tall fescue plants from 5 to 10 cm did not affect tiller density, but increased yield per tiller (Zarrough *et al.*, 1983a,b). Davies (1988) suggested that the self-thinning law does not cover circumstances in which tiller numbers are increasing or where (as in very short, hard-grazed swards) there is a loss of plant cover.

Severe defoliation (less than 2 cm stubble height) of ryegrass swards resulted in reduced growth and production of plants due to low tillering rates and small tiller sizes (Grant et. al., 1983; Bircham & Hodgson, 1983). Low tillering capacity in prairie grass was the major limitation to its performance in pastures relative to Italian ryegrass (*Lolium multiflorum*) (Hill *et al.*, 1985).

2.7.5 Meristem damage

The fate of apical meristems (growing points) during defoliation greatly affects subsequent regrowth. Defoliation that permits the apical meristem to remain intact allows continued shoot growth, whereas removal of apical meristem forces regrowth to occur from basal meristems or from meristems at the axils of leaves (Booysen *et al.*, 1963).

The presence of active meristems on plants after defoliation allows leaf expansion to result solely from expansion of already formed cells, rather than requiring new cell production (Briske, 1986, 1991; Richards, 1993; Culvenor *et al.*, 1989a). When defoliation allows growing tissues to remain intact, the compensatory processes of increased export from source tissues and increased proportional allocation to growing shoot sinks both contribute to rapid re-establishment of the photosynthetic canopy after defoliation (Richards, 1993). For example, in uniculm barley in which leaf laminae are removed to leave only two old leaves intact, the proportion of assimilate allocated to growing shoot tissue rapidly increased after defoliation. Previously older leaves exported their assimilate to root (Ryle & Powell, 1975). When actively growing tissues are absent, the available assimilate would be allocated to other sink tissues, such as roots and storage areas such as the sheath and stem bases in grasses (Bucher *et al.*, 1987a,b). Richards and Caldwell (1985) reported that the regrowth rate of two wheatgrass species (*Agropyron desertorum* and *Agropyron spicatum*) was reduced more than 5-fold when regrowth occurred from lateral meristems that had to be activated compared with regrowth from active intercalary and apical meristems remaining on the defoliated plants. However, removal of the stem apex of main tillers may terminate apical dominance, and allow development of lateral tillers that have been previously dormant at the basal nodes of the stem, thus resulting in an increase in tiller density (Jewiss, 1972).

The position of the stem apex is important in relation to defoliation management. For example, regrowth rate in *Paspalum dilatatum* is greater than in *Panicum coloratum* because the aerial shoots of the former species are less vulnerable to defoliation due to the presence of more basal shoots (Holt & McDaniel, 1963).

2.7.6 Carbohydrate reserves

Deregibus *et al.* (1982) pointed out that Graber *et al.* (1927) was the first to demonstrate that carbohydrate reserves in roots of alfalfa were utilized for maintenance and for regrowth of plants after defoliation. Numerous authors have confirmed this hypothesis for a range of plant species (McCarthy 1935; McIlvanie, 1942; Sullivan & Sprague, 1943). In contrast, May (1960) found that carbohydrate reserves were used as a respiratory substrate rather than for regrowth. Possible reasons for a lack of contribution of carbohydrate reserves to regrowth are (i) the contribution of current photosynthesis from the residual shoot is large, (ii) morphological or meristematic features limit regrowth, or (iii) carbohydrate reserves are inadequately assessed by common procedures (Richards & Caldwell, 1985).

The depletion in carbohydrate reserves following defoliation has been observed by many researchers such as Zarrough and Nelson (1980), and Volenec (1986) in tall fescue, Danckwerts and Gordon (1987) and Gonzalez *et al.* (1989) in perennial ryegrass and in some other species as reviewed by Deregibus *et al.* (1982). These results indicate that carbohydrate reserves are utilized for plant growth and maintenance when photosynthetic capacity is limited (Deregibus *et al.*, 1982).

Evidence that carbohydrate levels may directly influence regrowth has been provided by several authors. For example, Alberda(1966) kept perennial ryegrass in the dark for 3.5 days to reduce the level of carbohydrate reserves in the stubble before defoliation. Regrowth in these plants was substantially less than control plants receiving continuous light. Similarly, the amount of etiolated regrowth of tall fescue plants with shorter stubble height (25 mm) was lower than that with a taller stubble height (100 mm) (Matches, 1966).

It has not always been possible to show the correlation between carbohydrate reserves and regrowth. For example, Buwai and Trlica (1977) found that carbohydrate reserves in roots of bluegrass (*Bouteloua gracilis*) were not affected by defoliation, but total carbohydrate reserves of Western wheatgrass (*Agropyron smithii*) were reduced. Also, there was no correlation between total nonstructural carbohydrates and regrowth for *Agropyron desertorum* or *Agropyron spicatum* (Richards & Caldwell, 1985). Anderson *et al.*, (1989) reported that tiller development of *Panicum virgatum* was unrelated to total nonstructural carbohydrates after defoliation. However, when apical meristems were removed, total nonstructural carbohydrate in above ground tissue declined more during regrowth than when apical meristems remained intact (Anderson *et al.*, 1989).

The dependence of regrowth following defoliation upon carbohydrate reserves will be minimal and of short duration (2-4 days) if adequate leaf area remains for continuing photosynthesis (Caldwell, 1984). However, dependence on organic reserve componds, both protein and carbohydrates, will be magnified and prolonged as severity of defoliation increases, particularly when regrowth is dependent upon replacement by new tillers (Vickery, 1981). Carbohydrate concentrations of 1-6% have been suggested as minimum reserve levels in grasses (Caldwell, 1984). Caldwell (1984) concluded that relatively small quantities of carbohydrate reserves may be needed, but that they play a critical role in regrowth when the plant is unable to support regrowth directly from photosynthesis.

2.7.7 Stage of growth

During the vegetative stage, the growing points of tillers are normally located close to the ground surface with the result that regrowth can continue from both terminal and axillary meristems (Jewiss, 1972). However, during reproductive development internodes begin to extend and expose the stem apex to defoliation. Once defoliation removes the stem apex of reproductive tillers the remaining tiller stubs cannot grow and will ultimately lose weight and die (Davies, 1977). The persistence of the plant depends on the regrowth of existing tillers, or initiation of new tillers from axillary buds (Davies, 1977).

Defoliation management in relation to growth stages has a critical effect on the regrowth of plants. For example, in grasses tillering is restricted during the reproductive stages due to either apical dominance of reproductive tillers, or competition for available assimilate, or both (Jewiss, 1972; Colvill and Marshall, 1984). Close grazing of *Agropyron desertorum* resulted in termination of apical dominance and initiated growth of a second crop of tillers which were mostly vegetative (Hyder & Sneva, 1963). Tiller production was reduced more when reproductive tillers were cut to 1 cm above ground than when cut to 5 cm (Davies, 1988). In perennial ryegrass, Matthew (1992) suggested that leaving some reproductive tillers to develop to anthesis before defoliation promoted regrowth and survival of daughter tillers formed following flowering, by translocation of some assimilate from reproductive stubs to daughter tillers.

Brougham (1961) reported that during reproductive growth 'Grasslands Manawa' ryegrass apices were elevated more than those of 'Grasslands Ruanui' perennial ryegrass, and this was the reason for poor persistence of Manawa ryegrass under close grazing in summer. If seed production is the objective, close defoliation of the sward may be detrimental to seed production. Davies (1988) reported that very close defoliation (2-3 cm surface height) substantially reduced the total number of reproductive tillers per plant.

2.7.8 Root growth

Roots play an important role in plant function in terms of water and nutrient uptake. They also act as food reserves for regrowth in some herbaceous species. These root functions were affected when the growth of roots was suppressed as a result of defoliation of the shoot (Davidson & Milthorpe, 1966b; Clement *et al.*, 1978; Lambers, 1979; Caldwell *et al.*, 1987).

The effect of defoliation on root growth has been studied by many workers. Weaver and Darland (1947) found undefoliated plants had greater root weights, more lateral branching, deeper roots and less dead root material than did defoliated plants. Evans (1971, 1973) reported that a single defoliation of perennial ryegrass caused a rapid decrease in root elongation and then a gradual recovery. Repeated defoliation prolonged the suppression of elongation and even caused root death. Weinman and Goldsmith (1948) found no significant reduction in root weight of bermuda grass (*Cynodon dactylon*) when plants were clipped at monthly, biweekly or weekly intervals. However, when clipping continued for 25 weeks at weekly intervals, plants had lower root weights compared to the control. Ryle and Powell (1975) found from using radioactive tracer that for four days after defoliation, assimilate that would normally have gone to the roots was retained in the shoots. Caloin et al. (1990) found that after defoliation the shoots of *Dactylis glomerata* grow exponentially with time, whereas the growth rate of roots slowed markedly. A decrease in root fresh weight was observed under the severe defoliation.

Conversely, undefoliated *Bouteloua gracilis* and *Agropyron smithii* had only slightly greater root weights than did plants defoliated four times by removal of 90% of the foliage during each clipping (Buwai & Trilica, 1977). Matthew (1992) reported no significant differences between the root mass of perennial ryegrass swards under both lax and hard grazing systems (1800 kg ha^{-1} and 800 kg ha^{-1} residual herbage mass respectively).

2.7.9 Plant competition

Competition among plants mainly occurs for light, water and nutrients (Rhodes, 1968), although competition for oxygen, carbon dioxide, and space may also occur.

Species grazed less severely, capable of growing more rapidly following defoliation, or possessing a combination of these two resistance components, have a competitive advantage within a grazed community of plants. These species, through the possession of a greater leaf canopy area, are able to intercept greater amounts of solar energy and assimilate greater amounts of carbon, therefore further enhancing their competitive ability (Briske, 1991).

Cutting more frequently reduced the dominance of perennial ryegrass and aided the increase in competitiveness of paspalum (*Paspalum dilatatum*) due to the more prostrate habit of the latter species. This allowed paspalum to maintain more leaf area after defoliation and to achieve more efficient use of incident light than the perennial ryegrass (Harris *et al.*, 1981a,b). Tall fescue has been shown to be more competitive with perennial ryegrass under infrequent defoliation and poorly competitive under frequent defoliation (Sato et al., 1990). Crested wheatgrass (*Agropyron cristatum*) showed greater leaf replacement potential than bluebunch wheatgrass (*Elymus spicatum*) following similar defoliation intensity. This response was due in part to the ability of crested wheatgrass to rapidly initiate a greater number of tillers and to allocate carbon to re-establish photosynthetic surfaces while temporarily decreasing allocation below ground (Caldwell *et al.*, 1981; Richards, 1984). Brock *et al.* (1982) noted that ryegrass was markedly superior to tall fescue due to higher germination, root elongation, tillering rates and faster regrowth after defoliation.

The competitiveness of a species is dependent on the companion species with which it is grown (Harris *et al.*, 1981a,b; Alexander & Thomson, 1982). Production of bluebunch wheatgrass plants subjected to 50% canopy removal was equivalent to the production of undefoliated plants growing with competition. When associated vegetation was removed, defoliated plants produced three times the biomass of undefoliated plants growing with competition (Briske, 1991). These results indicated that the ability of plant to respond to defoliation is not only determined by an inherent suite of morphological and physiological characteristics, but also by competitive pressure from associated species (Caldwell, 1984). Laskey and Wakefield (1978) observed that reduced stands of birdsfoot trefoil (*Lotus comiculatus*), when grown with perennial ryegrass, appeared to be due to rapid seedling emergence of the grass at a critical stage in the early growth and development of the legume. The slower growing grasses, Kentucky bluegrass (*Poa pratensis*) and creeping fescue (*Festuca rubra*), did not inhibit growth of birdsfoot trefoil. Blaser *et al.* (1952) suggested that timothy and meadow fescue offer sufficiently low competition to enable tall fescue to thrive in a mixed sward. Frame and Hunt (1964) have shown the unsuitability of cooksfoot and perennial ryegrass as companion for tall fescue. Recently, Hunt and Dunn (1993) reported that in the tall fescue- perennial ryegrass mixture, tall fescue lacked competitiveness and had decreased from 51% in the first year to 11% of the plant population 5 years after planting, whereas tall fescue remained competitive with Kentuky bluegrass in the mixture by maintaining 44% of the plant population compared with 47% for Kentuky bluegrass.

2.8 Effects of defoliation on plant size and structure

The size and structure of a plant grown individually or in a sward is influenced by defoliation management. The magnitude of this effect varies between species, varieties or genotypes. The change in plant structure can modify the rate of dry matter production in terms of both quantity and quality (Davies, 1977).

Tiller number and tiller size of perennial ryegrass swards were different under contrasting sheep grazing managements. Under rotational grazing, tiller size increased at the expense of decrease in tiller population density, but continuous stocking resulted in a higher tiller population with smaller tillers (Chapman *et al.*, 1983; Brock & Fletcher, 1993). Grazed populations of several perennial grasses have been observed to consist of individuals with smaller basal area in comparison with ungrazed populations (Pond, 1960; Hickey, 1961) (See also Section 2.7.4).

There is conflicting evidence on the sensitivity of leaf appearance to defoliation management. Leaf appearance rate is mostly under the control of temperature, radiation, soil moisture and mineral nutrition (Anslow, 1966). Leaf appearance rate in perennial ryegrass was the same under two continuous stocking regimes, either 35 mm or 75 mm constant sward height (Tallowin *et al.*, 1989). Parsons *et al.* (1983) reported similar results in swards maintained at 1 or 3 LAI by continuous grazing. Removal of one leaf blade per tiller did not influence the rate of leaf appearance in *Phalaris arundinacea* (Begg & Wright, 1964) or in perennial ryegrass (Davies, 1974). But when two or more leaves were removed, the rate of leaf appearance was reduced, and the degree of reduction varied among genotypes (Davies, 1974). Hume (1991a) found that the leaf appearance rate of prairie grass and perennial ryegrass was reduced by both increased cutting frequency (1, 2 or 4 weeks) and lower cutting height (3 and 6 cm stubble height).

The main effect of defoliation is to change the size of leaves (Forde, 1966). For example, in an experiment on perennial ryegrass swards cut four times at 5 day intervals, the lengths of leaf laminae and sheaths reached 81 and 33 mm respectively after 3 weeks compared with 129 and 42 mm when cut only on the last of the four dates (Davies, 1977). Davies (1977) reported that when swards of S.23 perennial ryegrass were cut five times to heights of 10 cm and 2.5 cm, sheath lengths were 8.0 and 3.7 cm in a long-leaved genotype and 4.5 and 2.3 cm in a short-leaved genotype, respectively. Davies (1974) observed narrower leaves and lower leaf weights with increasing removal of leaf lamina for each tiller. Also, leaf lamina, leaf sheath and seed head weights of perennial ryegrass were lower under continuous grazing than rotational grazing (Brock & Fletcher, 1993). Plants also respond to defoliation by increasing specific leaf area (Chapman & Robson, 1988).

2.9 Summary and conclusion

In this chapter, the performance of tall fescue mainly under drought conditions has been compared with perennial ryegrass. The experiments reviewed demonstrate the potential of tall fescue as an alternative to perennial ryegrass, particularly in conditions of moisture limitation. However, they also show limitations in the growth and persistence of tall fescue in response to severe defoliation pressure under both intermittent and continuous defoliation.

Plant responses to defoliation are shown to be influenced by variation in tillering activity and leaf growth, residual leaf area, photosynthetic activity, root growth and carbohydrate reserves. The relative importance of these variables, and their influence upon plant persistence and production, differ between species. There is relatively little comparative information on the plant characteristics influencing regrowth of tall fescue and perennial ryegrass, particularly under conditions of continuous stocking. These factors are the basis for studies reported in the following chapters.

CHAPTER 3: Regrowth and competitiveness of tall fescue under grazing management

3.1 Introduction

Tall fescue has been suggested as having potential in New Zealand pastoral farming (Brock, 1983). The evaluation of this grass has mainly been under intermittent defoliation, although many grazing systems involve frequent grazing or continuous stocking. The available information indicated low competitive ability and poor persistence under continuous stocking (e.g. Vartha, 1977; Lancashire & Brock, 1983). Therefore, this experiment was conducted to study the behaviour of tall fescue under continuous stocking and to provide basic information for more detailed investigations on the physiological and morphological factors influencing the response of tall fescue to defoliation.

3.2 Materials and methods

3.2.1 Experimental conditions

The experiment was carried out between November 1990 and April 1991 at the Pasture and Crop Research Unit, Massey University, Palmerston North. The pasture had been sown as a mixture of tall fescue (*Festuca arundinacea* Schreb. cv. 'Grassland Roa') 25 kg ha^{-1} and white clover (*Trifolium repens* L. cv. 'Grasslands Tahora') 3 kg ha^{-1} in 1988. The soil at the site is Tokomaru silt loam (Cowie *et al.*, 1978). It is classified as an Aeric Fragiaqualf (gleyed, yellow-grey earth)(Cowie 1972).

Mean annual rainfall is 955 mm; the monthly rainfall, temperature and sunshine over the period of the trial is presented in Appendix 3.1.

The experiment was carried out on a 2-year old sward containing tall fescue and white clover as sown species and some volunteer grasses, especially perennial ryegrass (*Lolium perenne* L. cv. 'Grassland Nui'). The sward had been fenced to provide three plots each about 0.2 ha continuously stocked by sheep to maintain sward surface heights at 30-40 mm (H, hard), 50-60 mm (M, medium) and 90-100 mm (L, lax grazing) by manipulating animal numbers (see Plate 3.1 and Appendix 3.2). Treatments were randomly distributed to plots without replication, and were maintained from September 1989 until the measurement described here commenced in November 1990. Individual plots were divided into quarters as four internal replicates (blocks), and an area of about 1m by 2m for each treatment (with and without white clover) was marked in each quarter using pegs. Clover from the "no-clover" area in each quarter was removed by using 0.6 kg ai ha^{-1} of clopyralid about 10 days before starting measurements. Also, the height of the sward of marked areas was trimmed to the above mentioned sward heights and all measurements were carried out in each quarter (for both with and without clover areas) per plot. Measurements started on November 1990 and were repeated in December 1990 and April 1991 during the summer and autumn.

3.2.2 Measurements

In each treatment area the number of tillers of tall fescue was counted on 6 turf samples (5 cm by 10 cm). Turf samples were cut to ground level with a scalpel in the laboratory and then dissected into categories for estimation of herbage mass of tall fescue, white clover and other grasses. Pseudostem and laminae of tall fescue were separated from each other. All green laminae of tall fescue were cut from the point of emergence, and the total leaf area of all tillers in each turf was calculated using an electronic leaf area meter. The leaf area of each turf was used for calculating leaf area per tiller (LAT) by dividing by the total number of tall fescue tillers in the same turf, and leaf area index (LAI) by dividing by the turf area. The lamina and pseudostem mass of tall fescue and the masses of other grasses and white clover were washed free of soil and oven dried for 48h at 80°C before being weighed. Tiller weight was calculated by dividing the herbage mass of tall fescue in each turf by the tiller

Lax grazing plot

Hard grazing plot

Plate 3.1: General views of the grazing experiment

number for tall fescue in that turf.

In order to estimate leaf elongation rate (mm $tiller^{-1}$ day^{-1}), 10 to 12 tillers were marked along 2 transects (each 2 m in length) in each marked area (with and without clover) per quarter. Tillers were marked with plastic coated wire at 20 cm intervals. The length of all laminae (from the point of emergence to the tip of the lamina) on marked tillers was measured using a ruler with a precision of 1 mm on three consecutive occasions at intervals of 4, 5 and 7 days during November, December and April respectively (Davies, 1981). New tillers were marked to replace lost tillers. Leaves were measured individually, and recorded as immature, mature (when the lamina was subtended at an angle to the sheath, and the ligule was apparent), senescent (more than 80% of whole lamina chlorotic) and defoliated, for the following calculations:

Leaf elongation rate (LE) was estimated from leaves that had not been grazed during each interval (Davies, 1981) as;

$$LE = \frac{\Sigma(L2 - L1)}{(T2 - T1) \times N} \quad (\text{mm tiller}^{-1}\ \text{day}^{-1})$$

Where T1 and T2 are the times at which the measurements were made, L2 and L1 are the lengths of mature and immature leaves at T1 and T2, and N is the number of ungrazed tillers.

Leaf senescence (LS) was estimated from the differences in the senescent length of mature leaves as;

$$LS = \frac{\Sigma(S2 - S1)}{(T2 - T1) \times N} \quad (\text{mm tiller}^{-1}\ \text{day}^{-1})$$

Where T1 and T2 are the times at which the measurements are made, S2 and S1 are the length of senescent leaves at T1 and T2, and N is number of ungrazed tillers.

Net leaf elongation rate (NLE) was calculated as;

NLE = LE - LS (mm $tiller^{-1}$ day^{-1})

Net elongation rate per unit area (NLEA) was calculated as;

NLEA = (NLE x TN) / 1000 (m m^{-2} day^{-1})

Where TN is tiller population density per unit area.

Net leaf weight production per ha (NLP) was calculated as follows;

NLP = NLEA x SLL x 10000 (kg leaf dry weight ha^{-1})

Also SLW (specific leaf weight) was calculated as:

SLW = LW / LA (mg cm^{-2})

Where LW is leaf dry weight, and LA is the area of the same leaf.

Specific leaf weight per unit length (SLL) was calculated as;

SLL = SLW/100 (mg mm^{-1})

Leaf defoliation was defined by three parameters: frequency of defoliation (the proportion of marked tillers that had been grazed in each measurement interval), severity of defoliation (the proportion of leaf lamina removed from defoliated tillers), and leaf defoliation pressure (product of frequency and severity of defoliation).

Calculation of leaf length, leaf elongation and senescence rate and estimates of leaf defoliation parameters (frequency, severity and pressure) were done using a specially written computer program (Butler, pers. comm.).

3.2.3 Statistical analysis

The data were analysed by analysis of variance using the general linear model (GLM) procedure of SAS (SAS Institute Inc. 1991). Three levels of grazing intensity (lax, medium, hard), and two levels of clover (with clover (WC) and without clover (NC)) were considered as a factorial combination of treatments for analysis of variance. Because of internal replications of grazing treatment, a pooled randomised complete block design (RCB) with 4 replicates was used for analysis of variance. Data obtained from turf samples were considered as subsamples for analysis. The botanical composition of plots with and without clover was analysed separately as a single RCB with subsamples. The three measurements in November, December and April were analyzed separately.

3.3 Results

3.3.1 Herbage mass

The analysis of variance of tall fescue herbage mass in April based on a pooled randomised complete block design with subsamples is shown in Appendix 3.3. Total herbage mass of tall fescue and its leaf and pseudostem mass under different grazing treatments were significantly different in all measurement periods. Swards maintained lower herbage mass with increasing severity of grazing (Table 3.1). Overall, total herbage masses of treatments L and M were higher in November than in December and April (Table 3.1).

Leaf mass, pseudostem mass and total herbage mass of tall fescue grown with and without clover is shown in Table 3.2. Removal of white clover resulted in an increased leaf mass and total herbage mass in December and April, and increased pseudostem mass in April. The interaction between grazing and clover treatments was not statistically significant.

3.3.2 Botanical composition

Estimates of botanical composition were analysed within periods, and separately for treatments with and without clover (see Tables 3.3, 3.4 and Figures 3.1, 3.2). Overall, total biomass increased as sward surface height increased and was relatively unaffected by the presence or absence of white clover. In both conditions tall fescue had a lower herbage mass contribution to the sward under hard grazing than for the other treatments and tended to be replaced by white clover and other grasses, especially perennial ryegrass (Tables 3.3, 3.4 and Figures 3.1, 3.2).

Removal of white clover increased the proportion of tall fescue in the sward, but it also increased the proportion of other grasses, especially under hard grazing (Figures 3.1, 3.2). However, over all measurement periods the herbage mass of other grasses under the different grazing managements was

Table 3.1: Effect of grazing management on leaf, pseudostem and total herbage mass (g m^{-2}) of tall fescue.

	Leaf mass			Pseudostem mass			Total mass		
	NOV.	DEC.	APR.	NOV.	DEC.	APR.	NOV.	DEC.	APR.
Lax	80	80	58	134	80	104	214	160	162
Medium	54	43	36	74	64	62	128	108	98
Hard	22	19	17	16	21	22	38	40	39
SEM	4	5	3	9	9	6	11	13	8
F	***	***	***	***	**	***	***	*	***

*:P<0.05; **:P<0.01; ***:P<0.001; NS: No significant difference

Table 3.2: Effect of grazing management on leaf, pseudostem and total herbage mass of tall fescue grown with and without clover (g m^{-2}).

	Leaf mass			Pseudostem mass			Total mass		
	NOV.	DEC.	APR.	NOV.	DEC.	APR.	NOV.	DEC.	APR.
With clover	48	38	29	71	45	52	118	83	81
No clover	57	57	46	79	65	74	136	122	120
SEM	4	4	3	7	7	5	9	10	7
F	ns	*	**	ns	ns	*	ns	*	**

Table 3.3: Herbage mass of tall fescue, white clover, other grasses and total biomass (g m^{-2}) under different grazing management: with clover.

	NOV.					DEC.					APR.				
	L	M	H	SEM	F	L	M	H	SEM	F	L	M	H	SEM	F
Tall fescue	210	114	32	12	***	119	99	32	4	***	114	103	24	13	*
White clover	36	59	82	6	**	95	90	131	18	ns	54	56	102	17	ns
Other grasses	209	190	103	32	ns	292	132	95	52	ns	241	150	167	63	ns
Total biomass	455	363	217	37	**	506	321	258	46	*	409	309	293	18	**

L: Lax; M:Medium; H: Hard grazing

Table 3.4: Herbage mass of tall fescue, other grasses and total biomass (g m^{-2}) under different grazing management: without clover.

	NOV.					DEC.					APR.				
	L	M	H	SEM	F	L	M	H	SEM	F	L	M	H	SEM	F
Tall fescue	218	142	43	14	***	202	116	48	23	***	210	93	55	15	***
Other grasses	184	126	156	28	ns	361	245	192	54	ns	239	217	233	34	ns
Total biomass	402	269	199	31	**	554	361	239	47	**	449	309	288	33	*

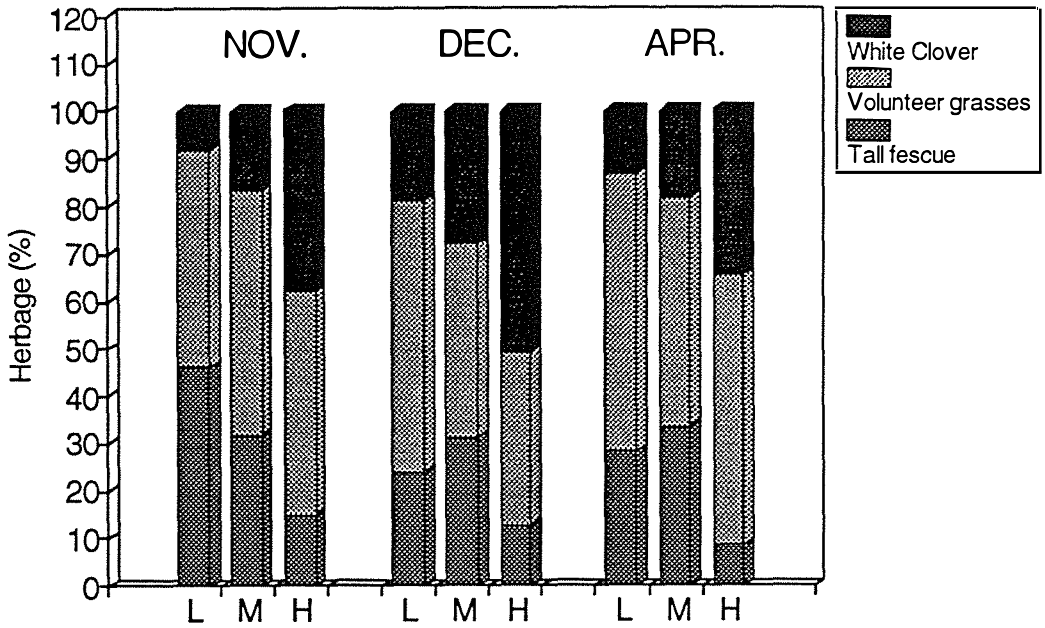

Figure 3.1: Botanical composition of pastures grown with clover

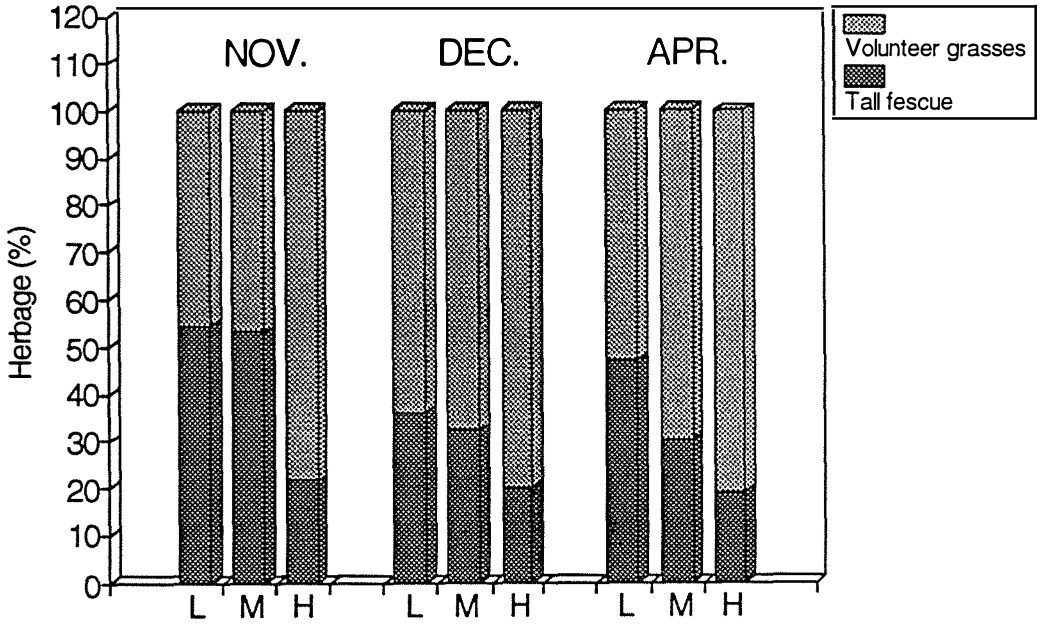

Figure 3.2: Botanical composition of pastures without clover

not significantly affected by the presence of clover (Tables 3.3, 3.4). Herbage mass of white clover was not significantly different between grazing treatments during December and April, but its contribution to herbage production increased as the severity of grazing increased, and was higher in December than in November or April (Table 3.3 and Fig 3.1).

3.3.3 Tiller population density and tiller weight

The effect of grazing management on tiller population density and tiller weight of tall fescue is shown in Table 3.5. There were no statistically significant differences between tiller number in the various grazing treatments during November and December, but treatment effects were significant by April (Table 3.5). Tiller population densities were higher under lax and, especially, medium grazing than under hard grazing. The effect of grazing treatments on tiller weight was significant in all three experimental periods (Table 3.5). Tiller weight decreased as the severity of defoliation increased. Tiller weight tended to decrease with time in the L and M treatments, but in the H treatment tiller weight was unchanged over time (Table 3.5).

The results for tiller number and tiller weight of tall fescue grown with clover and without clover are given in Table 3.6. Removal of white clover resulted in an increase in tiller population density for tall fescue by April, but there was no significant effect on tiller weight at any stage. The interaction between grazing treatment and removal of white clover was not statistically significant for either tiller number or tiller weight.

Table 3.5: Effect of grazing management on tall fescue tiller population density(tiller m^{-2}) and tiller weight (mg $tiller^{-1}$).

Treatments	Tiller number			Tiller weight		
	NOV.	DEC.	APR.	NOV.	DEC.	APR.
Lax	3450	3320	4460	65	51	38
Medium	4800	4040	4880	35	35	23
Hard	3150	3200	2990	13	13	14
SEM	501	247	452	2.2	2.9	1.9
F	ns	ns	*	***	***	***

Table 3.6: Tiller population density (tiller m^{-2}) and tiller weight (mg $tiller^{-1}$) of tall fescue grown with and without clover.

Treatments	Tiller number			Tiller weight		
	NOV.	DEC.	APR.	NOV.	DEC.	APR.
With clover	3460	3350	3480	38	28	24
No clover	4140	3690	4740	39	36	26
SEM	409	201	369	1.8	2.4	1.6
F	ns	ns	*	ns	ns	ns

3.3.4 Leaf area index and leaf area per tiller

In the mixed swards of tall fescue, white clover and other grass components only the leaf area of tall fescue was measured and used for determination of leaf area index (LAI) and leaf area per tiller (LAT). As Table 3.7 shows, grazing management had a significant effect on LAI and LAT of tall fescue during all three experimental periods. Both LAI and LAT were highest under lax grazing, lower under medium and lowest under hard grazing treatments. Removal of white clover resulted in an significant increase in LAI by December and April and for LAT by April (Table 3.8). The interaction between grazing treatments and clover treatments was not significant.

Table 3.7: Effect of grazing management on tall fescue leaf area index(LAI)(m^2) and leaf area per tiller(LAT)(mm^2).

Treatments	LAI			LAT		
	NOV.	DEC.	APR.	NOV.	DEC.	APR.
Lax	1.28	1.22	0.66	385	395	166
Medium	0.92	0.63	0.44	267	172	96
Hard	0.35	0.28	0.20	127	88	78
SEM	0.08	0.09	0.04	29	30	10
F	***	**	***	**	***	**

Table 3.8: Leaf area index(LAI)(m^2) and leaf area per tiller (LAT)(mm^2) of tall fescue grown with and without clover.

Treatments	LAI			LAT		
	NOV.	DEC.	APR.	NOV.	DEC.	APR.
With clover	0.76	0.56	0.33	255	198	102
No clover	0.94	0.86	0.54	270	243	131
SEM	0.07	0.08	0.04	24	24	8
F	ns	**	***	ns	ns	*

3.3.5 Leaf growth

Leaf elongation (LE), senescence (LS) and net leaf elongation rates per tiller per day (NLE) for the three experimental periods are shown in Tables 3.9 and 3.10. The rates were highest in November followed by December and April. Leaf elongation rate was highest under lax, and lowest under hard grazing (Table 3.9). The rate of leaf senescence increased with sward surface height, although the differences were not significant, and net leaf elongation (NLE=LE-LS) per tiller was still closely related to gross elongation rate (Table 3.9). The rates of leaf elongation, senescence and net leaf elongation were not affected by removal of white clover (Table 3.10). Also, for all rates the interactions between grazing treatments and clover were not significant.

Estimates of net leaf elongation rate per unit area per day (NLEA) and net leaf weight production per ha per day (NLP) of tall fescue under different grazing treatments, with and without clover, are presented in tables 3.11 and 3.12. Overall, NLP was higher in November than December and April, while NLEA showed a reduction over time. Both NLEA and NLP were affected by grazing management and were higher when swards were maintained at 50-60 mm (Medium) or 90-100 mm (Lax) than 30-40 mm (Hard) sward surface heights (Table 3.11). The NLEA and NLP were significantly higher in without clover than with clover by April (Table 3.12). There were no interactions between grazing management and clover treatments.

Table 3.9: Total leaf elongation(LE), senescence(LS) and net leaf elongation rates (NLE) (mm tiller^{-1} day^{-1}) under different grazing managements.

Treatments	LE			LS			NLE		
	NOV.	DEC.	APR.	NOV.	DEC.	APR.	NOV.	DEC.	APR.
Lax	11.7	8.3	5.2	0.45	0.44	0.19	11.1	7.9	5.0
Medium	8.8	6.1	3.7	0.31	0.11	0.06	8.5	5.9	3.7
Hard	5.8	3.7	3.2	0.13	0.08	0.05	5.6	3.6	3.2
SEM	0.7	0.3	0.1	0.14	0.13	0.05	0.7	0.3	0.1
F	***	***	***	ns	ns	ns	***	***	***

Table 3.10: Tall fescue total leaf elongation(LE), senescence (LS) and net leaf elongation rates (NLE) (mm tiller^{-1} day^{-1}) grown with and without clover.

Treatments	LE			LS			NLE		
	NOV.	DEC.	APR.	NOV.	DEC.	APR.	NOV.	DEC.	APR.
With clover	8.7	6.1	4.0	0.25	0.21	0.08	8.6	5.9	3.9
No clover	8.8	6.0	4.1	0.35	0.20	0.13	8.4	5.8	4.0
SEM	0.6	0.2	0.1	0.11	0.11	0.04	0.5	0.2	0.1
F	ns	ns	ns	ns	ns	ns	ns	ns	ns

Table 3.11: Estimation of net leaf elongation rates per unit area(NLEA)(m m^{-2} day^{-1}) and net leaf weight production (NLP)(kg ha^{-1} day^{-1}) of tall fescue under different grazing managements.

Treatments	NLEA			NLP		
	NOV.	DEC.	APR.	NOV.	DEC.	APR.
Lax	38.7	26.0	22.0	24.6	17.5	20.6
Medium	42.3	23.9	17.9	25.8	20.1	16.4
Hard	17.8	12.4	10.2	11.5	9.5	9.4
SEM	6.1	3.1	1.8	3.7	2.4	1.7
F	*	*	**	*	*	**

Table 3.12: Estimation of net leaf elongation rates per unit area(NLEA)(m m^{-2} day^{-1}) and net leaf weight production (NLP)(kg ha^{-1} day^{-1}) of tall fescue grown with and without clover.

Treatments	NLEA			NLP		
	NOV.	DEC.	APR.	NOV.	DEC.	APR.
With clover	29.7	20.0	14.0	18.7	15.3	13.0
No clover	36.9	21.5	19.4	22.6	16.2	18.0
SEM	5.0	2.5	1.8	3.1	1.9	1.4
F	ns	ns	*	ns	ns	*

3.3.6 Leaf defoliation

The results of defoliation parameters under different grazing managements are shown in Table 3.13. The proportion of marked tillers grazed at each interval differed significantly between grazing treatments in November, tillers being grazed more frequently under hard and medium than lax grazing (Table 3.13). The proportion of tillers defoliated daily under lax, medium and hard grazing treatments respectively were 12.2% 16.4% , 16.5% in November, 8.8%, 9.4%, 9.5% in December and 8.1%, 8.3%, 8.7% in April. Tillers were grazed less frequently during summer and autumn than in spring.

The severity of defoliation under H and M grazing was consistently greater than under L grazing, though the differences between grazing treatments were not statistically significant in November (Table 3.13). The results of leaf defoliation severity per day in November (12.0%, 13.1%, 13.8%), December (8.5%, 11.2%, 11.1%) and April (5.7%, 7.7%, 6.8%) under L, M and H grazing respectively, indicated decreasing severity of defoliation over the three measurement periods.

The defoliation pressure was greater under H and M grazing than under L grazing (Table 3.13). The defoliation pressure per day in November (5.9%, 8.6%, 9.2%) December (3.7%, 5.2%, 5.3%) and April (3.2%, 4.4%, 4.0%) under L, M and H grazing respectively, followed the same pattern of decline with time as severity of defoliation. Leaf defoliation parameters were not affected by removal of white clover (Table 3.14). Also, there were no interactions between grazing treatments and clover treatments for all the above mentioned parameters.

Table 3.13: Comparison of leaf defoliation (%) of marked tillers between different grazing treatments.

Defoliation	NOV.				
	L	M	H	SEM	F
Tiller defoliation frequency	48.9	65.7	66.0	2.7	***
Leaf defoliation severity	48.2	52.6	55.3	3.1	ns
Leaf defoliation pressure	23.6	34.5	36.8	2.2	***
	DEC.				
	L	M	H	SEM	F
Tiller defoliation frequency	44.3	47.3	47.6	3.5	ns
Leaf defoliation severity	42.5	56.4	55.7	3.8	*
Leaf defoliation pressure	18.8	26.3	26.7	2.4	ns
	APR.				
	L	M	H	SEM	F
Tiller defoliation frequency	56.9	58.1	60.7	3.1	ns
Leaf defoliation severity	40.0	53.9	47.8	2.7	**
Leaf defoliation pressure	22.8	31.2	28.6	1.7	*

Table 3.14: Comparison of leaf defoliation (%) of marked tillers of tall fescue grown with and without clover.

Defoliation	NOV.			
	WC	NC	SEM	F
Tiller defoliation frequency	63.5	57.3	2.2	ns
Leaf defoliation severity	53.3	50.8	2.5	ns
Leaf defoliation pressure	34.2	29.1	1.8	ns
	DEC.			
	WC	NC	SEM	F
Tiller defoliation frequency	48.0	44.8	2.8	ns
Leaf defoliation severity	53.4	49.6	3.1	ns
Leaf defoliation pressure	25.8	22.0	2.0	ns
	APR.			
	WC	NC	SEM	F
Tiller defoliation frequency	56.5	60.6	2.5	ns
Leaf defoliation severity	50.3	44.1	2.2	ns
Leaf defoliation pressure	28.2	26.9	1.4	ns

3.4 Discussion

3.4.1 Regrowth of tall fescue in response to defoliation

The tiller is considered to be the primary growth unit of a grassland community (Langer, 1990). Yield of the grass component of a pasture can be expressed as the product of the population density of tillers and production per tiller (Nelson & Zarrough, 1981; Zarrough *et al.*, 1983a). Therefore, management that can change tiller population density and the weight of tillers may effect productivity of pasture.

Tiller population density declined under hard grazing. Causes of low tiller population density under severe grazing may be due to a higher tiller death caused by an energy shortage (Troughton, 1957; Matches, 1966), uprooting (Bircham & Hodgson, 1983) or treading damage (Davies pers. comm.).

Plants under hard grazing had the lowest tiller weight which is consistent with observations of Spall (1977), Bircham and Hodgson (1983), Chapman *et al.*, (1983), Grant *et al.*, (1983), Sukpituksakul (1985) and Xia (1991). Sukpituksakul (1985) suggested that lower leaf area per tiller and lower dry matter production per tiller were the cause of low tiller weight under severe defoliation. In the case of this experiment, leaf area, leaf mass and total herbage mass per tiller (by dividing total leaf and herbage mass by tiller number of Tables 3.1 and 3.5) were lowest under hard grazing treatments. But leaf area per unit tiller weight was higher under hard grazing than other treatments. For example, at the end of the experiment leaf area per unit tiller weight under lax, medium and hard grazing was 4.36, 4.26 and 5.77 mm^2 mg^{-1} respectively. Possibly greater proportion of old leaf per tiller or short life-span of leaf area under hard grazing resulted in less contribution of these leaves to the tiller carbon economy and consequently lower tiller weight. However, this speculation needs to be verified by further investigations.

Tiller density of tall fescue in the present experiment was highest when the sward was maintained at 90-100 mm (Lax) and especially 50-60 mm (Medium) surface heights, and declined in swards maintained at 30-40 mm (Hard) surface height. In contrast, Bircham and Hodgson (1983) and Grant *et al.*, (1983) reported that under continuous stocking tiller density of perennial ryegrass was highest when the sward was maintained between 20-30 mm surface height and declined in swards maintained above and below this height. The results of these experiments indicate different sensitivity to continuous stocking of tall fescue and perennial ryegrass. The difference in response to defoliation of these species raises a question about the relative importance of physiological or morphological characteristics in influencing this behaviour, and therefore demands a comparative study for both species under the same management.

Leaf elongation rates are dependent on leaf area per tiller and associated tiller weight (Grant *et al.*, 1981; Carton & Brereton, 1983; Bircham & Hodgson, 1983; Chapman *et al.*, 1983; Agyare & Watkin, 1967; Volenec & Nelson, 1983). In the present experiment increasing the intensity of grazing decreased tiller weight (Table 3.5) and leaf area per tiller (Table 3.7), resulting in a reduction in both total and net leaf elongation rate per tiller in the three grazing treatments in the order H > M > L (Table 3.9). Bircham and Hodgson (1983) and Grant *et al.* (1983) also reported that leaf elongation rate per tiller decreased linearly as the severity of defoliation increased. On the other hand, adjusting net leaf elongation rate for differences in tiller density showed high and relatively similar net leaf elongation per unit area per day and net leaf weight production per ha per day in treatments L and M, but lower values in treatment H (Table 3.11). This compensatory response of M grazing was due to higher tiller population density in this treatment, which corresponds with results of Bircham and Hodgson (1983) and Grant *et al.* (1983) for ryegrass swards under continuous stocking management.

However leaf defoliation frequency, severity and pressure (Table 3.13) were similar under treatments M and H, but plants under treatment M which had higher stubble and tiller weight had higher tillering activity and leaf growth, and consequently produced higher regrowth than treatment H. This is indicative of a critical sward height for tall fescue.

In general, tall fescue showed less regrowth and productivity under hard grazing treatment than under lax and medium grazing. Hart *et al.* (1971), Zarrough *et al.* (1983a), and Sugiyama *et al.* (1985) found a positive relationship between leaf growth and tiller weight with regrowth and the productivity of tall fescue. Under continuous grazing Bircham and Hodgson (1983) reported that a severe reduction in net herbage production of perennial ryegrass occurred when swards were maintained below 20 mm surface height. The low productivity of tall fescue under severe grazing was due to low tiller weight and less leaf growth, and inadequate tiller density that maintained swards at low LAI which were less efficient in intercepting light and producing assimilate for regrowth. However, the magnitude of the above components in determining regrowth differed; for example, at the end of the experiment, leaf elongation rate, tiller density and tiller weight under hard grazing were 1.5. 1.6 and 2.8 times less relative to lax grazing. This observation indicates different sensitivity in response to defoliation for these components and needs to be investigated in more detail.

3.4.2 Botanical composition

In agreement with these results an increase in total herbage mass accumulation with a decrease in the severity of defoliation has been reported by many workers including Agyare and Watkin (1967), Alexander and Thomson (1982), Harris *et al.* (1981a) for ryegrass, and Zarrough *et al.* (1983a) for tall fescue.

The contribution of tall fescue to the herbage mass was severely affected by grazing intensity. It contributed less to herbage mass accumulation under hard grazing than in the other grazing treatments, and tended to be replaced by other species. The proportion of other grasses was relatively similar between treatments when clover was present, and increased with increasing severity of defoliation in the absence of clover (Fig 3.1, 3.2). These results indicated poor adaptability of tall fescue, and greater compatibility of other grasses (mainly ryegrass) to continuous stocking, which corresponds with results obtained by Lancashire and Brock (1983) and Moloney *et al.* (1993). In a mixed sward Bell (1985) reported that tall fescue exhibited less competitive ability than ryegrass under frequent defoliation. Harkess (1970) showed a depression in the proportion of tall fescue in a mixed sowing with ryegrass. Brock (1982) reported that tall fescue pastures were more sparse and heavily infested with volunteer grasses than ryegrass pastures under the same grazing management. These results all indicate low compatibility of tall fescue with perennial ryegrass under hard defoliation, but there is no comprehensive study to distinguish which physiological or morphological features are responsible for this behaviour.

The contribution of white clover to herbage mass was affected by grazing management, herbage mass of white clover increased as the intensity of grazing increased (Table 3.3, Fig 3.1). Brock *et al.* (1989) and Davies (1992) suggested that close, frequent defoliation favours white clover and lax infrequent defoliation increases the content of ryegrass. White clover was not as competitive with tall fescue as was observed in studies by Pederson & Brink (1988) and Woledge *et al.* (1992). Because tall fescue is a high nitrogen demanding species for high productivity, the existence of white clover in the sward may benefit tall fescue in terms of providing nitrogen for its growth.

3.5 Summary

This study indicated that grazing management had more effect on the growth and productivity of tall fescue and the proportion of tall fescue in a mixed sward than removing or leaving white clover.

Tall fescue is susceptible to competition from companion species, mainly perennial ryegress. It was also shown to be sensitive to continuous stocking, especially when grazed below 50-60 mm surface height. The sensitivity was shown by effects on tiller density, tiller weight and leaf production per tiller.

It seems that the plasticity in terms of tiller density and tiller weight of tall fescue and perennial regress differs, and possibly different management strategies are needed for these species. The response of the two species to a range of defoliation treatments under controlled conditions were considered in series of trials which are reported in the following sections.

CHAPTER 4: Effect of cutting on regrowth of tall fescue and perennial ryegrass

4.1 Introduction

The results of the initial grazing experiment (Chapter 3) showed some limitations in tall fescue under hard grazing. Under grazing, management factors such as treading, tiller uprooting, grazing selectivity and returning dung and urine to the soil may interact with physiological or morphological responses to defoliation (Watkin & Clements, 1978; Hodgson, 1982). Therefore, the experiment described in this chapter was set up to study the response of tall fescue and perennial ryegrass to a range of cutting treatments. The individual plants were cut frequently and to similar heights in a management designed to simulate continuous stocking. The response of the two species to defoliation was measured in terms of tillering activity, leaf growth and consequently shoot and root growth.

4.2 Material and methods

4.2.1 Experimental conditions

Individual plants of Roa tall fescue and Nui perennial ryegrass were grown from seed in pots (20 X 20 cm wide, 20 cm deep) filled with 50/50 fine-loam-mixed-mesic (Haplquept) and sand. Nutrients were supplied as 240g superphosphate, 240g lime, 180g osmocote (N, P, K release over 3-4 months), 120g dolomite and 48g micromax (trace elements) per 100 litre of potting media. Pots were placed in a glasshouse with 20/15°C day/night temperature at the Plant Growth Unit (PGU), Massey University in Palmerston North. Plants were grown under natural light intensity, but a 250W mercury light was used for illumination in early morning (2 hours) and late afternoon (2 hours) to provide a 12h photoperiod. Seedlings of each pot were thinned to one uniform plant per pot once established. Pots were placed on a bench covered by plastic and foam, and watered by automatic irrigation from below.

Each individual plant was considered as a replicate. For each species 16 plants provided four replicates of four cutting treatments. The cutting treatments consisted of cutting plants to stubble heights of 100 mm (L, Lax), 60 mm (M, Medium), 30 mm (H1, Hard1) and 30 mm (H2, Hard2). Treatments L, M and H1 were initiated at an average of 11 tillers per plant for each species; treatment H2 commenced at an earlier stage, with 6 tillers per plant. Cutting treatments were repeated 9 times at 5 day intervals over a period of 45 days (see Plate 4.1).

4.2.2 Measurements

Leaf elongation was measured from 4 marked tillers per plant. The lengths of laminae of expanding leaves (from the point of emergence to the tip of the lamina) of marked tillers was measured using a ruler with a precision of 1 mm just before and after each cutting harvest. Leaf extension rates (mm tiller^{-1} day^{-1}) were calculated by the difference between leaf length at the beginning and the end of each cutting interval divided by the number of days in the interval. Tiller number per plant was counted at each harvest. Tillering rate (TIR) was calculated as:

$$\mathrm{TIR} = \frac{\ln TN2 - \ln TN1}{T2 - T1} \qquad \text{(tiller tiller}^{-1}\text{ day}^{-1}\text{)}$$

Where T2 and T1 were the times at which the measurements are made,TN1 and TN2 are the tiller number per plant at T1 and T2.

Herbage removed at each cutting was dried at 80°C for 48h and then weighed. At the end of the experiment, plants were cut to ground level. Plant stubble was also dried and weighed. Total shoot mass harvested per plant (TSM) was calculated by adding the stubble dry matter, total herbage harvested (THH) and herbage dry matter removed at the beginning of the cutting treatments. The herbage harvested per tiller at each harvest was

Plate 4.1: A general view of cutting experiment 40 days after first defoliation

calculated by dividing herbage harvested per plant by its tiller number. Mean tiller weight per plant at the final harvest was calculated by adding residual stubble and herbage harvested, and dividing by final tiller number for each plant. Roots were washed free of soil, dried and weighed. Root material was then combusted at 500°C in a muffle furnace, and organic matter of the roots calculated by subtracting the root ash from the total root dry weight. This was regarded as the total root mass (TRM).

4.2.3 Statistical analysis

The data were examined by analysis of variance using the General Linear Model (GLM) procedure of SAS (SAS Institute Inc. 1991). Two species with four cutting treatments were analysed as a factorial combination with a randomised complete block (RCB) design (Steel & Torrie, 1981). Time was considered as a factor by analysing the data as repeated measurements (Rowell & Walters, 1976).

4.3 Results

4.3.1 Herbage harvested

Herbage harvested at each cutting period was analyzed as herbage per plant and per tiller. As an example, the general results of analysis of variance of herbage harvested per plant over time is shown in Appendix 4.1. Herbage harvested per plant differed between species and cutting treatments (Appendix 4.1). It was significantly greater for perennial ryegrass than tall fescue after the sixth harvest (Table 4.1). Increasing cutting height resulted in greater herbage harvested per plant at all harvests (Table 4.2). There were no statistically significant differences between herbage harvested in H1 and H2 cutting treatments at any harvest (Table 4.2). The interactions of time x species, time x cutting treatment and time x species x treatment were all significant ($P< 0.001$) (Appendices 4.1 & 4.2).

The general results of analysis of variance over all cutting periods indicated no differences between species in herbage harvested per tiller, but the results of individual cuttings at C1 and C4 showed significantly greater herbage harvested per tiller for tall fescue than perennial ryegrass (Table 4.3). These variations over time were responsible for the significant time x species interaction ($P< 0.01$).

Both species showed statistically similar herbage harvested per tiller at all cuttings except at C1 and C4 where more herbage mass was harvested for tall fescue than for perennial ryegrass (Table 4.3). Herbage harvested per tiller was significantly greater under treatment L than under the treatments M, H1 and H2 at all harvests except at C3, where the difference was not significant from treatment M (Table 4.4). Herbage harvested per tiller for treatment H1 and H2 was similar to treatment M until the third cutting, but thereafter was significantly lower than treatment M (Table 4.3). The time x cutting treatments, and time x species x cutting treatments interactions were not significant.

Table 4.1: Comparison between herbage harvested per plant (mg) of perennial ryegrass and tall fescue.

Cutting	Ryegrass	Fescue	SEM	F
C1	55.4	73.3	6.8	ns
C2	57.4	62.6	6.4	ns
C3	79.2	70.9	13.2	ns
C4	72.4	78.3	13.2	ns
C5	92.3	80.6	13.6	ns
C6	145.2	72.6	8.8	***
C7	167.9	75.5	11.1	***
C8	131.6	90.3	10.9	*
C9	118.7	79.9	11.0	*

Table 4.2: Effect of cutting treatments on herbage harvested per plant (mg) of perennial ryegrass and tall fescue.

Cutting	Treatments				SEM	F
	L	M	H1	H2		
C1	108.5	74.8	51.1	23.1	9.7	***
C2	107.3	75.6	39.1	18.0	9.1	***
C3	155.9	101.8	26.8	15.7	18.7	***
C4	174.8	95.7	18.9	11.9	18.6	***
C5	219.6	99.2	18.5	8.6	19.6	***
C6	286.4	124.5	13.9	10.9	12.4	***
C7	339.2	129.6	13.0	5.1	15.7	***
C8	322.4	111.7	6.7	2.9	15.5	***
C9	293.8	94.5	6.4	2.6	15.6	***

L: Lax; M: Medium; H1: Hard1; H2: Hard2 cutting treatments

Table 4.3: Herbage harvested per tiller (mg) of perennial ryegrass and tall fescue.

Cutting	Ryegrass	Fescue	SEM	F
C1	4.0	6.8	0.7	**
C2	4.2	4.6	0.6	ns
C3	4.5	4.8	0.9	ns
C4	2.7	4.1	0.7	*
C5	3.2	3.3	0.7	ns
C6	3.8	3.8	0.3	ns
C7	3.9	2.4	0.5	ns
C8	2.6	2.6	0.4	ns
C9	2.2	2.0	0.5	ns

Table 4.4: Effect of cutting treatments on mean herbage harvested per tiller (mg) of perennial ryegrass and tall fescue.

Cutting	Treatments				SEM	F
	L	M	H1	H2		
C1	8.5	5.2	4.2	3.9	1.0	*
C2	6.7	4.4	3.4	3.2	0.6	**
C3	7.0	5.1	2.2	4.1	1.2	ns
C4	6.2	4.2	1.9	1.5	1.0	*
C5	6.3	3.5	1.3	1.8	1.0	*
C6	6.2	3.7	1.6	1.7	0.4	***
C7	6.4	3.4	1.1	1.7	0.7	***
C8	5.8	2.8	0.8	1.0	0.5	***
C9	4.7	2.2	0.6	0.8	0.6	***

4.3.2 Tiller number and tiller weight

Tillering activity for species and cutting treatments was compared in terms of tiller number per plant and tillering rate (tiller $tiller^{-1}$ day^{-1}).

Tiller number per plant for species is depicted in Figure 4.1. Perennial ryegrass was superior to tall fescue over time, and tiller number per plant was greater at cutting harvests 7, 8, 9 and 10 than tall fescue. Tiller number in treatments L and M increased over time for each species, but the differences between L and M became substantially greater in perennial ryegrass than in tall fescue (Fig 4.2 and Appendix 4.3). In contrast tiller number per plant under treatments H1 and H2 was at first constant and then tended to decrease, particularly in tall fescue. The interactions time x species, time x treatments, and time x species x treatments were all significant ($P< 0.001$).

There was virtually no tillering activity under treatments H1 and H2 in either species (Figure 4.2). Tillering rates of treatments L and M were therefore considered separately for comparison between species. The time x species interaction was significant ($P< 0.01$). Perennial ryegrass showed significantly higher tillering rate than tall fescue at C1, C6 and on average but lower at C9 (Table 4.5). Tillering rate was higher under L treatment than under M at C5, C8 and on average (Table 4.6). The interactions of the time x treatments, and time x species x treatments were not significant.

Tiller weight was greater in tall fescue than perennial ryegrass (29 vs 18 ±1.3 mg $tiller^{-1}$, $P< 0.001$). Tiller weight of both species decreased as intensity of defoliation increased (Table 4.7). The species x treatment was significant ($P< 0.001$). The lax treatment of tall fescue had significantly greater tiller weight than all other treatments for both species.

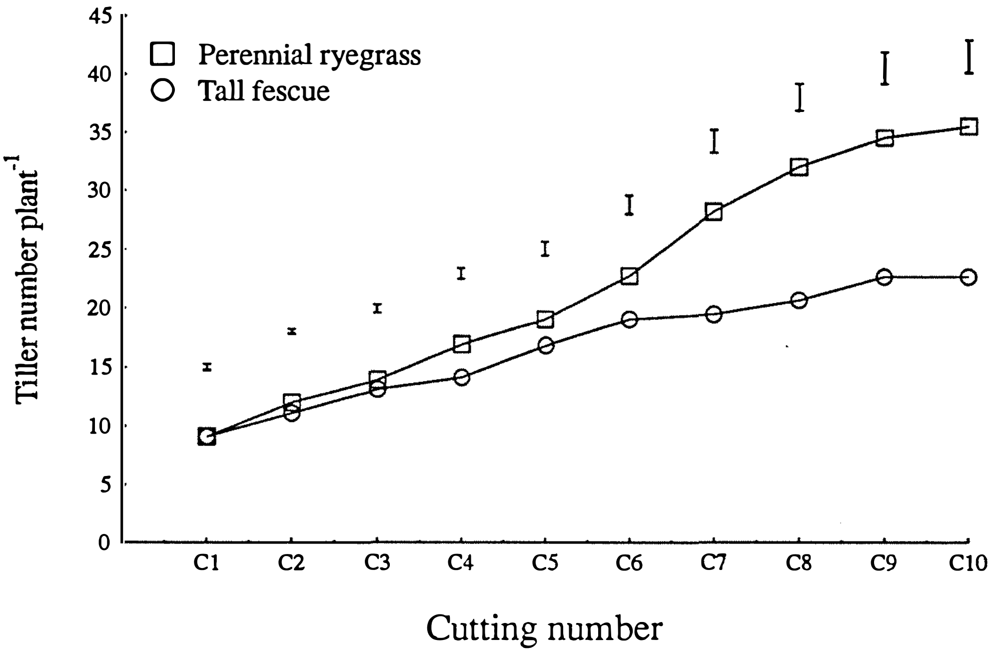

Figure 4.1 Tiller number per plant of perennial ryegrass and tall fescue over time. Bar shows SEM

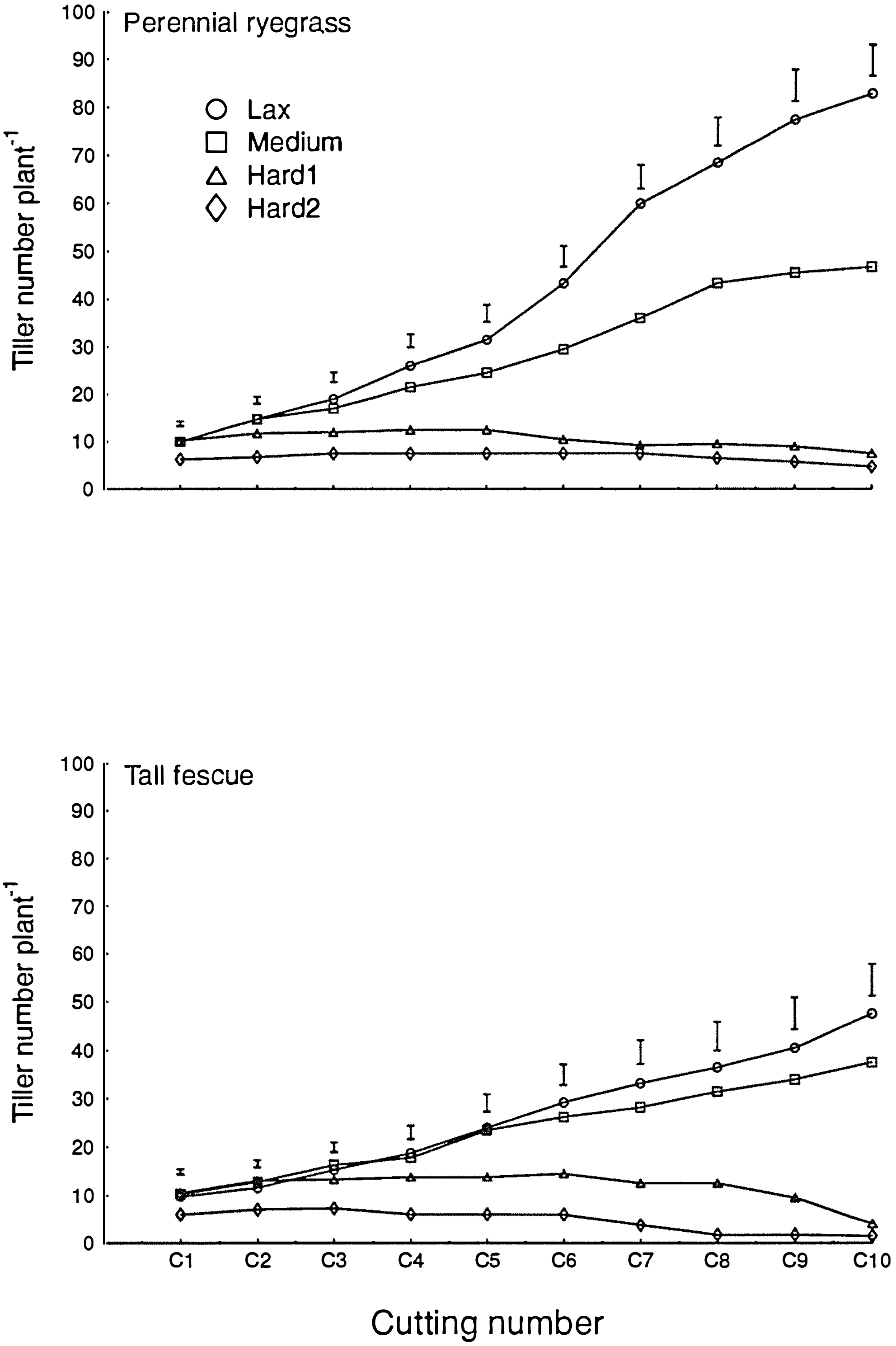

Figure 4.2 Effect of cutting heights on tiller number per plant of perennial ryegrass and tall fescue. Bar shows SEM

Table 4.5: Tillering rates (tiller tiller^{-1} day^{-1}) of perennial ryegrass and tall fescue; mean of treatments L and M.

Cutting	Ryegrass	Fescue	SEM	F
C1	0.079	0.048	0.010	*
C2	0.038	0.041	0.008	ns
C3	0.054	0.039	0.006	ns
C4	0.033	0.039	0.008	ns
C5	0.049	0.033	0.007	ns
C6	0.054	0.019	0.007	**
C7	0.031	0.017	0.005	ns
C8	0.017	0.016	0.005	ns
C9	0.009	0.031	0.005	*
Mean	0.040	0.031	0.002	*

Table 4.6: The effect of cutting treatments on tillering rates (tiller tiller^{-1} day^{-1}) of perennial ryegrass and tall fescue.

Cutting	Treatments			
	L	M	SEM	F
C1	0.062	0.065	0.010	ns
C2	0.046	0.033	0.008	ns
C3	0.055	0.038	0.006	ns
C4	0.040	0.032	0.008	ns
C5	0.052	0.029	0.007	*
C6	0.047	0.026	0.007	ns
C7	0.022	0.025	0.005	ns
C8	0.023	0.009	0.005	*
C9	0.023	0.017	0.005	ns
Mean	0.041	0.030	0.002	*

Table 4.7: Tiller weight (mg tiller^{-1}) of perennial ryegrass and tall fescue under different cutting treatments at final harvest.

	Ryegrass				Fescue					F values for		
	L	M	H1	H2	L	M	H1	H2	SEM	SP	TR	SPxTR
Tiller weight	36	18	10	8	62	26	13	13	2.7	***	***	***

4.3.3 Leaf growth

Leaf elongation rates (mm $tiller^{-1}$ day^{-1}) decreased over time (Fig 4.3 and 4.4), but were consistently higher in ryegrass than tall fescue (Fig. 4.3). The effect of cutting treatment on leaf elongation rates was significant. The taller the stubble the higher the leaf elongation rates, with the order for the treatments being L > M > H1 or H2 at all harvests. Leaf elongation rate did not differ between H1 and H2. Also, the interactions of species x cutting treatments, and time x species x cutting treatment were not significant.

4.3.4 Total herbage harvested and plant shoot and root mass

Total herbage harvested per plant on perennial ryegrass was greater than tall fescue, but total shoot mass and root mass per plant did not differ between species (Table 4.8). Total herbage harvested and total shoot and root mass per plant decreased as cutting height declined (Table 4.9). No interactions were observed between species and cutting treatments for the above factors.

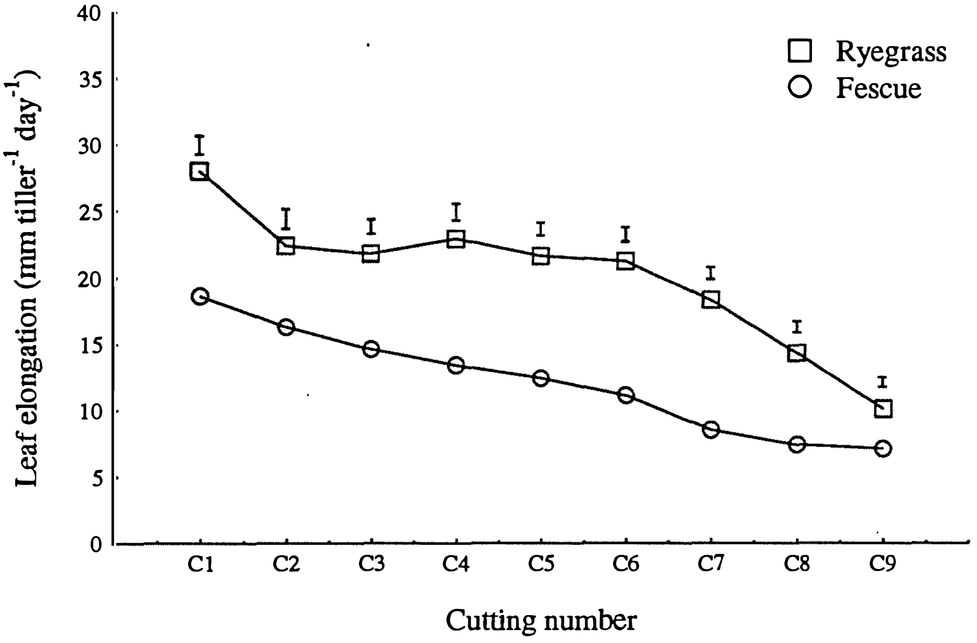

Figure 4.3: Leaf elongation rates of perennial ryegrass and tall fescue over time. Bar shows SEM

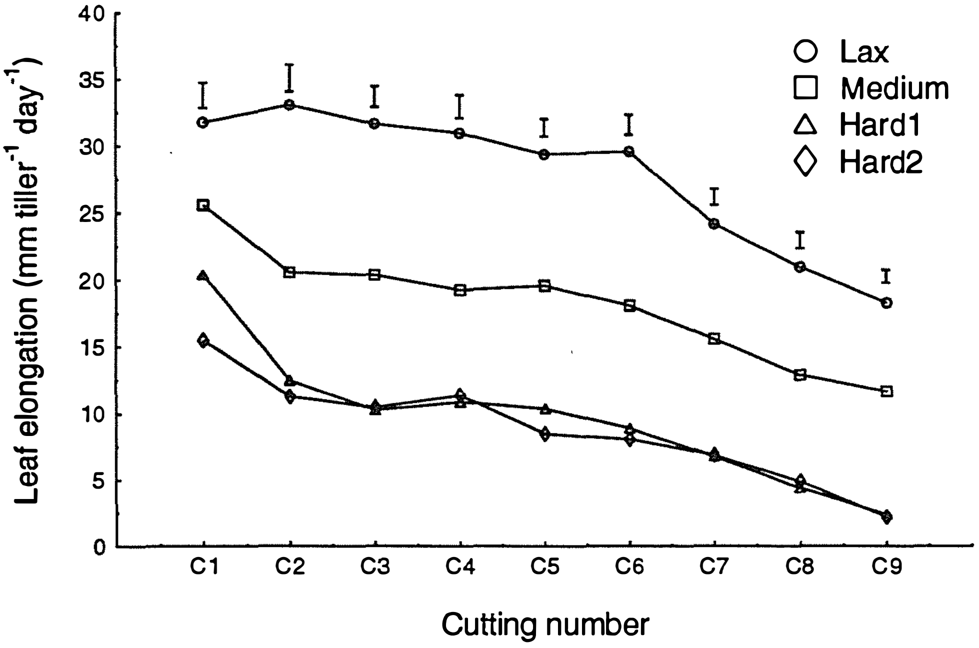

Figure 4.4: Leaf elongation rates of perennial ryegrass and tall fescue under different cutting treatments. Bar shows SEM

Table 4.8: Comparison of total herbage harvested, total plant shoot mass and root mass (mg plant^{-1}) of perennial ryegrass and tall fescue.

Cutting	Ryegrass	Fescue	SEM	F
Herbage harvested	920	684	80	*
Shoot mass	1921	1928	148	ns
Root mass	228	254	32	ns

Table 4.9: Total herbage harvested, total plant shoot mass and root mass (mg plant^{-1}) of perennial ryegrass and tall fescue under different cutting treatments.

Cutting	Treatments				SEM	F
	L	M	H1	H2		
Herbage harvested	2008	907	195	99	114	***
Shoot mass	4747	1907	647	398	210	***
Root mass	632	224	66	44	45	***

4.4 Discussion

The productivity and sustained production of grasses are conferred by the successive production of relatively short-lived tillers (Langer, 1963; Jewiss, 1972). In the current experiment tillering was affected by defoliation intensity, particularly when plants were cut frequently to 30 mm stubble height either in H1 or H2 treatment (Table 4.5, Figure 4.2). Mitchell and Coles (1955) reported that cutting perennial ryegrass to 20 mm repeatedly checked the tillering rate. Tillering of tall fescue was reduced 100% relative to uncut plants when plants were defoliated repeatedly to a 25 mm stubble height (Matches, 1966).

Decreasing leaf elongation rate with increasing severity of defoliation (Figure 4.4) is consistent with the results of Ryle (1964), Davies (1977), Bircham and Hodgson (1983), Grant *et al.* (1983) and Butler and Hodgson (1993). Herbage mass harvested per tiller for both species decreased over time and with increasing severity of defoliation (Table 4.4) which corresponds with results obtained by Mitchell and Coles (1955) under close and repeated defoliation on perennial ryegrass. Reduction in tiller weight with decreasing defoliation height (Table 4.7) is in agreement with the findings of Bircham and Hodgson (1983), Xia (1993) and Brock & Hay (1993) in ryegrass, and Zarrough *et al.* (1983a) in tall fescue. Although tall fescue had heavier tillers they were more sensitve to cutting than perennial ryegrass. Study on the causes of reduction in leaf growth and tiller weight is followed in experiments under controlled environment.

The number of tillers per plant for perennial ryegrass plants was greater than for tall fescue plants (Figure 4.1). A slightly higher tillering rate in perennial ryegrass resulted in an accumulating advantage in tiller number with time, thus at plant harvest perennial ryegrass plants had 1.6 times more tillers than tall fescue. On the other hand, tall fescue had about 1.6 times heavier tillers than perennial ryegrass, indicating that tall fescue invests more assimilate in individual tiller development, and less in tiller initiation, than does perennial ryegrass. It is generally accepted that perennial ryegrass is a more vigorous plant than tall fescue in terms of tillering activity (e.g. Ryle, 1964; Rhodes, 1968; Brock, 1983), but the physiological or morphological mechanism responsible for the different behaviour of tall fescue and perennial ryegrass are not fully understood and need further investigation.

A reduction in herbage yield in response to increasing severity of defoliation can reflect a lower tiller number (Davies, 1971), a lower tiller weight (Zarrough *et al.*, 1983a; Bartholomew & Chestnutt, 1978), or both (Korte *et al.*, 1985). In the present experiment, reduction in herbage harvested per plant was due to both reduction in tiller number and tiller weight. Also, lower tiller numbers per plant and lower leaf elongation rates (65% of perennial ryegrass) in tall fescue than perennial ryegrass were the causes of lower levels of herbage harvested per plant in tall fescue relative to perennial ryegrass. However, tiller weight of tall fescue was higher than perennial ryegrass.

Reduction in plant root growth as the severity of defoliation is increased has often been reported (Davidson & Milthorpe, 1966b; Schuster, 1964; Wilson, 1988). Apparently reduction in supply of photosynthate to the roots because of reduced photosynthesis, and also greater allocation to shoot meristematic and leaf growth regions after defoliation (Richards, 1993), results in a reduction in root growth under more intense defoliation. Root mass of both species decreased as intensity of defoliation increased (Table 4.9).

Removal of top growth in tall fescue is almost always associated with a drop in total plant weight (Booysen & Nelson, 1975) and the recovery of plants from the effects of defoliation takes time and depends on its severity (Booysen & Nelson, 1975). If plants are defoliated again before recovery is complete, then recovery will be even more prolonged and plant death may result. The recovery of perennial ryegrass and tall fescue plants cut to 30 mm every 5 days from different initial stages of development (H1 and H2) declined progressively and resulted in death of 75% of tall fescue plants and 50% of perennial ryegrass plant by the end of experiment. However, plants cut to 60 mm stubble or higher were able to recover sufficiently to survive the same interval between cuts (see Plate 4.1), in accord with the results obtained by Matches (1966) on tall fescue. Cutting to leave 60 mm of stubble height on a prostrate ryegrass did not affect the amount of regrowth (Wilson & Robson, 1970), but closer cutting progressively reduced regrowth compared with uncut plants.

It was thought that plants under H1 and H2 might behave differently under defoliation due to smaller and shorter tillers in H2, so leaving a greater proportion of leaf after defoliation relative to treatment H1. In fact treatments H1 and H2 produced similar results. Apparently less development of the root system and low initial stubble weight under H2 resulted in failure of the plants to recover after repeated defoliation.

In general, results obtained in this experiment with 5 day cutting intervals together with the findings of Matches (1966) on tall fescue with 10 day cutting intervals with similar cutting heights, confirmed the responses of plants to defoliation under grazing conditions (Chapter 3). Under the hard cutting treatment with 30 mm cutting height at 5 day intervals in the present experiment, and under 25 mm cutting height with 10 day intervals in the study of Matches (1966), plants failed to recover over short defoliation intervals. However, under grazing conditions (Chapter 3) with a tiller grazing interval of about 9 days, plants tolerated hard grazing better. For example, tillering rates remained constant under hard grazing from November until April (Table 3.5). The fact that close grazing is less detrimental than uniformly close cutting may be because grazing typically leaves some ungrazed tillers on a plant while removing others (Vallentine, 1991), thus allowing for the transfer of assimilate from undefoliated tillers to the defoliated tillers (Ryle & Powell, 1975; Ong, 1978). Greater growth rates are observed in tall fescue plants following defoliation as the percentage of undefoliated tillers within the plant increased (Matches, 1966).

4.5 Summary

The results of cutting treatments on individual plants indicated sensitivity in both perennial ryegrass and tall fescue to severe cutting treatments. There were reductions in tiller number, tiller weight and leaf growth, and consequently less shoot and root growth.

There were some species differences in terms of leaf elongation rates, tillering activity, tiller weight and herbage harvested per plant, with perennial ryegrass superior to tall fescue except in tiller weight.

Further investigations of the physiological and morphological responses to defoliation in both species are described in the next chapter.

CHAPTER 5: Response of tall fescue and perennial ryegrass to leaf defoliation

5.1 Introduction

The results of previous grazing (Chapter 3) and cutting (Chapter 4) experiments indicated some differences between tall fescue and perennial ryegrass in response to defoliation management. Also, the effects of defoliation treatments on regrowth of plants were different and related to severity of defoliation.

To understand the differences in the response to defoliation of grass species, and the physiological or morphological causes of such responses in more detail, two experiments were conducted at the vegetative and two at the reproductive growth stage under controlled environment conditions. For the vegetative stage perennial ryegrass and tall fescue were subjected to (1) leaf defoliation treatments at the same time after sowing (different tiller number per plant per species) and (2) to leaf defoliation treatments with similar tiller number per plant per species. For the reproductive stage leaf defoliation was applied to perennial ryegrass and tall fescue at the same time after establishment.

Response to defoliation was measured in terms of tillering activity, leaf growth characteristics, leaf photosynthesis and respiration, carbohydrate reserves and root and shoot growth.

In this Chapter the material and methods and the results for each experiment are explained sequentially, and the results are then considered in a combined discussion.

5.2 Vegetative stage

5.2.1 Material and methods- experiment 1

5.2.1.1 Experimental conditions

Individual plants of perennial ryegrass and tall fescue were grown from seed in plastic pots (15 cm diameter by 20 cm deep). The pot media contained peat, sand and pumice (3:1:1). Nutrients were supplied as 240g superphosphate, 240g lime, 180g osmocote (release by 3-4 months), 120g dolomite and 48g micromax per 100 litre of potting media. Seedlings were thinned to one uniform plant per pot after establishment. Plants were grown in a controlled environment room at the Horticulture Crown Research Institute (CRI) in Palmerston North.

The controlled environment room (CE) was maintained at 20 ±0.5°C for 12h during the day and 15 ±0.5°C for 10h at night; the photoperiod was 14h. The day/night, night/day temperature changeovers took 60 minutes.

The photosynthetic photon flux density (PPFD) of 675 μmol m^{-2} s^{-1} was provided at the surface of standard trolley height using 4 x 1000 W Sylvania 'Metalarc' high pressure discharge lamps, together with 4 x 1000 W Philips tungsten iodide lamps. Further details on the lighting systems are provided in Warrington *et al.* (1978).

CO_2 levels during the course of the experiment ranged from 341-460 ppm during day conditions and 356-482 ppm during night conditions. The CO_2 levels were higher than normal because of pepole working in the room for extended periods each day and sometimes during the night time. Relative humidity during the day and night was 65 ±5%. Plants were watered by hand daily.

Leaf defoliation treatments were applied to both species when plants were 33 days old, and there was a mean of 36 and 12 tillers per plant for perennial ryegrass and tall fescue respectively. Each individual plant per pot was considered as a replicate. For each species there were 24 plants which provided six replicates with four leaf defoliation treatments in a randomized complete block design. The preliminary observations of mature tillers on individual plants under glasshouse conditions showed up to 4 live leaves per tiller. Therefore, the four initial defoliation treatments were applied (Figure 5.1);

Control (C): no defoliation
Lax (L): the oldest leaf lamina removed (L4)
Medium (M): the two oldest leaf laminae removed (L3,L4)
Hard (H): all fully expanded leaf laminae removed (L2,L3,L4)

Subsequently, after each leaf appearance the oldest leaf lamina was removed on all tillers for six leaf appearance intervals to maintain a consistent condition during the experiment. After each defoliation treatments H, M, L and C had up to 1, 2, 3 and 4 live leaves per tillers respectively. Plants were defoliated when more than 80% of the tillers had produced a new expanded leaf. The leaf appearance sequences are abbreviated as LAS1 LAS2 and so on in the text and tables.

5.2.1.2 Measurements

Leaf elongation rates (LE)(mm tiller^{-1} day^{-1}) were estimated on 3 marked tillers per plant. The lengths of laminae of expanding leaves (from the point of emergence to the tip of the lamina) of marked tillers was measured at each leaf defoliation interval using a ruler with a precision of 1 mm. Leaf elongation rates were calculated by the difference between leaf lengths at successive measurements divided by the number of days in the interval. Leaf lamina growth rates (LGR)(mg tiller^{-1} day^{-1}) was calculated by using leaf elongation rate and specific leaf weight (SLW) (mg cm^{-2}) of the uppermost fully expanded leaves as:

$LGR=(LE \times SLW)/100$ (mg tiller^{-1} day^{-1})

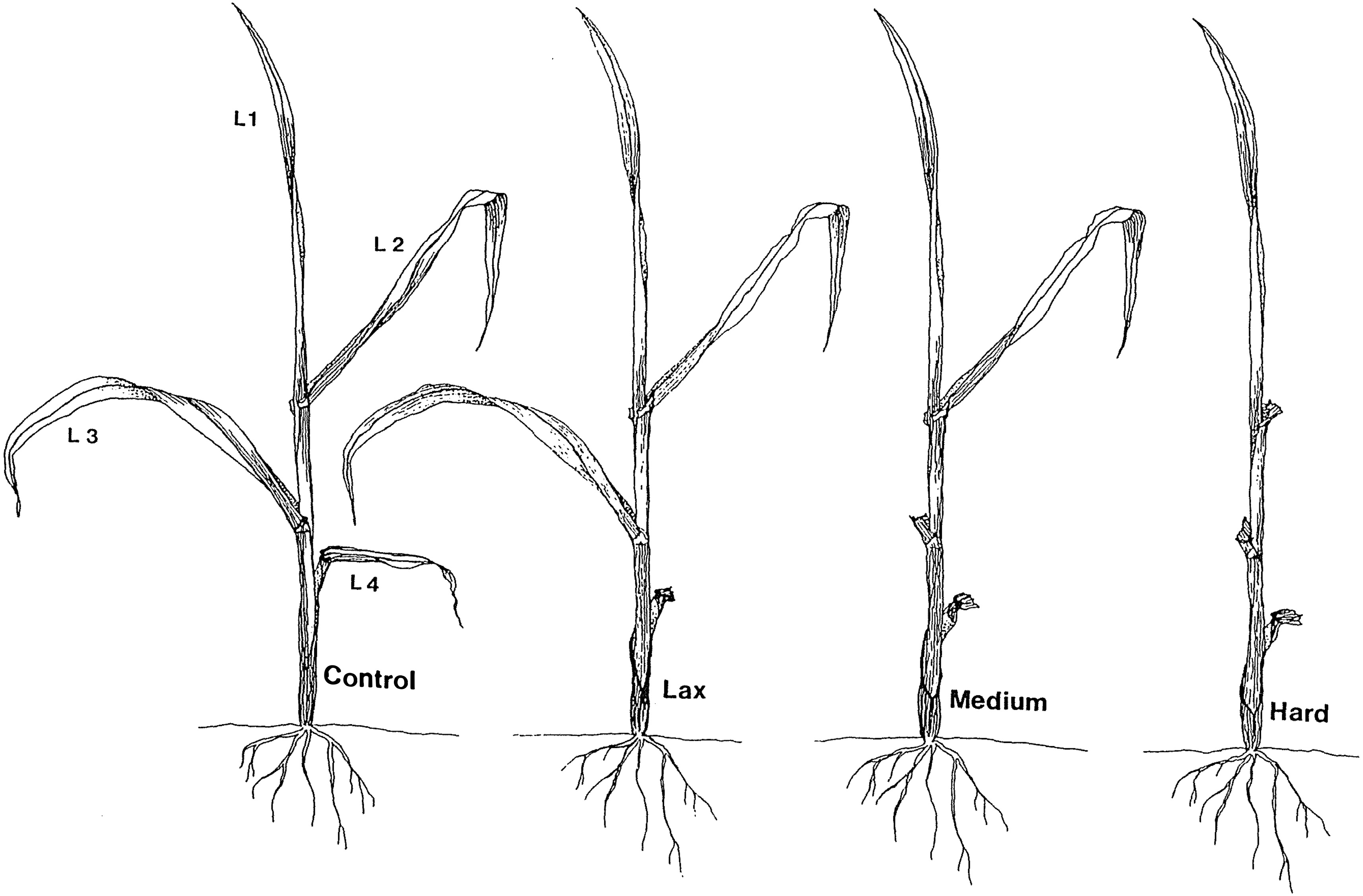

Figure 5.1 LEAF DEFOLIATION TREATMENTS (Drawn by Cally McKenzie)

Tiller numbers per plant were counted at each leaf defoliation sequence. Tillering rates (TIR) were calculated as:

$$TIR= \frac{\ln TN2 - \ln TN1}{T2 - T1} \quad (\text{tiller tiller}^{-1}\ \text{day}^{-1})$$

Where T2 and T1 are the times at which the measurements were made, and TN1 and TN2 were the tiller number per plant at T1 and T2.

To determine the initial shoot dry mass (ISM), 5 plants for each species were cut randomly to soil surface level at the beginning of the experiment, dried at 80°C for 48h and then weighed. At the end of the experiment, plants were cut to soil surface level, dissected into different categories (green leaf, senescent leaf and psuedostem) and then dried separately as above. Total shoot dry mass accumulation (TSM) included plant dry weight at the end of the experiment plus the leaves that were removed during the experiment. For the control treatment the senescent leaves that fell to the ground were collected and added to the final dry weight. Tiller weight per plant was calculated by dividing the total plant dry weight by its final tiller number.

The mean shoot relative growth rate (RGR) for the period of the experiment was calculated (Hunt, 1978; Davies pers. comm.) using the following equation:

$$RGR = \frac{TSM - ISM}{TSM \times D} \quad (\text{mg g}^{-1}\ \text{day}^{-1})$$

Where ISM and TSM are the initial and total plant shoot mass at the beginning and end of the measurement period respectively, and D is the number of days in this period.

The number of fully expanded leaves that appeared on three marked tillers per plant was used to provide estimates of leaf number per tiller (LN). The mean leaf appearance rates (A_L) (leaf tiller^{-1} day^{-1}) were calculated by dividing LN by the duration of the experimental for each species.

Site filling (F_s), defined as the number of tillers appearing per tiller during a single leaf appearance interval (Davies & Thomas, 1983), was calculated from the following equation:

$F_s = TIR / A_L$ (Tillers leaf^{-1})

Where TIR is tillering rate, and A_L is leaf appearance rate. Site filling was also estimated over the 6 leaf appearance intervals as above.

At the final defoliation (LAS6) the five uppermost fully expanded leaves from five tillers per plant were cut to estimate the following individual leaf characteristics; leaf length (mm) using a ruler with a precision of 1 mm, leaf area (cm^2) using leaf area meter, leaf dry weight (mg), specific leaf area (SLA) (cm^2 g^{-1}) by dividing individual leaf area by leaf weight, and specific leaf weight (SLW) (mg cm^{-2}) by dividing leaf weight by leaf area.

The photosynthetic activity of the uppermost fully expanded leaf of two tillers per plant was measured at LAS1, LAS3 and LAS6 by an infra-red gas analyzer (Li-cor 6200) with a quarter litre chamber. To measure leaf photosynthesis individual leaves were placed transversely in the chamber. The first half of the each leaf from the collar was chosen for measuring leaf photosynthesis because of its relatively rectangular shape. The area of leaf inside the chamber was calculated by multiplying leaf width by chamber width (see Plate 5.1). Net photosynthetic rate per unit leaf area (PNa) (μmol CO_2 m^{-2} s^{-1}) of individual leaves was recorded after 25 seconds inside the chamber. Net photosynthetic rate per unit leaf weight (PNw) (μmol CO_2 kg^{-1} s$^{-1)}$ was calculated as follows:

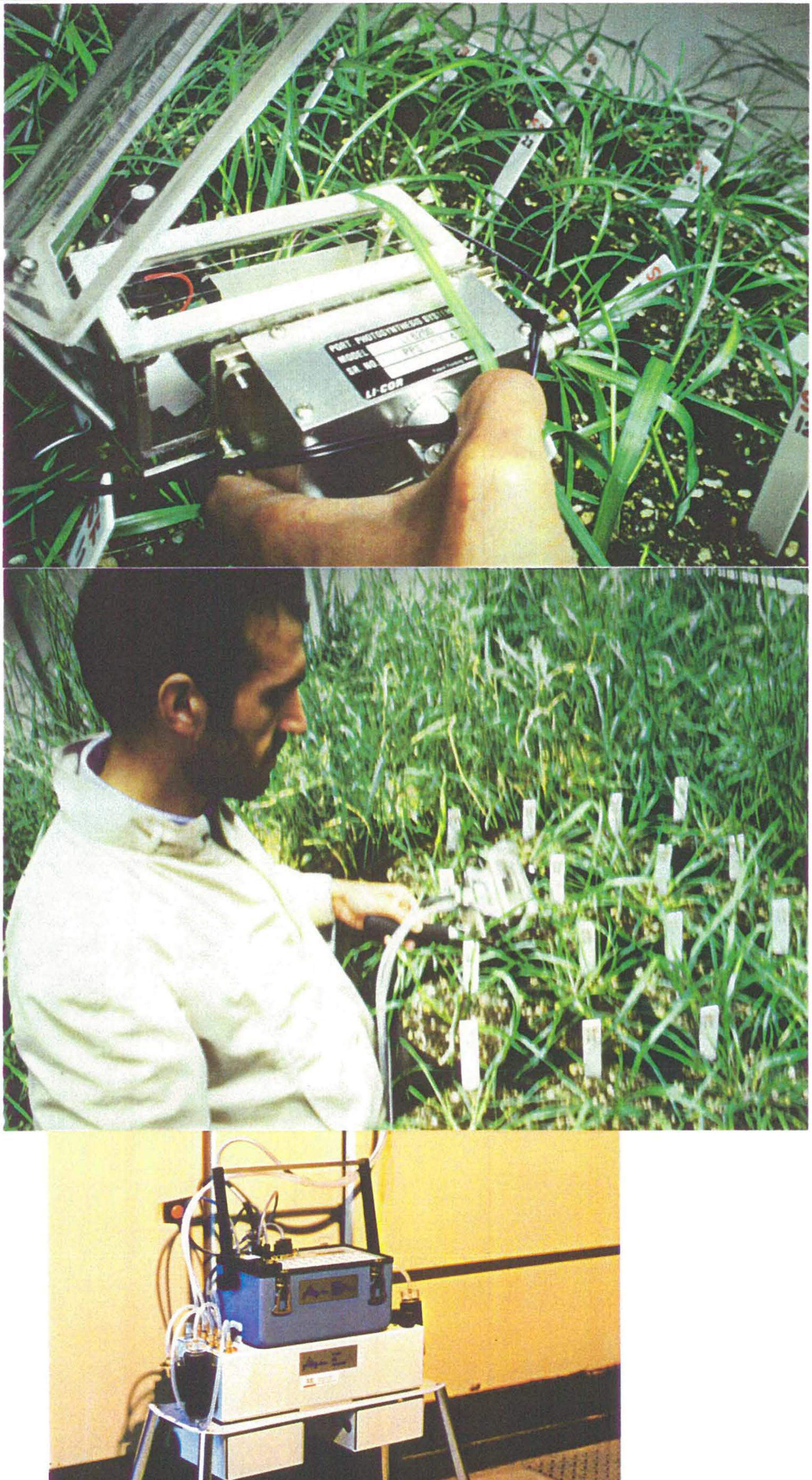

Plate 5.1: Measurement of leaf carbon exchange by Infra-red Gas Analyzer (Li-cor 6200)

$$\mathrm{PNw} = \frac{\mathrm{PNa} \times \mathrm{LA}}{\mathrm{LW} \times 10} \quad (\mu\mathrm{mol\ CO_2\ kg^{-1}\ s^{-1}})$$

Where PNa is photosynthetic rate per unit leaf area (μmol CO_2 m^{-2} s^{-1}), LA is the area of the individual leaf (cm^2) and LW is the dry weight of the same leaf (g) which was used for measuring PNa.

Dark respiration rates (Rd) were measured during the night periods on the leaves used for photosynthesis at LAS6. Respiration rate was calculated per unit leaf area (μmol CO_2 m^{-2} s^{-1}) and unit leaf weight (μmol CO_2 kg^{-1} s^{-1}).

Carbohydrate reserves in the stem bases of the plants were measured as water soluble carbohydrate concentrations (WSC) at the end of experiment. Starch is present in small quantities in perennial ryegrass and tall fescue(<2%) (Volenec & Nelson, 1984; Thom *et al.*, 1989), so estimates of starch were not made in this study. To estimate water soluble carbohydrate concentration (WSC) plants were cut to the surface level, washed, clipped free of roots, and a proportion of the basal tillers with lengths of up to 4 cm containing crown and stubble were cut free of leaves and immediately frozen in liquid nitrogen. Samples were kept in a flask containing ice, transferred to the laboratory and stored in a freezer. Samples was freeze dried and ground to pass through a 40-mesh sieve, put in sealed plastic bags and stored for carbohydrate analysis.

Sugars were extracted from the samples with 2.5 mM H_2SO_4 (Smith *et al.*, 1964; Smith, 1969) and reduced with *p*-hydroxybenzoic acid hydrazide (PAHBAH) based on the reaction with reducing sugars(Blakeney & Mutton, 1980;Trent & Christiansen, 1986).

100 mg of dried and ground plant material for each sample was weighed to an accuracy of 4 decimal places, put in a 20 ml test tube and 10 ml of 2.5 mM H_2SO_4 added. The tubes were capped to minimize evaporation, heated gently in a boiling water bath for 60 minutes with agitation at the beginning

and after 30 minutes to ensure thorough extraction. The samples were centrifuged at 2000 rpm for 5 minutes then diluted by putting an 1 ml aliquot into 19 ml of 2.5 mM H_2SO_4. 200 µl aliquot from this solution was added to 2 ml PAHBAH regent (see Appendix 5.1), capped, mixed and heated in boiling water for 5 minutes. It was then cooled to the room temperature, and 4 ml of distilled water added to each sample before recording absorbance at 420 nm in an spectrophotometer. The amount of water soluble carbohydrates was calculated from a standard curve (Appendix 5.2) as mg g^{-1} of dry matter.

Fructose was used for the standard solutions. Five samples of each standard solution concentration were reduced by PAHBAH as above and read in the spectrophotometer. The standard curve was formed by plotting the relationship between known concentrations of fructose and absorbance of standards at 420 nm (Appendix 5.2).

5.2.1.3 Statistical analysis

The data were examined by analysis of variance using the General Linear Model (GLM) procedure of SAS (SAS Institute Inc. 1991). The two species with four cutting treatments were analyzed as a factorial combination with a randomised complete block (RCB) design. Because the species had different tiller numbers per plant at the beginning of the experiment, initial tiller number was used as a covariate (Steel & Torrie, 1981). Both data adjusted and unadjusted for initial tiller number were used for the comparisons of the species and treatments. Time was considered as a factor by analysing the data as repeated measurements analysis.

5.2.2 Results- experiment 1

5.2.2.1 Plant herbage mass components and relative growth rate

The accumulated green leaf, senescent leaf, total leaf, pseudostem and consequently shoot mass were higher in perennial ryegrass than in tall fescue, though shoot relative growth rate was similar for both species (Table 5.1). The order of the defoliation treatments for green leaf mass of perennial ryegrass was M>H>L>C, whereas for tall fescue the order was M>L>C>H (Table 5.2), which resulted in a significant interaction for species x defoliation treatments.

Under treatments M and H the oldest leaf was removed before becoming senescent. In general, senescent leaf mass was higher on treatment C than under treatment L (Table 5.2). The accumulated senescent leaf for treatments C and L in perennial ryegrass were higher than for treatments C and L of tall fescue (Table 5.2, Plate 5.2). The interaction of species x defoliation treatment was significant.

Total leaf mass for both species was highest under M and lowest under H treatments (Table 5.2). Pseudostem mass decreased with increasing severity of defoliation; treatment H had significantly lower pseudostem mass than the other treatments. Shoot mass in both species was lower in treatment H than in treatments C, L and M, which did not differ significantly (Table 5.2). The reduction in shoot mass under hard defoliation was greater for tall fescue (52%) than for perennial ryegrass (38%), consequently, shoot relative growth rate was significantly lower under treatment H than the other treatments (Table 5.2).

The mean proportion of leaf lamina to shoot mass for both species was 55%. The proportion of leaf increased as the severity of defoliation increased (Figure 5.2).

Table 5.1: Accumulated dry mass of green leaf, senescent leaf, total leaf, pseudostem, total shoot (g plant^{-1}), and mean shoot relative growth rates (RGR) (mg g^{-1} day^{-1}) of perennial ryegrass and tall fescue.

	Ryegrass	Fescue	SEM	F
Green leaf	13.9	12.0	0.40	**
Senescent leaf	3.1	0.4	0.19	***
Total leaf	17.0	12.4	0.40	***
Pseudostem	13.9	10.0	0.62	***
Total shoot	30.9	22.3	0.89	***
Shoot RGR	20.6	20.6	0.06	ns

Table 5.2: Accumulated dry mass of green leaf senescent leaf, total leaf, pseudostem, total shoot (g plant^{-1}), and mean shoot relative growth rates (RGR) (mg g^{-1} day^{-1}) of perennial ryegrass and tall fescue under different leaf defoliation treatments.

	Ryegrass				Fescue					F values for		
	C	L	M	H	C	L	M	H	SEM	SP	TR	SPxTR
Green leaf	9.9	13.6	17.6	14.4	12.0	12.9	14.6	8.2	0.79	**	***	***
Senescent leaf	6.9	3.9	1.4	0.4	1.3	0.2	0.0	0.0	0.38	***	***	***
Total leaf	16.8	17.5	19.0	14.5	13.3	13.1	14.7	8.2	0.80	***	***	ns
Pseudostem	18.9	15.1	13.9	7.8	13.1	12.0	10.4	4.5	1.24	***	***	ns
Total shoot	35.7	32.6	33.0	22.2	26.4	25.0	25.1	12.8	1.79	***	***	ns
Shoot RGR	20.9	20.6	20.7	20.2	20.9	20.9	20.6	20.0	0.10	ns	***	ns

C: Control; M: Medium; L: Lax; H:Hard defoliation

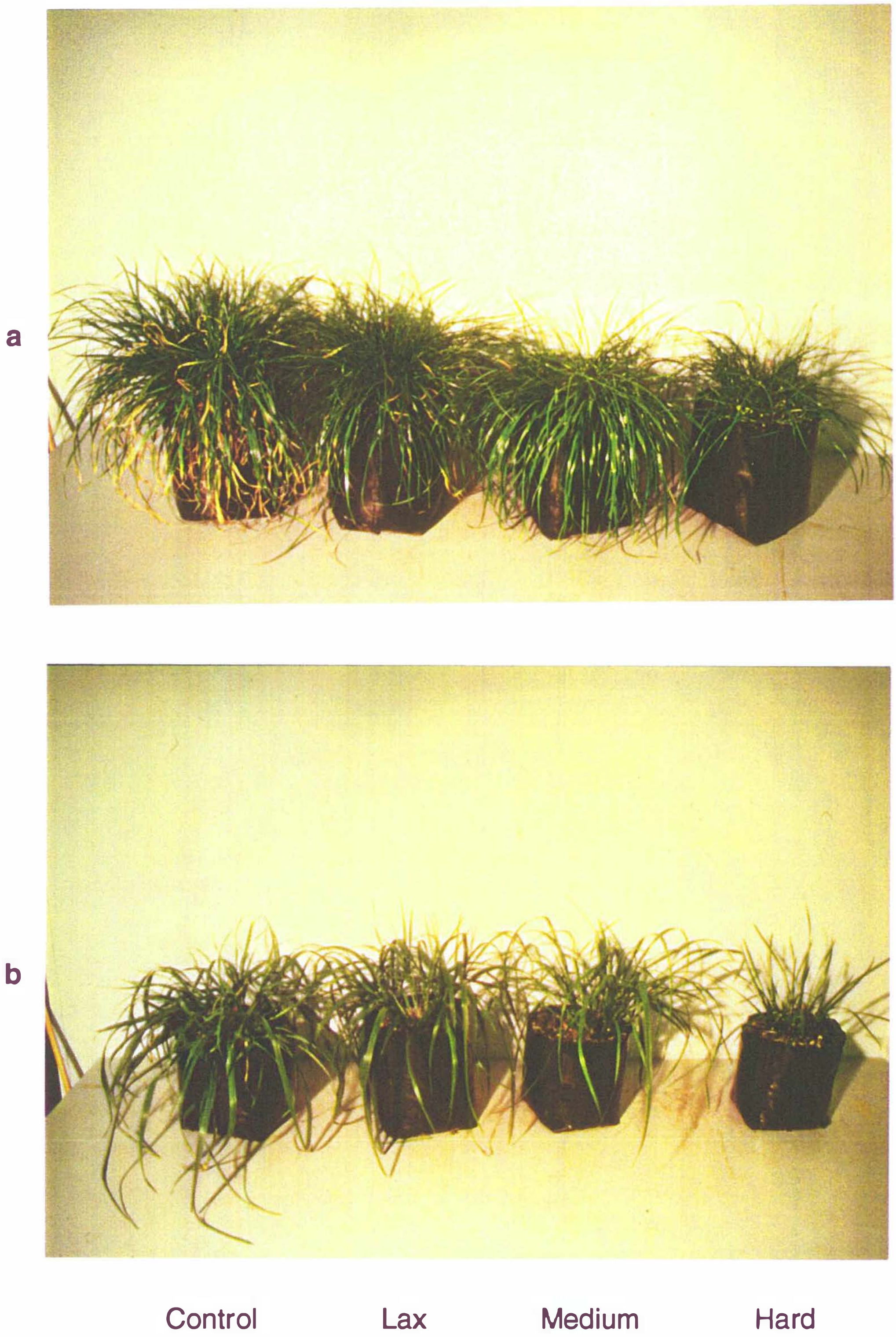

Plate 5.2: A general views of individual plants of (a) perennial ryegrass and (b) tall fescue nine weeks after sowing. Note differences in tiller number and proportion of senesced leaves.

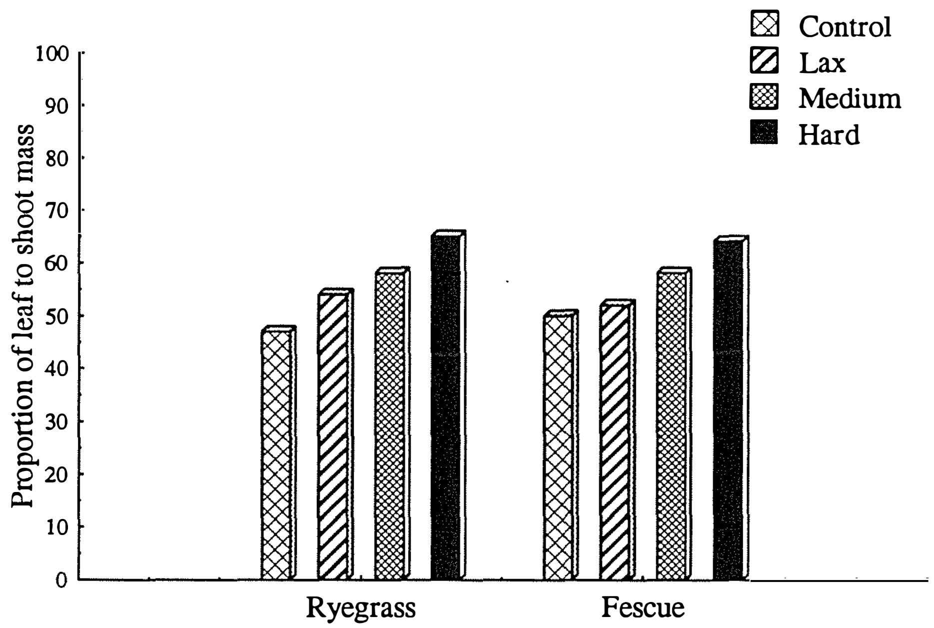

Figure 5.2: Proportion of leaf to shoot mass of perennial ryegrass and tall fescue under different defoliation treatments.

5.2.2.2 Tiller number and tiller weight

Tiller number per plant of the two species was initially different. So, both adjusted and unadjusted tiller number was used for comparison of species. Changes in tiller number(unadjusted) between species are shown in Table 5.3. Perennial ryegrass had significantly more tillers per plant than tall fescue throughout the measurement period (also see Plate 5.2). There were no differences between defoliation treatments (Table 5.4) and the interaction of species x defoliation treatments was not significant. The interaction of time x species ($P<0.001$) was significant.

Species and treatment comparisons, after adjustment for differences in tiller number at the start of the experiment, are shown in Tables 5.5 and 5.6. Neither species nor defoliation treatments showed differences in tiller number per plant. There were no interactions of species x defoliation treatments, time x species, time x defoliation treatments, or time x species x defoliation treatment. At the time of final harvest some of the perennial ryegrass tillers were in the reproductive stage with a node near the pot surface.

Overall, tillering rate (tiller tiller^{-1} day^{-1}) decreased over time (Tables 5.7 and 5.8). Perennial ryegrass had significantly higher tillering rates at LAS1 and LAS2, and lower tillering rates at LAS4, LAS5 and LAS6 than tall fescue (Table 5.7). On average, tillering rates for tall fescue were greater than for perennial ryegrass (Table 5.7). Tillering rates under different defoliation treatments were statistically similar, except at LAS5 and LAS6. Treatment M had the lowest tillering rate (Table 5.8). The interaction of time x species ($P< 0.001$) was significant.

Tiller weight of tall fescue was 1.7 times greater than perennial ryegrass (218 vs. 130 ±11 mg tiller^{-1} $P< 0.001$). Tiller weight for treatment H was lower than the other treatments. The magnitude of reduction relative to undefoliated plants was greater for tall fescue(48%) than for perennial ryegrass(28%) (Table 5.9). The species x defoliation treatments interaction was not significant.

Table 5.3: Tiller number per plant of perennial ryegrass and tall fescue (unadjusted mean).

Leaf appearance sequence	Ryegrass	Fescue	SEM	F
LAS0	36	12	1.32	***
LAS1	66	20	2.74	***
LAS2	116	33	4.81	***
LAS3	167	50	7.51	***
LAS4	219	71	9.06	***
LAS5	244	90	9.53	***
LAS6	259	109	9.64	***

Table 5.4: Effect of leaf defoliation treatments on tiller number per plant of pooled perennial ryegrass and tall fescue (unadjusted mean).

Leaf appearance sequence	Treatmeants					
	C	L	M	H	SEM	F
LAS0	23	25	25	23	1.86	ns
LAS1	42	46	44	41	3.88	ns
LAS2	74	75	80	69	6.80	ns
LAS3	107	109	117	103	10.63	ns
LAS4	142	144	152	140	12.82	ns
LAS5	174	163	173	162	13.48	ns
LAS6	195	181	184	175	13.63	ns

Table 5.5: Tiller number per plant of perennial ryegrass and tall fescue (adjusted mean).

Leaf appearance sequence	Ryegrass	Fescue	SEM	F
LAS1	43	44	1.78	ns
LAS2	75	74	3.26	ns
LAS3	110	108	7.38	ns
LAS4	156	134	10.83	ns
LAS5	183	153	12.15	ns
LAS6	201	167	13.48	ns

Table 5.6: Effect of leaf defoliation treatments on tiller number per plant of pooled perennial ryegrass and tall fescue (adjusted mean).

Leaf appearance sequence	Treatmeants				SEM	F
	C	L	M	H		
LAS1	43	44	42	43	1.38	ns
LAS2	77	72	77	72	2.53	ns
LAS3	111	104	112	108	5.73	ns
LAS4	147	139	147	146	8.41	ns
LAS5	178	158	168	166	9.44	ns
LAS6	199	176	180	179	10.48	ns

Table 5.7: Tillering rates (tiller tiller^{-1} day^{-1}) of perennial ryegrass and tall fescue.

Leaf appearance sequence	Ryegrass	Fescue	SEM	F
LAS1	0.087	0.077	0.003	*
LAS2	0.080	0.070	0.003	*
LAS3	0.052	0.050	0.003	ns
LAS4	0.034	0.042	0.002	**
LAS5	0.014	0.031	0.002	***
LAS6	0.007	0.023	0.002	***
Mean	0.046	0.049	0.001	*

Table 5.8: Effect of leaf defoliation treatments on mean tillering rates (tiller tiller^{-1} day^{-1}) of perennial ryegrass and tall fescue.

Leaf appearance sequence	Treatmeants					
	C	L	M	H	SEM	F
LAS1	0.082	0.084	0.081	0.081	0.004	ns
LAS2	0.077	0.069	0.082	0.071	0.004	ns
LAS3	0.053	0.052	0.051	0.048	0.004	ns
LAS4	0.040	0.035	0.036	0.041	0.002	ns
LAS5	0.030	0.022	0.018	0.024	0.003	*
LAS6	0.018	0.019	0.010	0.015	0.002	*
Mean	0.050	0.047	0.046	0.047	0.001	ns

Table 5.9: Tiller weight(mg tiller^{-1}) of perennial ryegrass and tall fescue under different leaf defoliation treatments

	Ryegrass				Fescue					F values for		
	C	L	M	H	C	L	M	H	SEM	SP	TR	SPxTR
Tiller weight	134	152	137	97	239	274	232	125	23	***	***	ns

5.2.2.3 Leaf appearance and site filling

The number of fully expanded leaves that appeared on three marked main tillers per plant was statistically similar in the two species, and consequently leaf appearance rates were similar (Table 5.10). Site filling based on either three marked tillers (F_s3T) or on 6 leaf defoliations (F_s6I) was higher in tall fescue than perennial ryegrass (Table 5.10). Leaf number, leaf appearance rate, F_s3T and F_s6I were not affected by defoliation treatments (Table 5.11). There were no interactions between species and defoliation treatments for all the above mentioned parameters.

Table 5.10: Leaf number appearance per tiller, leaf appearance rates (leaf tiller^{-1} day^{-1}) of three marked tillers per plant, and site filling (tiller leaf^{-1}) based on three marked tillers (F_s3T) and six leaf appearance intervals (F_s6I) of perennial ryegrass and tall fescue.

Characters	Ryegrass	Fescue	SEM	F
Leaf number	5.583	5.486	0.059	ns
Leaf appearance rate	0.126	0.125	0.001	ns
F_s3T	0.355	0.405	0.007	***
F_s6I	0.331	0.369	0.010	***

Table 5.11: Leaf number appearance per tiller (LN), leaf appearance rates (A_L) (leaf tiller^{-1} day^{-1}) of three marked tillers per plant, and site filling (tiller leaf^{-1}) based on three marked tillers (F_s3T) and six leaf appearance intervals (F_s6I) of mean of perennial ryegrass and tall fescue under different leaf defoliation treatments.

Characters	Treatmeants				SEM	F
	C	L	M	H		
LN	5.527	5.416	5.638	5.555	0.084	ns
A_L	0.125	0.124	0.128	0.126	0.002	ns
F_s3T	0.402	0.384	0.361	0.373	0.010	ns
F_s6I	0.370	0.345	0.339	0.345	0.010	ns

5.2.2.4 Leaf growth

Leaf elongation rates (mm tiller^{-1} day^{-1}) decreased over time (Table 5.12 and 5.13). Leaf elongation rates of both species at each leaf appearance sequence and on average over time were statistically similar, except in LAS1 and LAS2 where values for perennial ryegrass were greater than for tall fescue (Table 5.12). Leaf elongation rates were not affected by leaf defoliation over time (Table 5.13). No significant interactions were observed between species x defoliation treatments, time x defoliation treatments, and time x species x defoliation treatments, but time x species was significant ($P < 0.001$).

Leaf lamina growth rates (mg tiller^{-1} day^{-1}) for species and for treatments are shown in Tables 5.14 and 5.15, respectively. Overall, leaf growth rate reduced over time. Perennial ryegrass had greater leaf growth rate at LAS1 and lower leaf growth rate at LAS3 than tall fescue. Leaf growth rate decreased as severity of defoliation increased. The mean values indicated more reduction for tall fescue than perennial ryegrass. The interactions of species x defoliation treatments for the LAS3 and for the mean , time x species ($P < 0.001$), and time x species x defoliation treatments ($P < 0.05$) were significant.

Table 5.12: Leaf elongation rates (mm tiller^{-1} day^{-1}) of perennial ryegrass and tall fescue.

Leaf appearance sequence	Ryegrass	Fescue	SEM	F
LAS1	40	34	1.05	***
LAS2	38	33	1.25	*
LAS3	30	30	1.27	ns
LAS4	23	25	1.10	ns
LAS5	20	21	1.01	ns
LAS6	17	17	0.89	ns
Mean	29	28	0.96	ns

Table 5.13: Effect of leaf defoliation treatments on leaf elongation rates (mm tiller^{-1} day^{-1}) of grass species.

Leaf appearance sequence	Treatmeants					
	C	L	M	H	SEM	F
LAS1	38	37	38	34	1.48	ns
LAS2	37	36	36	31	1.77	ns
LAS3	31	31	30	29	1.79	ns
LAS4	26	25	23	24	1.55	ns
LAS5	23	22	19	20	1.43	ns
LAS6	18	18	15	16	1.25	ns
Mean	30	29	28	26	1.35	ns

Table 5.14: Leaf lamina growth rates (mg tiller^{-1} day^{-1}) of perennial ryegrass and tall fescue.

Leaf appearance sequence	Ryegrass	Fescue	SEM	F
LAS1	1.9	1.7	0.05	**
LAS3	1.3	1.6	0.06	**
LAS6	0.8	0.9	0.05	ns
Mean	1.3	1.4	0.04	ns

Table 5.15: Effect of leaf defoliation treatments on leaf lamina growth rates (mg tiller^{-1} day^{-1}) of perennial ryegrass and tall fescue.

	Ryegrass				Fescue					F values for		
	C	L	M	H	C	L	M	H	SEM	SP	TR	SPxTR
LAS1	2.1	2.0	1.8	1.8	1.9	2.0	1.7	1.2	0.1	**	***	ns
LAS3	1.4	1.3	1.3	1.2	2.0	1.8	1.4	1.0	0.1	**	***	*
LAS6	0.9	0.9	0.8	0.6	1.2	1.0	0.8	0.6	0.1	ns	***	ns
Mean	1.4	1.4	1.3	1.2	1.7	1.6	1.3	1.3	0.1	ns	***	*

5.2.2.5 Leaf characteristics

Mature leaf length was not statistically different between species (Table 5.16) but it was affected by the leaf defoliation treatments. Individual leaf length of plants under treatments M and especially H, became shorter relative to plants under treatments L and C (5.17).

Individual leaf area of tall fescue plants was 1.7 times higher than perennial ryegrass (Table 5.16). In all treatments leaf area decreased as severity of defoliation increased, except for treatment L in tall fescue, and resulted in the interaction of species x treatment defoliation. The decrease in leaf area for treatments M and H of tall fescue was more intensive than perennial ryegrass (Table 5.17).

Leaf weight of tall fescue was 2 times greater than that of perennial ryegrass (Table 5.16). The trend was for leaf weight to decrease as severity of defoliation increased, but decrease was greater for tall fescue than perennial ryegrass (Table 5.17). The interaction of species x defoliation treatments was significant.

Specific leaf area was lower in tall fescue than perennial ryegrass, though the difference was not statistically significant (Table 5.16). Specific leaf weight was greater for tall fescue than for perennial ryegrass (Table 5.16). Specific leaf area under treatment H was significantly greater than the other treatments. In contrast specific leaf weight under treatments M and H in tall fescue and treatment H in perennial ryegrass were lower than the other treatments (Table 5.17). The interactions of species x defoliation treatments for both measurements were not significant.

Table 5.16: Individual leaf length (mm), leaf area (cm^2), leaf weight (mg), specific leaf area (SLA)(cm^2 g^{-1}) and specific leaf weight (SLW)(mg cm^{-2}) of perennial ryegrass and tall fescue.

Characters	Ryegrass	Fescue	SEM	F
Leaf length	240	234	4.5	ns
Leaf area	7.8	13.1	0.4	***
Leaf weight	36	73	3.0	***
SLA	224	209	9.2	ns
SLW	4.7	5.3	0.1	**

Table 5.17: Individual leaf length (mm), leaf area (cm^2), leaf weight (mg), specific leaf area (SLA) (cm^2 g^{-1}) and specific leaf weight (SLW)(mg cm^{-2}) of perennial ryegrass and tall fescue under different leaf defoliation treatments.

	Ryegrass				Fescue					F values for		
	C	L	M	H	C	L	M	H	SEM	SP	TR	SPxTR
Length	257	255	232	222	258	265	221	189	8.9	ns	***	ns
Area	9.8	7.5	7.3	6.6	16.9	16.9	10.7	8.1	0.9	***	***	**
Weight	46	37	34	26	107	95	60	31	6.1	***	***	**
SLA	216	204	222	254	192	182	188	271	18.8	ns	**	ns
SLW	4.7	5.0	4.7	4.1	6.3	6.3	5.6	5.5	0.4	**	**	ns

5.2.2.6 Leaf photosynthesis and respiration

Rates of photosynthesis per unit area and per unit weight of the uppermost fully expanded leaf (L2) were not significantly different between species, and the photosynthetic activity of the leaves of both species decreased at LAS6 (Table 5.18). The rate of photosynthesis per unit area was not affected by leaf defoliation (Table 5.19). Rates of leaf photosynthesis per unit weight increased under treatment H, although the increase was not significant at the first and third measurements (Table 5.19). There were no interactions between species and defoliation treatments in terms of rates of leaf photosynthesis per unit leaf area and unit leaf weight. The species x treatments, and all combinations of time, species and defoliation treatments interactions were not significant.

Dark respiration rates per unit leaf area of the same leaves were similar for both species, but dark respiration rate per unit leaf weight was higher in ryegrass than tall fescue (Table 5.18). Both species under different defoliation treatments had statistically similar rates of dark respiration, but the rates per unit weight were higher under treatments M and H than treatments C and L (Table 5.19). There was no interaction between species and defoliation treatments.

5.2.2.7 Water soluble carbohydrate

Water soluble carbohydrate (WSC) concentrations in stem bases were higher in perennial ryegrass than tall fescue (269 vs. 209 ±12 mg/g dry weight $P< 0.01$). A sharp depletion of carbohydrate occurred under hard defoliation treatments; WSC concentrations under this treatment were lower than under the other treatments which did not differ significantly (Table 5.20). The reduction under hard defoliation was 56% and 44% for tall fescue and for perennial ryegrass respectively, relative to control plants.

Table 5.18: Leaf photosynthetic and dark respiration rates per unit leaf area (μmol CO_2 m^{-2} s^{-1}) and unit leaf weight (μmol CO_2 kg^{-1} s^{-1}) of the uppermost fully expanded leaf (L2) of perennial ryegrass and tall fescue.

	Ryegrass		Fescue	SEM	F
		μmol CO_2 m^{-2} s^{-1}			
Photosynthesis					
LAS1	13.8		13.5	0.50	ns
LAS3	14.7		14.7	0.34	ns
LAS6	11.0		11.6	0.45	ns
Respiration					
LAS6	1.5		1.4	0.06	ns
		μmol CO_2 kg^{-1} s^{-1}			
Photosynthesis					
LAS1	288		274	11	ns
LAS3	356		319	17	ns
LAS6	239		228	17	ns
Respiration					
LAS6	34		29	2	*

Table 5.19: Leaf photosynthetic and dark respiration rates per unit leaf area (μmol CO_2 m^{-2} s^{-1}) and unit leaf weight (μmol CO_2 kg^{-1} s^{-1}) of the uppermost fully expanded leaf (L2) of perennial ryegrass and tall fescue under different leaf defoliation treatments.

	Treatments					
	C	L	M	H	SEM	F
		μmol CO_2 m^{-2} s^{-1}				
Photosynthesis						
LAS1	13.7	13.7	13.8	13.5	0.74	ns
LAS3	14.0	14.5	14.6	15.8	0.53	ns
LAS6	11.3	11.4	11.1	11.4	0.70	ns
Respiration						
LAS6	1.5	1.4	1.5	1.4	0.09	ns
		μmol CO_2 kg^{-1} s^{-1}				
Photosynthesis						
LAS1	264	254	292	315	17	ns
LAS3	272	272	363	412	26	*
LAS6	228	228	218	276	27	ns
Respiration						
LAS6	26	28	35	37	2.63	*

Table 5.20: Water soluble carbohydrate concentrations (WSC) (mg g^{-1} dry weight) in the stem bases of perennial ryegrass and tall fescue under different leaf defoliation treatments.

	Ryegrass				Fescue					F values for		
	C	L	M	H	C	L	M	H	SEM	SP	TR	SPxTR
WSC	309	278	312	175	259	252	209	114	24.5	**	***	ns

5.2.3 Material and methods- experiment 2

5.2.3.1 Experimental conditions

Individual plants of tall fescue and perennial ryegrass were grown from seed in pots (15 cm diameter by 16 cm deep) filled with 50/50 fine-loam-mixed-mesic soil (Haplquept) and sand. Nutrients were supplied as 240g superphosphate, 240g lime, 180g osmocote (release over 3-4 months), 120g dolomite and 48g micromax per 100 litre of potting media. Pots were placed in two growth cabinets at the Plant Growth Unit (PGU), Massey University in Palmerston North.

The growth cabinet conditions were maintained at 21 ±1°C during the day and 15 ±1°C at night; with 12h photoperiod. The photosynthetic photon flux density(PPFD) of about 600 μmol m^{-2} s^{-1} was provided at bench height in cabinets using 2 x 1000 W Phillips tungsten halogen lamps together with 6 x 400 W Phillips HPI/T mercury iodide high-pressure discharge lamps, and also 3 x 100 W incandescent lamps. Relative humidity during day and night was 60 ±5%. Plants were watered from the bottom by adding water into trays underneath the pots when needed.

Leaf defoliation treatments were applied to both species when there was an average of 11 tillers per plant (plants were 38 and 26 days old in tall fescue and perennial ryegrass respectively. Each individual plant per pot was considered as a replicate. Because plants of both species under lax defoliation treatment showed similar responses to the control plants (experiment 1), this treatment was discarded. For each species 18 plants provided six replicates of three leaf defoliation treatments which consisted of control (C), and medium (M) and hard (H) defoliation. Leaf defoliation treatments were carried out as in experiment 1 (Section 5.2.1.1) for seven leaf appearance sequences. There was a factorial combination of treatments in a randomised complete block design for each species with each three replicates placed in one growth cabinet.

5.2.3.2 Measurements

Leaf elongation rates (mm tiller^{-1} day^{-1}) were estimated as for experiment 1 from 5 marked tillers per plant, with three of them being parent tillers which were continuously measured throughout the trial, and two being new daughter tillers with a fully expanded leaf which were measured for one defoliation interval. Leaf lamina growth rates (mg tiller^{-1} day^{-1}) were calculated as for experiment 1.

All measurements including tiller number per plant, tillering rates, tiller weight, leaf number per tiller (LN), and leaf appearance rates (A_L) were based on three main marked tillers, site filling (F_s) was based on leaf appearance rates on three marked tillers and 7 leaf appearance intervals, initial shoot dry mass was based on 4 random plants for each species, total accumulated shoot dry mass and its components, mean shoot RGR, and WSC in stem bases of plants were attained as explained for experiment 1. Leaf area per plant (PLA)(cm^2), was measured using a leaf area meter. Leaf area ratios based on shoot mass (SLAR) and total plant biomass (BLAR) were calculated by dividing PLA by shoot mass and by total biomass respectively.

Roots of the plants were washed free of soil, dried at 80°C for 48h and weighed. Root material was then combusted at 500°C in a muffle furnace, and organic matter of the roots calculated by subtracting the root ash from the total root dry mass. This was regarded as the total root mass. The mean root RGR was also estimated, as for shoot RGR, from initial root mass of plants which had been cut at the beginning of experiment and total root mass at final harvest.

Individual leaf characteristics including leaf length, leaf weight, leaf area, SLA and SLW were measured on five uppermost fully expanded leaves per plant at final harvest as explained in experiment 1 (Section 5.2.1.2). Individual leaf width (of first half from the base of leaf lamina) of the same leaves was measured using a ruler with 1 mm precision.

Leaf photosynthesis of all leaves of two tillers per plant was measured at LAS1, LAS3 and LAS6 by an infra-red gas analyzer (Li-cor 6200) apparatus as mentioned in the previous experiment (Section 5.2.1.2). Net photosynthetic rates were calculated per unit leaf area and unit leaf weight.

The change in photosynthetic and respiration rates as leaves aged was measured on 6 intact plants for each species. Two new emerging leaves per plant were marked. Leaf photosynthetic and respiration rates per unit leaf area of these leaves were measured at day 5 after emergence, at full expansion (day 8), day 10 and then at 4 day intervals until leaf senescence (more than 80% necrotic). The time from leaf emergence to senescence was considered as leaf life-span for both species.

5.2.3.3 Statistical analysis

The data were examined by analysis of variance using the General Linear Model (GLM) procedure of SAS (SAS Institute Inc. 1991) as explained in experiment 1.

5.2.4 Results- experiment 2

5.2.4.1 Plant herbage mass components and relative growth rate

The time elapsed between seedling emergence and final experimental defoliation was 70 and 87 days for perennial ryegrass and tall fescue plants respectively. The longer time of growth for tall fescue was to get to 11 tillers per plant. Its longer time of growth resulted in higher plant biomass, root mass, shoot mass, pseudostem and green leaf relative to perennial ryegrass, although the shoot relative growth rate was significantly lower in tall fescue than ryegrass during the experimental period (Table 5.21). The accumulated senescent leaf of control plants was greater in perennial ryegrass than tall fescue, although the difference was not significant (Table 5.21). The absence of senescent leaf under treatment M and H was due to the removal of the oldest leaf before senescence (Table 5.22). Relative root growth rates for the two grasses were statistically similar (Table 5.21).

Leaf defoliation treatments had a significant effect on all the above components. Both species under treatment H had significantly lower leaf, pseudostem, shoot, root (see Plate 5.3), and total biomass, shoot relative growth rate and root relative growth rate than under treatments C and M (Table 5.22). The interaction of species x defoliation treatments was significant for green leaf, total leaf pseudostem, shoot, root and total biomass and shoot relative growth rate (Table 5.22).

The proportions of leaf lamina and root mass to shoot mass are depicted in figures 5.3 and 5.4. Tall fescue had a slightly lower proportion of leaf lamina to shoot, and a higher proportion of root to shoot mass than perennial ryegrass. Higher leaf lamina to shoot ratio and lower root to shoot ratio were observed under the hard defoliation than for plants with no defoliation or plants under moderate defoliation.

Table 5.21: The accumulated dry mass of green leaf, senescent leaf, total leaf, pseudostem, shoot mass, root mass and total biomass(g plant^{-1}), and mean shoot and root relative growth rates(RGR)(mg g^{-1} day^{-1}) of perennial ryegrass and tall fescue.

	Ryegrass	Fescue	SEM	F
Green leaf	11.2	15.5	0.67	***
Senescent leaf	0.7	0.5	0.16	ns
Total leaf	11.8	16.0	0.65	***
Pseudostem	8.8	13.7	0.67	***
Shoot mass	20.7	29.7	1.26	***
Root mass	4.5	9.0	0.46	***
Total biomass	25.1	38.6	1.61	***
Shoot RGR	21.2	18.7	0.07	***
Root RGR	17.0	16.2	0.30	ns

Table 5.22: Effect of leaf defoliation treatments on accumulated dry mass of green leaf, senescent leaf, total leaf, pseudostem, shoot mass, root mass and total biomass (g plant^{-1}), and mean shoot and root relative growth rates(RGR)(mg g^{-1} day^{-1}) of perennial ryegrass and tall fescue.

	Ryegrass			Fescue				F values for		
	C	M	H	C	M	H	SEM	SP	TR	SPxTR
Green leaf	12.1	12.8	8.6	19.8	17.4	9.4	1.16	***	***	*
Senescent leaf	2.0	0.0	0.0	1.5	0.0	0.0	0.27	ns	***	ns
Total leaf	14.1	12.8	8.6	21.3	17.4	9.4	1.13	***	***	*
Pseudostem	13.9	9.1	3.5	21.2	15.1	4.7	1.14	***	***	*
Shoot mass	28.0	21.9	12.1	42.4	32.5	14.1	2.19	***	***	*
Root mass	6.4	5.3	1.7	14.1	10.4	2.4	0.80	***	***	***
Total biomass	34.4	27.2	13.8	56.6	42.9	16.5	2.79	***	***	**
Shoot RGR	21.7	21.4	20.5	19.4	19.1	17.6	0.12	***	***	*
Root RGR	19.2	18.4	13.6	18.6	17.9	12.1	0.51	ns	***	ns

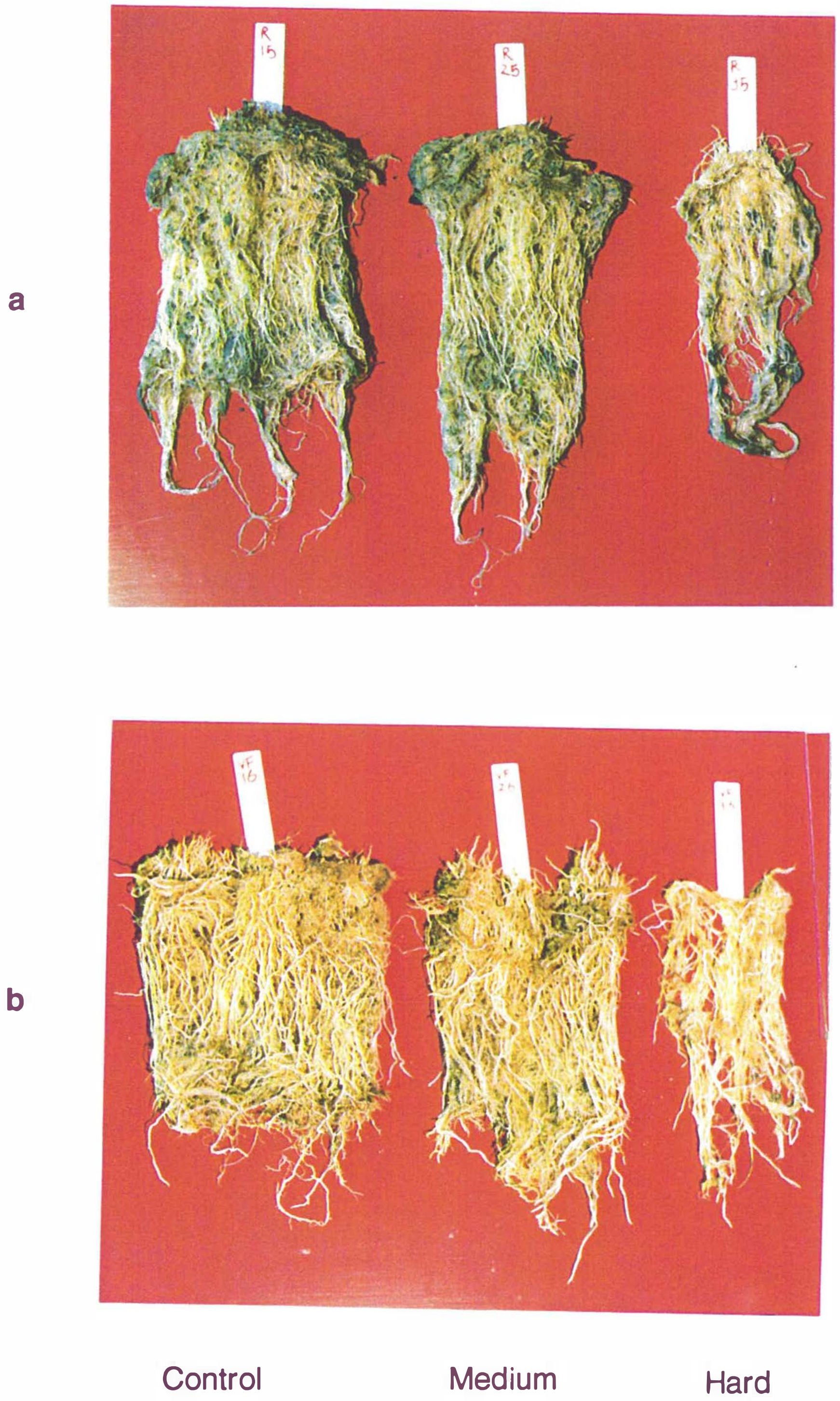

Plate 5.3: Accumulation of root mass of (a) perennial ryegrass and (b) tall fescue under different defoliation treatments

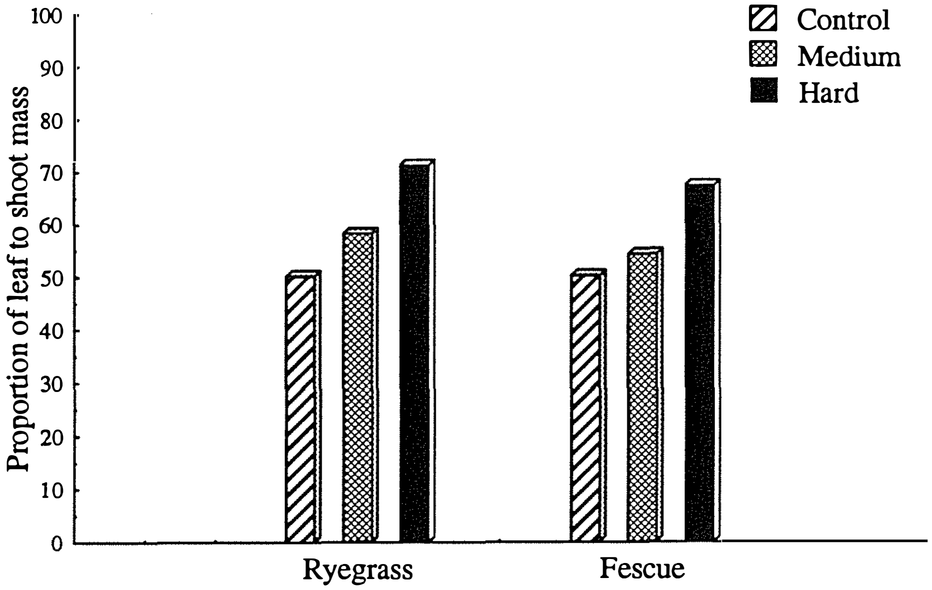

Figure 5.3: Proportion of leaf to shoot mass of perennial ryegrass and tall fescue under different defoliation treatments.

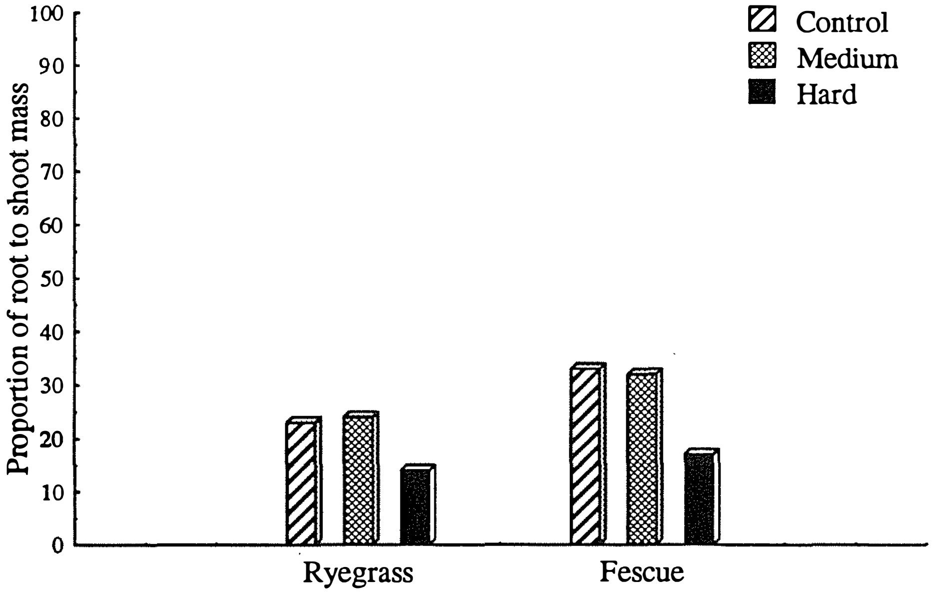

Figure 5.4: Proportion of root to shoot mass of perennial ryegrass and tall fescue under different defoliation treatments.

5.2.4.2 Leaf area per plant and leaf area ratio

Leaf area per plant (PLA) was 11% higher for tall fescue than for perennial ryegrass, although the difference was not significant (Table 5.23). Differences between the defoliation treatments were not significant, but PLA was lower under treatment H relative to the other treatments (Table 5.23). Both leaf area ratio per shoot (SLAR) and per total biomass (BLAR) were about 14% and 18% lower in tall fescue than perennial ryegrass, respectively (Table 5.23). Plants of both species responded to hard defoliation by increasing SLAR and BLAR relative to moderately defoliated plants and control plants (Table 5.23).

Table 5.23: Leaf area per plant (PLA) (cm^2), leaf area ratio per shoot mass (SLAR) and per biomass (BLAR) (cm^2 g^{-1}) of perennial ryegrass and tall fescue under different leaf defoliation treatments.

	Ryegrass			Fescue				F values for		
	C	M	H	C	M	H	SEM	SP	TR	SPxTR
PLA	2862	2804	2562	3297	3269	2687	345	ns	ns	ns
SLAR	104	127	210	80	106	191	11	*	***	ns
BLAR	84	102	182	61	80	163	9	**	***	ns

5.2.4.3 Tiller number and tiller weight

Tiller number per plant of both species was initially similar but differences became significant after the third defoliation. Perennial ryegrass produced significantly higher tiller numbers than tall fescue over the rest of the experiment, and produced 1.8 times more tillers by the end of the experiment (Table 5.24). The effect of defoliation treatment on tiller number was progressive and treatment H had significantly lower tiller numbers than treatments C and M at LAS6 and LAS7 (Table 5.25). The interactions of time x species ($P<0.001$), time x treatment ($P< 0.001$) and time x species x treatment ($P< 0.05$) were all significant.

Overall, tillering rate (tiller tiller^{-1} day^{-1}) decreased over time (Tables 5.26 and 5.27). Perennial ryegrass was superior to tall fescue throughout the experiment and on average had 1.4 times greater tillering rate than tall fescue (Table 5.26). The tillering rate for treatment H was significantly lower at LAS2, LAS4 and LAS5 than for other treatments (Table 5.27). A sharp reduction in tillering in treatment C at LAS6 and LAS7 for tall fescue resulted in a significant interaction of species x treatment at these times. There were no significant interactions between time x species, time x treatment, and time x species x treatment.

Table 5.24: Tiller number per plant of perennial ryegrass and tall fescue.

Leaf appearance sequence	Ryegrass	Fescue	SEM	F
LAS0	11	11	0.59	ns
LAS1	18	17	0.92	ns
LAS2	30	26	1.41	*
LAS3	50	38	2.36	***
LAS4	77	54	3.75	***
LAS5	113	71	5.08	***
LAS6	145	84	6.23	***
LAS7	174	98	6.41	***

Table 5.25: Effect of leaf defoliation treatments on tiller number per plant: mean of perennial ryegrass and tall fescue data.

Leaf appearance sequence	Treatmeants				
	C	M	H	SEM	F
LAS0	11	11	11	0.72	ns
LAS1	18	18	18	1.12	ns
LAS2	29	28	26	1.73	ns
LAS3	46	45	40	2.88	ns
LAS4	68	69	59	4.59	ns
LAS5	98	99	80	6.22	ns
LAS6	123	123	98	7.68	*
LAS7	146	146	115	7.85	*

Table 5.26: Tillering rates (tiller tiller^{-1} day^{-1}) of perennial ryegrass and tall fescue.

Leaf appearance sequence	Ryegrass	Fescue	SEM	F
LAS1	0.100	0.072	0.006	**
LAS2	0.083	0.061	0.005	**
LAS3	0.087	0.061	0.004	***
LAS4	0.072	0.051	0.003	***
LAS5	0.055	0.034	0.002	***
LAS6	0.036	0.022	0.002	***
LAS7	0.026	0.019	0.002	**

Table 5.27: Effect of leaf defoliation treatments on tillering rates (tiller tiller^{-1} day^{-1}) of perennial ryegrass and tall fescue

	Ryegrass			Fescue				F values for		
	C	M	H	C	M	H	SEM	SP	TR	SPxTR
LAS1	0.106	0.101	0.093	0.074	0.072	0.071	0.011	**	ns	ns
LAS2	0.085	0.092	0.071	0.074	0.064	0.044	0.008	**	*	ns
LAS3	0.084	0.085	0.092	0.067	0.064	0.052	0.006	***	ns	ns
LAS4	0.077	0.072	0.065	0.046	0.060	0.045	0.005	***	*	ns
LAS5	0.057	0.055	0.052	0.036	0.038	0.027	0.003	***	*	ns
LAS6	0.043	0.033	0.031	0.014	0.024	0.026	0.003	***	*	**
LAS7	0.029	0.027	0.023	0.015	0.019	0.023	0.003	**	ns	*

Tiller weight of tall fescue was 2.9 times greater than perennial ryegrass (336 vs. 114 ±24 mg tiller^{-1} $P< 0.001$). In general, tiller weight of both species decreased as severity of defoliation increased; the reduction in tiller weight was greater for tall fescue than for perennial ryegrass (Table 5.28). The species x treatment interaction was not significant.

Table 5.28: Tiller weight(mg tiller^{-1}) of perennial ryegrass and tall fescue under different leaf defoliation treatments.

	Ryegrass			Fescue				F values for		
	C	M	H	C	M	H	SEM	SP	TR	SPxTR
Tiller weight	138	122	83	460	345	201	41	***	**	ns

5.2.4.4 Leaf appearance and site filling

The number of fully expanded leaves which appeared on three marked main tillers per plant was used to provide estimates of leaf number per tiller and rate of leaf appearance. These values were not necessarily representative of the whole plant, but provided a basis for comparison of leaf appearance on tillers of the same age. Perennial ryegrass produced 6.44 fully expanded leaves per tiller over 44 days, whereas tall fescue produced 5.92 leaves over 49 days during the experiment (Table 5.29). The leaf appearance rate (leaf tiller^{-1} day^{-1}) was significantly greater in perennial ryegrass than tall fescue (Table 5.29). Neither leaf number per tiller (LN) nor leaf appearance rate (A_L) were affected by defoliation (Table 5.30). The interaction of species x treatment was not significant.

In perennial ryegrass and tall fescue leaf appearance interval was faster in the early vegetative stage of tiller development. For this reason there were differences in the number of leaves produced per tiller on the three marked tillers (Tables 5.29 and 5.30) and the number of defoliations (7 leaf appearance intervals) which were based on the appearance of a new fully expanded leaf on more than 80% of tillers per plant. Therefore, site filling estimates were based on both the leaf appearance on three marked tillers (F_s3T) and on the number of times which plants were defoliated (F_s7I).

Both estimates of site filling were significantly greater in ryegrass than tall fescue (Table 5.29). Values based on Fs7I were slightly lower than those based on Fs3T in both species (Table 5.29). Plants defoliated severely failed to fill sites relative to treatments C and M in both species, and showed significantly lower site filling rates (Table 5.30). There was no interaction between species and treatment.

Table 5.29: Leaf number appearance per tiller, leaf appearance rates (leaf $tiller^{-1}$ day^{-1}) of three marked tillers per plant, and site filling (tiller $leaf^{-1}$) based on three marked tillers and seven leaf appearance intervals of perennial ryegrass and tall fescue.

Characters	Ryegrass	Fescue	SEM	F
Leaf number	6.440	5.920	0.070	**
Leaf appearance rate	0.146	0.121	0.002	***
Site filling(3 tillers)	0.440	0.360	0.002	***
Site filling(7 intervals)	0.400	0.300	0.008	***

Table 5.30: Leaf number appearance per tiller (LN), leaf appearance rates(A_L) (leaf $tiller^{-1}$ day^{-1}) of three marked tillers per plant, and site filling (tiller $leaf^{-1}$) based on three marked tillers (F_s3T) and seven leaf appearance intervals (F_s7I) of perennial ryegrass and tall fescue under different leaf defoliation treatments.

	Ryegrass			Fescue				F values for		
	C	M	H	C	M	H	SEM	SP	TR	SPxTR
LN	6.500	6.388	6.444	5.778	5.944	6.055	0.121	**	ns	ns
A_L	0.148	0.145	0.146	0.118	0.121	0.123	0.003	***	ns	ns
F_s3T	0.490	0.440	0.400	0.370	0.380	0.320	0.026	***	*	ns
F_s7I	0.420	0.400	0.370	0.310	0.320	0.280	0.014	***	**	ns

5.2.4.5 Leaf growth

Leaf elongation was measured on three main tillers and two daughter tillers at each leaf appearance interval. Main and daughter tillers behaved similarly throughout the experiment, though main tillers showed greater (33% on average) leaf elongation rate (mm $tiller^{-1}$ day^{-1}) than daughter tillers. The average leaf elongation rate for each tiller category is shown in Table 5.31 for species and Table 5.32 for treatments. The data for five tillers per plant were combined and analyzed for estimation of leaf elongation rate for species and for different defoliation treatments.

Leaf elongation rate decreased over time (Table 5.31 and 5.32). It was significantly greater in perennial ryegrass than tall fescue at all defoliations except LAS2 and LAS3. On average leaf elongation rate of ryegrass was 17% more than tall fescue (Table 5.31). The interaction of species x defoliation treatment was not significant. Leaf elongation of treatment H was lower than treatments C and M at LAS2, LAS3 and LAS4, but greater at LAS7 (Table 5.32). On average leaf elongation rate of treatment H was slightly lower than the other treatments, but the differences were not statistically significant (Table 5.32). The interactions of time x species, time x treatment were significant ($P< 0.001$).

Leaf lamina growth rates (mg tiller^{-1} day^{-1}) was calculated on the basis of 5 marked tillers. Perennial ryegrass produced greater leaf dry matter per tiller for all periods than tall fescue, though the difference was not significant at LAS3 (Table 5.33). Leaf lamina production was influenced by defoliation treatment, decreasing with increasing severity of defoliation (Table 5.34). There was no interaction between species and defoliation treatments, but time interacted with defoliation treatments ($P< 0.05$).

Table 5.31: Leaf elongation rates (mm tiller^{-1} day^{-1}) of perennial ryegrass and tall fescue.

Leaf appearance sequence	Ryegrass	Fescue	SEM	F
LAS1	45	39	1.32	**
LAS2	38	37	1.33	ns
LAS3	40	38	1.34	ns
LAS4	39	34	1.36	*
LAS5	39	31	1.35	***
LAS6	35	28	0.89	***
LAS7	32	22	1.10	***
Mean	38	33	0.91	***
MeanPT	43	36	1.14	***
MeanDT	31	28	0.87	**

PT and DT are means of parent and daughter tillers over time respectively.

Table 5.32: Effect of leaf defoliation treatments on mean leaf elongation rates (mm tiller^{-1} day^{-1}) of perennial ryegrass and tall fescue

Leaf appearance sequence	Treatmeants				
	C	M	H	SEM	F
LAS1	43	42	40	1.62	ns
LAS2	39	39	34	1.55	*
LAS3	41	41	35	1.64	*
LAS4	37	39	33	1.66	*
LAS5	35	37	33	1.66	ns
LAS6	31	31	31	1.09	ns
LAS7	24	26	30	1.35	*
Mean	36	36	34	1.12	ns
MeanPT	40	41	37	1.40	ns
MeanDT	30	30	29	1.07	ns

PT and DT are means of parent and daughter tillers over time respectively.

Table 5.33: Leaf lamina growth rates (mg tiller^{-1} day^{-1}) of perennial ryegrass and tall fescue.

Leaf appearance sequence	Ryegrass	Fescue	SEM	F
LAS1	1.9	1.7	0.06	*
LAS3	1.7	1.6	0.06	ns
LAS6	1.4	1.3	0.04	*
LAS7	1.4	1.1	0.06	**

Table 5.34: Effect of leaf defoliation treatments on leaf lamina growth rates (mg tiller^{-1} day^{-1}) of perennial rygrass and tall fescue.

	Ryegrass			Fescue				F values for		
	C	M	H	C	M	H	SEM	SP	TR	SPxTR
LAS1	2.3	1.8	1.7	1.9	1.9	1.4	0.11	*	***	ns
LAS3	2.1	1.7	1.3	2.1	1.6	1.2	0.10	ns	***	ns
LAS6	2.0	1.3	0.9	1.6	1.3	0.9	0.07	*	***	ns
LAS7	1.7	1.5	1.0	1.3	1.2	1.0	0.10	**	***	*

5.2.4.6 Leaf characteristics

Individual leaf characteristics of the uppermost fully expanded leaves are shown in Tables 5.35 and 5.36. Tall fescue had longer and wider leaves and consequently higher individual leaf area than perennial ryegrass, although the difference in leaf length was not significant (Table 5.35). Leaf weight of tall fescue was 2.9 times greater than perennial ryegrass (Table 5.35). Ryegrass had higher specific leaf area and consequently lower specific leaf weight than tall fescue (Table 5.35). Perennial reygrass had a shorter leaf life-span than tall fescue (Table 5.35).

The effect of the defoliation treatments on all the above characteristics was significant (Table 5.36). Leaves from treatment H were shorter and narrower, and therefore smaller in area than leaves from treatment C and M in both species (Table 5.36).

Overall, leaf weight decreased with increasing severity of defoliation. The difference between treatments M and C was not statistically significant in either species, but treatment H leaves were 51% and 71% lighter than treatment C leaves in perennial ryegrass and tall fescue respectively (Table 5.36).

Specific leaf area was substantially increased when plants were defoliated to leave only one expanding leaf.The SLA under treatment H was 1.7 and 1.8 times greater than SLA of undefoliated plants in perennial ryegrass and tall fescue respectively (Table 5.36). Conversely, SLW was lower under treatment H than treatment C and M in both species (Table 5.36). The species x treatment interaction was only significant for leaf weight.

Table 5.35: Individual leaf length and width(mm), leaf area(cm^2), leaf weight(mg), specific leaf area (SLA)(cm^2 g^{-1}) and specific leaf weight (SLW)(mg cm^{-2}) and leaf life-span (day) of perennial ryegrass and tall fescue plants.

Characters	Ryegrass	Fescue	SEM	F
Leaf length	248.4	263.1	9.36	ns
Leaf width	4.0	7.6	0.23	***
Leaf area	6.4	13.6	0.71	***
Leaf weight	27.6	79.8	6.00	***
SLA	244.8	205.1	9.61	**
SLW	4.5	5.5	0.30	*
Leaf life-span	31.0	41.8	0.47	***

Table 5.36: Individual leaf length and width(mm), leaf area(cm^2), leaf weight(mg), specific leaf area(SLA)(cm^2 g^{-1}) and specific leaf weight(SLW)(mg cm^{-2}) of perennial ryegrass and tall fescue plants under different leaf defoliation treatments.

	Ryegrass			Fescue				F values for		
	C	M	H	C	M	H	SEM	SP	TR	SPxTR
Length	267	256	221	289	274	224	16	ns	**	ns
Width	4.2	4.2	3.6	8.4	8.3	6.1	0.4	***	**	ns
Area	6.6	6.8	5.7	16.3	14.8	9.6	1.2	***	*	ns
Weight	36.4	28.5	17.9	118.6	86.1	34.6	10.4	***	***	*
SLA	183	231	320	150	189	276	16.6	**	***	ns
SLW	5.6	4.7	3.1	7.2	5.6	3.6	0.6	*	***	ns

5.2.4.7 Leaf photosynthesis and respiration

Overall, rates of leaf photosynthesis per unit leaf area (μmol m^{-2} s^{-1}) and unit leaf weight (μmol kg^{-1} s^{-1}) of control plants decreased over time (Table 5.37). The rates of leaf photosynthesis per unit leaf area and per unit leaf weight of both species were similar for all measurement periods, except at LAS6 when perennial ryegrass had higher photosynthetic rates per unit leaf weight than tall fescue (Table 5.37). Rates of photosynthesis per unit area and per unit weight were higher for leaf 2 than for leaf 1, 3 and 4 in both species (Table 5.38). There was no interaction between species and leaf position on tiller.

The results for leaf photosynthesis of leaf 1 of all treatments and leaf 2 of treatments C and M are shown in Tables 5.39 and 5.40. The results indicated no significant difference between species or treatments in terms of leaf photosynthesis per unit area at any measurement and for any leaf category (Table 5.39 and 5.40). The interaction of time x defoliation treatment ($P< 0.01$) and time x species x defoliation treatment ($P< 0.05$) were significant for leaf L2.

Leaf photosynthesis per unit leaf weight was higher for perennial ryegrass than for tall fescue at LAS6 (Table 5.39). Leaf photosynthesis of leaf 1 of plants under treatment H was significantly greater than plants under treatments C and M, and it was also higher for leaf 2 at the third measurement (Table 5.40). There were interactions between time x species ($P< 0.05$) for L1, L2 and L3, and time x treatment ($P< 0.05$) for L2 and time x species x defoliation treatment ($P< 0.001$) for L2.

The change in photosynthetic and respiration rates as leaves aged are depicted in figures 5.5 and 5.6 respectively. Leaf photosynthesis of both species was about 11 μmol m^{-2} s^{-1} at day 5 after emergence (expanding stage). It increased by day 8 (fully expanded) and for 2 days later, then decreased during leaf aging. Leaf photosynthesis in perennial ryegrass declined to a low value at day 30 after emergence, whereas in tall fescue photosynthetic efficiency persisted to 42 days from emergence. There were no differences in leaf photosynthesis between the species until day 26 after emergence. Tall fescue had higher leaf photosynthesis than perennial ryegrass after this time (Figure 5.5). Leaf respiration in both species decreased linearly with leaf age. It was statistically different between species at day 30, when tall fescue had higher leaf respiration than perennial ryegrass (Figure 5.6).

Table 5.37: The leaf photosynthetic rates per unit leaf area (μmol CO_2 m^{-2} s^{-1}) and unit leaf weight (μmol CO_2 kg^{-1} s^{-1}) of control plants in perennial ryegrass and tall fescue.

	Ryegrass		Fescue	SEM	F
		μmol CO_2 m^{-2} s^{-1}			
LAS1	14.0		13.1	0.40	ns
LAS3	12.6		13.0	0.54	ns
LAS6	9.7		9.5	0.37	ns
		μmol CO_2 kg^{-1} s^{-1}			
LAS1	304		290	12	ns
LAS3	283		266	12	ns
LAS6	222		171	9	**

Table 5.38: Leaf photosynthetic rates per unit leaf area (μmol CO_2 m^{-2} s^{-1}) and leaf weight (μmol CO_2 kg^{-1} s^{-1}) of leaves in different position (L) in a tiller of control plants in perennial ryegrass and tall fescue.

	Ryegrass					Fescue					F values for		
	L1	L2	L3	L4		L1	L2	L3	L4	SEM	SP	L	SPxL
					μmol CO_2 m^{-2} s^{-1}								
LAS1	13.1	17.7	11.3			11.6	16.0	11.5		0.70	ns	***	ns
LAS3	12.3	14.7	11.0			11.4	16.0	11.8		0.93	ns	***	ns
LAS6	12.2	13.9	8.9	3.6		10.9	12.8	9.3	4.7	0.71	ns	***	ns
					μmol CO_2 kg^{-1} s^{-1}								
LAS1	283	398	231			240	366	262		11	ns	***	ns
LAS3	252	321	275			223	304	272		20	ns	**	ns
LAS6	290	267	261	70		207	230	174	73	18	**	***	ns

Table 5.39: Leaf photosynthetic rates per unit leaf area (µmol CO_2 m^{-2} s^{-1}) and leaf weight (µmol CO_2 kg^{-1} s^{-1}) of perennial ryegrass and tall fescue.

	Ryegrass		Fescue	SEM	F
		µmol CO_2 m^{-2} s^{-1}			
LAS1			11.9	0.45	ns
L1	12.7		15.2	0.44	ns
L2	16.5				
LAS3			10.9	0.50	ns
L1	11.4		15.4	0.55	ns
L2	14.5				
LAS6			10.9	0.43	ns
L1	12.0		13.3	0.44	ns
L2	14.5				
		µmol CO_2 kg^{-1} s^{-1}			
LAS1					
L1	324		277	17	ns
L2	398		357	21	ns
LAS3					
L1	292		261	14	ns
L2	365		378	18	ns
LAS6					
L1	363		248	17	**
L2	416		318	18	**

Table 5.40: Effect of leaf defoliation on leaf photosynthetic rates per unit leaf area (μmol CO_2 m^{-2} s^{-1}) and leaf weight (μmol CO_2 kg^{-1} s^{-1}) of perennial ryegrass and tall fescue.

		Ryegrass				Fescue				F values for		
		C	M	H		C	M	H	SEM	SP	TR	SPxTR
					μmol CO_2 m^{-2} s^{-1}							
LAS1	L1	13.1	12.9	12.2		11.6	12.4	11.7	0.78	ns	ns	ns
	L2	17.7	15.3			16.0	14.4		0.52	ns	ns	ns
LAS3	L1	12.3	11.5	10.5		11.4	11.3	9.9	0.90	ns	ns	ns
	L2	14.7	14.6	14.2		16.0	16.1	14.0	0.86	ns	ns	ns
LAS6	L1	12.2	12.5	11.4		10.9	10.8	11.1	0.77	ns	ns	ns
	L2	13.9	14.0	15.6		12.8	13.5	13.8	0.64	ns	ns	ns
					μmol CO_2 kg^{-1} s^{-1}							
LAS1	L1	283	306	381		240	273	317	28	ns	*	ns
	L2	398	399			366	348		33	ns	ns	ns
LAS3	L1	252	287	338		223	261	299	25	ns	**	ns
	L2	321	250	289		304	252	296	7	ns	ns	ns
LAS6	L1	290	391	427		200	224	319	28	**	***	ns
	L2	267	407	571		230	297	440	22	**	***	ns

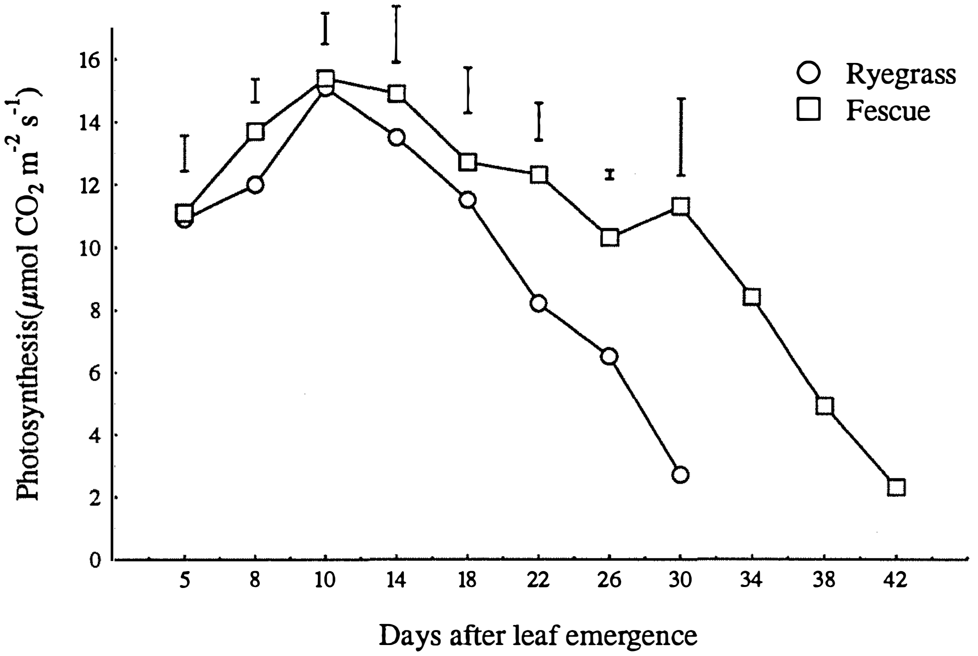

Figure 5.5: Effect of leaf age on photosynthetic efficiency of perennial ryegrass and tall fescue. Bar shows SEM

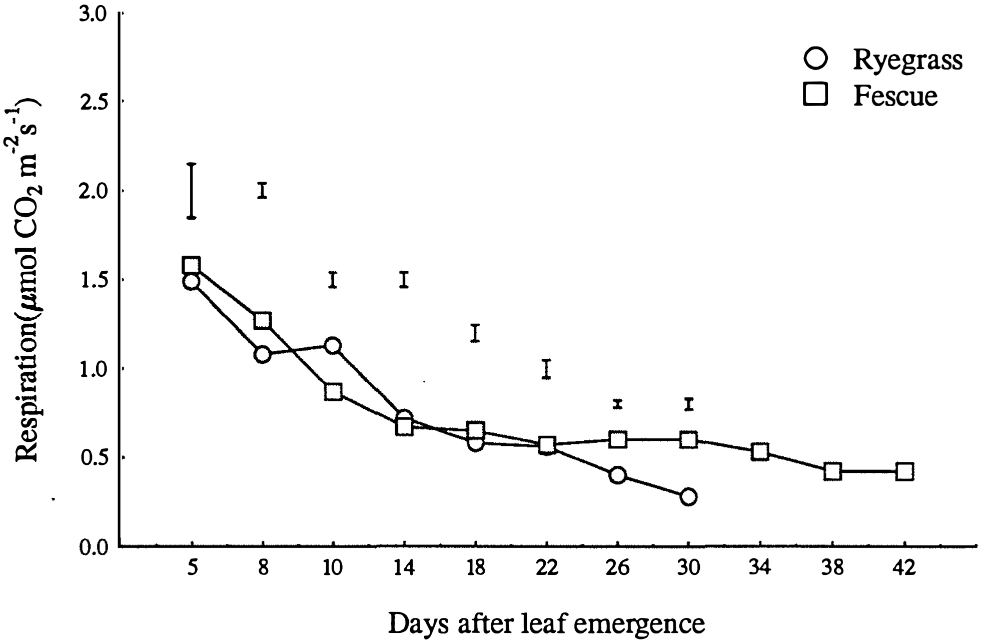

Figure 5.6: Effect of leaf age on respiratory activity of perennial ryegrass and tall fescue. Bar shows SEM

5.2.4.8 Water soluble carbohydrate

Water soluble carbohydrate (WSC) concentrations in stem bases of plants were higher in tall fescue than perennial ryegrass, though the differences were not statistically significant (171 vs. 149 ± 24 mg g^{-1} dry weight $P< 0.52$). WSC concentrations were lower in treatment H than in treatments M and C, which did not differ significantly (Table 5.41). The reduction under hard defoliation was greater for tall fescue (69%) than for perennial ryegrass (47%).

Table 5.41: Water soluble carbohydrate (WSC) concentrations (mg g^{-1} dry weight) in stem bases of perennial ryegrass and tall fescue under different leaf defoliation treatments.

	Ryegrass			Fescue				F values for		
	C	M	H	C	M	H	SEM	SP	TR	SPxTR
WSC	188	170	88	255	178	81	42	ns	*	ns

5.3 Reproductive stage

5.3.1 Material and methods- experiment 3

5.3.1.1 Experimental conditions

Two experiments were conducted for continued study of responses to defoliation of reproductive plants. To prepare plants for these experiments, turf samples (30 by 30 cm) of perennial ryegrass and tall fescue were transferred to the glasshouse for using as transplant material in June 1991. Individual plants of perennial ryegrass and tall fescue were grown by transplanting a single vegetative tiller per plastic pot (15 cm by 20 cm). The same media and nutrients were used for growing plants as in experiment 1. Also, plants were fertilized with a nutrient solution (Yates, liquid Lush contains 10% N, 3% P, 6% K, plus trace elements Mg, Fe, Cu, Zn, Mn, Mo and Br) of 5 ml litre^{-1} every fortnight during the course of the experiment. Uniform plants were selected for the experiments after establishment. Plants were grown in a glasshouse with 20/15°C day/night temperature and natural photoperiod for 66 days before being transferred to a controlled environment room (CE) with the same conditions as experiment 1 at CRI Palmerston North.

Fifty plants were transferred to the CE on 26/08/1991. From these plants 32 were used for the defoliation experiment, 8 plants were used to determine the initial plant shoot mass and 10 plants were used to determine leaf photosynthetic efficiency and leaf life-span as leaves aged. The experiment were started after 9 days acclimatization in the CE room.

Each individual plant was considered as a replicate. For each species 16 plants provided four replicates of four defoliation treatments. The factorial combination of species and defoliation treatments was arranged in a randomised complete block design. The four leaf defoliation treatments were control (C), lax (L), medium (M) and hard (H) as described for experiment 1 (see Fig 5.1). The treatments were applied for six leaf appearance sequences.

5.3.1.2 Measurements

Leaf elongation rates were initially estimated from 3 marked tillers per plant. The marked tillers stopped producing leaves between the second and third leaf appearance sequences, so new tillers (secondary tillers) were marked for estimating leaf elongation rates. Similarly tertiary tillers were marked when secondary tillers stopped producing leaves after LAS4. Both leaf elongation rates (mm tiller^{-1} day^{-1}) and leaf lamina growth rates(mg tiller^{-1} day^{-1}) were estimated with the same procedures as in experiment 1 (see Section 5.2.1.2).

Tiller number per plant (adjusted and unadjusted), tillering rates, and tiller weights were also measured as explained previously (see Section 5.2.1.2). At harvest, plants were dissected into categories; green leaf, senescent leaf, pseudostem and seed head which had appeared on the stem at harvest time, were dried and weighed separately. The initial plant shoot mass, total plant shoot mass accumulation and mean shoot relative growth rates (RGR) were measured as mentioned in experiment 1. The number of tillers with seed heads was counted and considered as a percentage of total tillers per plant at harvest.

At the final defoliation (LAS6) the 5 uppermost fully expanded leaves per plant were cut to estimate individual leaf length, leaf area, leaf weight, SLA and SLW as was explained in Section 5.2.1.2.

Leaf photosynthesis of the uppermost fully expanded leaf of two tillers per plant was measured at LAS1, LAS3 and LAS6 with an infra-red gas analyzer (Li-cor 6200). Leaf photosynthetic rates were calculated per unit leaf area and unit leaf weight.

Photosynthetic efficiency during leaf aging was measured on three marked leaves of the main tillers per plant of four plants per species. The photosynthetic rates per unit area of marked leaves were measured at full expansion and then at 4 day intervals until leaf senescence. Leaf life-span was considered as the time from leaf emergence until senescence.

Water soluble carbohydrate concentrations (WSC) of reproductive tillers were determined with the method explained in experiment 1 (Section 5.2.1.2).

5.3.1.3 Statistical analysis

The data were analyzed as in experiment 1 (Section 5.2.1.3).

5.3.2 Results- experiment 3

5.3.2.1 Plant herbage mass components and relative growth rate

The accumulated green leaf mass was significantly higher in tall fescue than perennial ryegrass, but there were no significant differences between species in terms of senescent leaf and total leaf mass accumulation (Table 5.42). On the other hand, tall fescue plants produced lower pseudostem mass and head mass than perennial ryegrass (Table 5.42). Both total shoot mass and the mean shoot relative growth rate were 25% lower in tall fescue than in perennial ryegrass (Table 5.42).

The green leaf mass in perennial ryegrass decreased as the severity of defoliation decreased, but for the tall fescue it was lower under treatments C and H than the other treatments (Table 5.43), which resulted in the interaction for species x defoliation treatments. The highest accumulated senescent leaf mass in both species was under treatment C (Table 5.43). The small senescent leaf mass for tall fescue under treatment H was due to leaf accumulation before the start of the experiment (Table 5.43). Total leaf mass accumulated was not significantly different between defoliation treatments, but it was highest and lowest under treatment H for perennial ryegrass and tall fescue respectively (Table 5.43), which resulted in the interaction for species x defoliation treatments.

Pseudostem mass, seed head mass, total shoot mass and the mean shoot RGR were significantly lower under the hard defoliation treatment than the other treatments (Table 5.43). The degree of reduction was greater in pseudostem (60% vs. 50%) and total shoot mass (47% vs. 29%) for tall fescue than for perennial ryegrass when compared with the control treatment. The mean shoot relative growth rate was significantly lower under treatment H than the other treatments (Table 5.43). There were no interactions for species x defoliation treatments for all the above components.

Table 5.42: Accumulated dry mass of green leaf, senescent leaf, total leaf, pseudostem, head, total shoot(g plant^{-1}), and mean shoot relative growth rates (mg g^{-1} day^{-1}) of perennial ryegrass and tall fescue.

	Ryegrass	Fescue	SEM	F
Green leaf	10.9	12.7	0.43	**
Senescent leaf	2.2	1.8	0.19	ns
Total leaf	13.1	14.5	0.50	ns
Pseudostem	26.0	17.6	1.17	***
Seed head	8.8	4.0	0.44	***
Shoot mass	47.9	36.0	1.73	***
Shoot RGR	21.1	15.9	0.10	***

Table 5.43: Accumulated dry mass of green leaf, senescent leaf, total leaf, pseudostem, head and total shoot (g plant^{-1}), and mean shoot relative growth rates(mg g^{-1} day^{-1}) of perennial ryegrass and tall fescue under different leaf defoliation treatments.

	Ryegrass				Fescue					F values for		
	C	L	M	H	C	L	M	H	SEM	SP	TR	SPxTR
Green leaf	5.9	10.8	13.0	14.0	10.1	14.1	15.4	11.0	0.87	**	***	**
Senescent leaf	5.8	2.9	0.0	0.0	4.1	2.7	0.0	0.5	0.39	ns	***	ns
Total leaf	11.7	13.7	13.1	14.0	14.2	16.9	15.4	11.5	1.00	ns	ns	*
Pseudostem	31.0	30.5	26.7	15.9	21.9	19.8	19.6	8.8	2.34	***	***	ns
Seed head	11.9	10.7	9.1	3.3	5.0	4.7	5.0	1.4	0.88	***	***	ns
Shoot mass	54.6	54.9	48.9	33.3	41.2	41.4	40.0	21.7	3.47	***	***	ns
Shoot RGR	21.4	21.4	21.4	20.4	16.3	16.0	16.0	15.2	0.20	***	***	ns

The proportion of leaf mass to shoot mass was higher for tall fescue than for perennial ryegrass (Figure 5.7). Under the hard defoliation treatment the proportion of leaf mass to shoot mass increased relative to the other treatments (Figure 5.7).

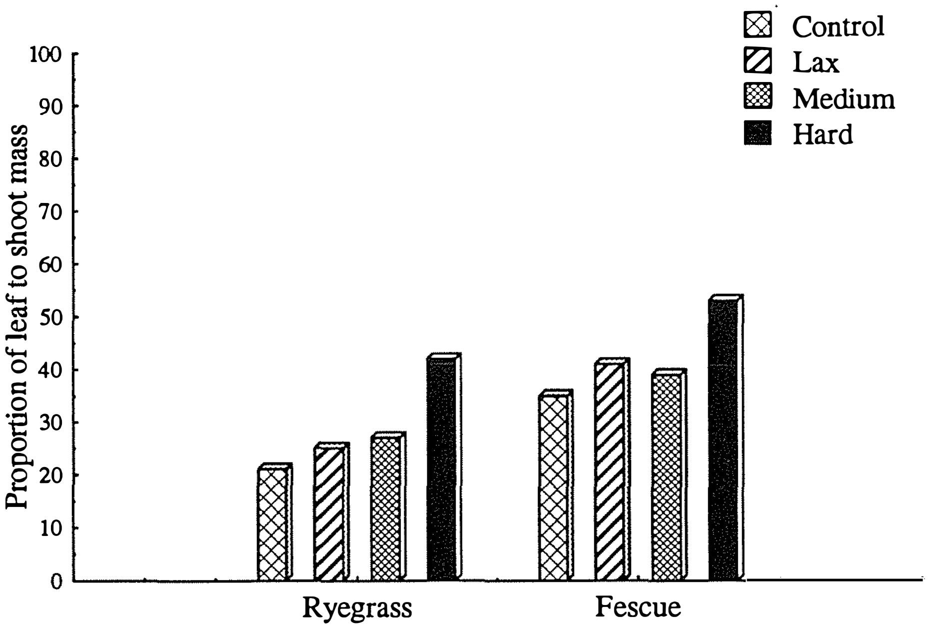

Figure 5.7: Proportion of leaf to shoot mass of perennial ryegrass and tall fescue under different defoliation treatments.

5.3.2.2 Tiller number and tiller weight

Both adjusted and unadjusted tiller number per plant were significantly different between the species. In both cases tall fescue had a lower tiller number per plant than perennial ryegrass over time (Tables 5.44 and 5.46). However, tiller numbers per plant (unadjusted) in each defoliation treatment were similar at all measurement times except at LAS6 where it was lower under treatment H than the other treatments (Table 5.45). In contrast, when tiller numbers per plant were adjusted for initial tiller numbers then they were significantly lower in treatment H than the other treatments (Table 5.47). The interactions of species x defoliation treatments were not significant. The interactions of time x species, time x defoliation ($P< 0.001$ and $P<0.01$) for adjusted tillers, and time x species, time x defoliation treatments ($P< 0.001$) for unadjusted tillers were significant.

Overall, tillering rate (tiller tiller^{-1} day^{-1}) decreased over time (Table 5.48). Tall fescue had lower tillering rates than perennial ryegrass on average and at all measurement periods, though it was not significantly lower at LAS2, LAS3 and LAS5 (Table 5.48). On average, tillering rate was lower under treatment H than under the other treatments (Table 5.49). Tillering rates were significantly different between treatments at LAS1, LAS5 and LAS6. At the first measurement time the lowest tillering rates for both species were under treatment H, whereas at the fifth measurement time treatment L for perennial ryegrass and treatment H for tall fescue had the lowest tillering rates. This resulted in a interaction of species x treatment for this period (Table 5.49). At LAS6 treatment M in perennial ryegrass and treatments L and M in tall fescue exhibited lower tillering rates than the other treatments (Table 5.49). The interaction of time x defoliation treatments ($P< 0.01$) was significant.

The percentages of reproductive tillers that had visible heads at the time of harvest are shown in Table 5.50. Tall fescue had a significantly lower percentage of tillers with heads (17%) than perennial ryegrass (53%). In both species seed head percentage was lowest under treatment H. There was no interaction between species and defoliation treatments.

Tiller weight of tall fescue was 1.3 times greater than perennial ryegrass (411 vs. 316 ± 21 mg tiller^{-1} P< 0.01). Tiller weight of treatment H was lower than the other treatments though the difference was not statistically significant (Table 5.51). The species x defoliation treatments interaction was not significant.

Table 5.44: Tiller number per plant of perennial ryegrass and tall fescue (unadjusted mean).

Leaf appearance sequence	Ryegrass	Fescue	SEM	F
LAS0	32	21	1.97	***
LAS1	51	31	2.74	***
LAS2	87	54	4.15	***
LAS3	114	71	4.82	***
LAS4	130	81	4.87	***
LAS5	140	86	5.57	***
LAS6	153	89	5.39	***

Table 5.45: Effect of leaf defoliation treatments on mean tiller number per plant of perennial ryegrass and tall fescue (unadjusted mean).

Leaf appearance sequence	Treatmeants				SEM	F
	C	L	M	H		
LAS0	25	28	25	26	2.80	ns
LAS1	44	44	41	37	3.87	ns
LAS2	72	78	73	60	5.87	ns
LAS3	95	103	94	78	6.81	ns
LAS4	106	115	108	92	6.89	ns
LAS5	120	123	115	97	7.88	ns
LAS6	131	133	117	103	7.63	*

Table 5.46: Tiller number per plant of perennial ryegrass and tall fescue (adjusted mean).

Leaf appearance sequence	Ryegrass	Fescue	SEM	F
LAS1	44	38	1.20	**
LAS2	77	65	1.65	***
LAS3	102	83	2.22	***
LAS4	119	92	3.42	***
LAS5	129	98	4.14	***
LAS6	142	100	4.44	***

Table 5.47: Effect of leaf defoliation treatments on mean tiller number per plant of perennial ryegrass and tall fescue (adjusted mean).

Leaf appearance sequence	Treatmeants					
	C	L	M	H	SEM	F
LAS1	45	42	42	37	1.47	**
LAS2	74	74	75	60	2.01	***
LAS3	97	99	96	78	2.70	***
LAS4	108	112	109	92	4.15	*
LAS5	122	119	115	97	5.52	*
LAS6	133	130	119	104	5.38	**

Table 5.48: Tillering rates (tiller tiller^{-1} day^{-1}) of perennial ryegrass and tall fescue.

Leaf appearance sequence	Ryegrass	Fescue	SEM	F
LAS1	0.070	0.051	0.004	**
LAS2	0.068	0.061	0.003	ns
LAS3	0.033	0.027	0.002	ns
LAS4	0.019	0.013	0.002	*
LAS5	0.011	0.006	0.001	ns
LAS6	0.012	0.004	0.001	***
Mean	0.036	0.027	0.001	***

Table 5.49: Tillering rates (tiller tiller^{-1} day^{-1}) of perennial ryegrass and tall fescue under different defoliation treatments.

Leaf appearance sequence	Ryegrass				Fescue					F values for		
	C	L	M	H	C	L	M	H	SEM	SP	TR	SPxTR
LAS1	0.086	0.068	0.077	0.050	0.059	0.061	0.045	0.038	0.008	**	*	ns
LAS2	0.060	0.070	0.076	0.066	0.065	0.064	0.066	0.050	0.005	ns	ns	ns
LAS3	0.032	0.035	0.033	0.033	0.031	0.031	0.024	0.021	0.005	ns	ns	ns
LAS4	0.015	0.022	0.019	0.022	0.013	0.010	0.013	0.017	0.004	*	ns	ns
LAS5	0.022	0.005	0.007	0.009	0.007	0.009	0.005	0.003	0.003	ns	*	**
LAS6	0.017	0.019	0.004	0.010	0.005	0.002	0.003	0.005	0.003	***	*	ns
Mean	0.038	0.036	0.036	0.032	0.030	0.029	0.026	0.022	0.002	***	*	ns

Table 5.50: Percentage of tillers with seed heads for perennial ryegrass and tall fescue under different leaf defoliation treatments.

	Ryegrass				Fescue					F values for		
	C	L	M	H	C	L	M	H	SEM	SP	TR	SPxTR
Seed head tillers	64	57	57	33	17	16	20	14	5.8	***	*	ns

Table 5.51: Tiller weight(mg $tiller^{-1}$) of perennial ryegrass and tall fescue under different leaf defoliation treatments.

	Ryegrass				Fescue					F values for		
	C	L	M	H	C	L	M	H	SEM	SP	TR	SPxTR
Tiller weight	344	351	344	236	451	389	460	345	42	**	ns	ns

5.3.2.3 Leaf growth

Leaf elongation rates (mm tiller^{-1} day^{-1}) decreased substantially over time (Tables 5.52 and 5.53). Tall fescue had significantly lower leaf elongation rates at LAS2, LAS6, and on average (14%) than perennial ryegrass (Table 5.52). Leaf elongation rates for the different defoliation treatments were similar at all periods except at LAS6 when it was greater under treatment H than the other treatments (Table 5.53). No interactions were observed for species x defoliation treatments, time x defoliation treatments, and time x species x defoliation treatments, but time x species was significant ($P< 0.001$).

Leaf lamina growth rate (mg tiller^{-1} day^{-1}) of both species was similar at LAS2 and LAS6 and overall, but it was higher for tall fescue than for perennial ryegrass at LAS4 (Table 5.54). Leaf lamina growth rate was lowest under treatment H at LAS2 and on average, but in the other periods leaf lamina growth in the defoliation treatments was similar (Table 5.55). There was no interaction for species x defoliation treatments, but time interacted with both species and defoliation treatments ($P< 0.001$).

5.3.2.4 Leaf characteristics

Individual leaf length, leaf area, leaf weight and specific leaf weight for tall fescue plants were greater than for perennial ryegrass, but specific leaf area of perennial ryegrass was higher than tall fescue (Table 5.56). Tall fescue had a longer leaf life-span relative to perennial ryegrass (Table 5.56). The lowest leaves were infected with powdery mildew (*Erysiphe graminis*) which caused faster leaf senescence in both species.

No statistical differences were observed between defoliation treatments in terms of the above measurements (Table 5.57). There was no interaction of species x defoliation treatments for any measurements, except for SLA and SLW.

Table 5.52: Leaf elongation rates (mm tiller^{-1} day^{-1}) of perennial ryegrass and tall fescue.

Leaf appearance sequence	Ryegrass	Fescue	SEM	F
LAS2	48	38	1.16	***
LAS4	24	22	0.97	ns
LAS6	14	11	0.82	*
Mean	28	24	0.59	***

Table 5.53: Effect of leaf defoliation treatments on mean leaf elongation rates (mm tiller^{-1} day^{-1}) of perennial ryegrass and tall fescue.

Leaf appearance sequence	Treatmeants					
	C	L	M	H	SEM	F
LAS2	44	43	43	41	1.65	ns
LAS4	21	23	23	26	1.37	ns
LAS6	10	11	12	16	1.16	*
Mean	25	26	26	28	0.84	ns

Table 5.54: Leaf lamina growth rates (mg tiller^{-1} day^{-1}) of perennial ryegrass and tall fescue.

Leaf appearance sequence	Ryegrass	Fescue	SEM	F
LAS2	1.9	1.6	0.05	ns
LAS4	1.1	1.4	0.05	***
LAS6	0.5	0.4	0.03	ns
Mean	1.3	1.4	0.04	ns

Table 5.55: Effect of leaf defoliation treatments on mean leaf lamina growth rates (mg tiller^{-1} day^{-1}) of perennial ryegrass and tall fescue.

Leaf appearance sequence	Treatmeants					
	C	L	M	H	SEM	F
LAS2	1.8	1.6	1.8	1.4	0.07	***
LAS4	1.2	1.4	1.2	1.2	0.07	ns
LAS6	0.4	0.4	0.4	0.5	0.04	ns
Mean	1.6	1.5	1.3	1.1	0.06	***

Table 5.56: Individual leaf length(mm), leaf area(cm^2), leaf weight(mg), specific leaf area(SLA)(cm^2 g^{-1}), specific leaf weight (SLW) (mg cm^{-2}) and leaf life-span(day) of perennial ryegrass and tall fescue.

Characters	Ryegrass	Fescue	SEM	F
Leaf length	188	252	8.66	***
Leaf area	7.8	14.0	0.63	***
Leaf weight	26	55	2.90	***
SLA	299	269	7.83	**
SLW	3.5	3.9	0.08	**
Leaf life-span	31	38	0.56	***

Table 5.57: Individual leaf length(mm), leaf area(cm^2), leaf weight(mg), specific leaf area(SLA)(cm^2 g^{-1}) and specific leaf weight (SLW) (mg cm^{-2}) of perennial ryegrass and tall fescue under different leaf defoliation treatments.

Characters	Ryegrass				Fescue					F values for		
	C	L	M	H	C	L	M	H	SEM	SP	TR	SPxTR
Leaf length	174	183	182	215	267	259	257	224	17.3	***	ns	ns
Leaf area	6.0	9.0	8.0	8.2	14.7	14.4	14.0	12.9	1.27	***	ns	ns
Leaf weight	25	28	24	26	47	60	56	55	6.60	***	ns	ns
SLA	249	304	321	323	289	254	256	279	15.6	**	ns	*
SLW	4.2	3.4	3.3	3.1	3.6	4.0	4.0	3.8	0.18	**	ns	**

5.3.2.5 Leaf photosynthesis

Rates of photosynthesis per unit area of the uppermost fully expanded leaf (L2) were not significantly different between species, but the rates of photosynthesis per unit leaf weight were lower in tall fescue than perennial ryegrass at LAS3 and LAS6 (Table 5.58). The rate of photosynthesis per unit area was not affected by leaf defoliation (Table 5.59). Rates of leaf photosynthesis per unit weight increased under treatment H, although the increase was not significant at the first and third measurements (Table 5.59). There were no interactions between species and defoliation treatments in terms of rates of leaf photosynthesis per unit leaf area and unit leaf weight. The species x defoliation treatments, and all combinations of time, species and defoliation treatments interactions were not significant.

The change in photosynthetic rates as leaves aged is shown in Figure 5.8. Leaf photosynthetic rates of both species were highest at full expansion (day 7) and then decreased linearly over time. Differences in the leaf photosynthetic rates per unit area of the species first appeared at day 27 after leaf emergence. Tall fescue had a higher leaf photosynthetic rate than perennial ryegrass after this time (Figure 5.8).

Table 5.58: Leaf photosynthetic rates per unit leaf area (μmol CO_2 m^2 s^{-1}) and unit leaf weight (μmol CO_2 kg^{-1} s^{-1}) of the uppermost fully expanded leaf (L2) of perennial ryegrass and tall fescue.

Leaf appearance sequence	Ryegrass		Fescue	SEM	F
		μmol CO_2 m^{-2} s^{-1}			
LAS1	13.8		13.4	0.45	ns
LAS3	15.1		14.1	0.52	ns
LAS6	14.5		13.4	0.74	ns
		μmol CO_2 kg^{-1} s^{-1}			
LAS1	393		345	19	ns
LAS3	330		225	14	***
LAS6	422		353	42	*

Table 5.59: Leaf photosynthetic rates per unit leaf area (μmol CO_2 m^2 s^{-1}) and unit leaf weight (μmol CO_2 kg^{-1} s^{-1}) of the uppermost fully expanded leaf (L2) of perennial ryegrass and tall fescue under different leaf defoliation treatments.

Leaf appearance sequence	Ryegrass					Fescue				SEM	F values for		
	C	L	M	H		C	L	M	H		SP	TR	SPxTR
					μmol CO_2 m^2 s^{-1}								
LAS1	13.4	14.2	13.8	13.7		13.0	13.2	14.3	13.2	0.91	ns	ns	ns
LAS3	14.6	14.6	16.5	14.8		13.8	13.6	14.4	14.6	1.05	ns	ns	ns
LAS6	13.4	14.7	15.3	14.6		12.8	13.4	13.6	13.7	1.48	ns	ns	ns
					μmol CO_2 kg^{-1} s^{-}								
LAS1	373	406	355	436		317	303	321	440	37.1	ns	ns	ns
LAS3	302	306	332	378		216	196	223	266	24.4	***	**	ns
LAS6	334	449	456	449		338	361	342	370	43.4	*	ns	ns

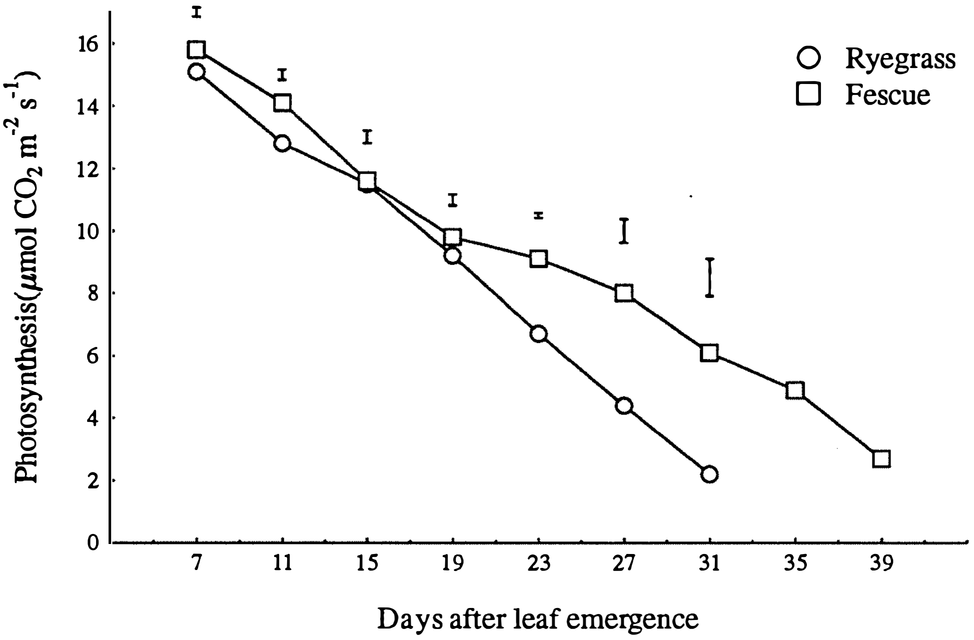

Figure 5.8: Effect of leaf age on photosynthetic efficiency of perennial ryegrass and tall fescue. Bar shows SEM

5.3.2.6 Water soluble carbohydrate

Water soluble carbohydrate (WSC) concentrations in stem bases of plants were lower in tall fescue than in perennial ryegrass (170 vs. 254 ±13 mg g^{-1} dry weight $P< 0.001$). Water soluble carbohydrate concentrations were significantly lower under treatment H than the other treatments (Table 5.60). WSC of treatment H was only 19% (tall fescue) and 31% (perennial ryegrass) of treatment C. There was no interaction of species x defoliation treatments.

Table 5.60: Water soluble carbohydrate (WSC)(mg g^{-1} dry weight) in stem bases of perennial ryegrass and tall fescue under different leaf defoliation treatments.

	Ryegrass				Fescue					F values for		
	C	L	M	H	C	L	M	H	SEM	SP	TR	SPxTR
WSC	318	307	293	99	243	173	216	47	25	***	***	ns

5.3.3 Material and methods- experiment 4

5.3.3.1 Experimental conditions

The main aim of this study was to determine water soluble carbohydrate concentrations (WSC) in stem bases of plants at different leaf appearance sequences. For this experiment 106 plants of both perennial ryegrass and tall fescue were transferred to the same CE room at the same time as experiment3.

At the beginning of the experiment five plants per species were cut to ground level for determination of WSC. The same defoliation treatments as used in experiment 1 (see figure 5.1) were applied to the rest of plants which provided 3 replicates and four harvests in a factorial treatment combination in a randomized complete block design.

5.3.3.2 Measurements

Plants were harvested after the 1st, 3rd, 4th and 5th leaf appearance sequence. WSC was measured with the procedure used in experiment 1 (see Section 5.2.1.2). In addition to WSC, tiller number per plant, tiller weight and total accumulated shoot mass of plants were also measured (see section 5.2.1.2).

5.3.3.3 Statistical analysis

Data for each harvest were analyzed separately as explained for experiment 1 (Section 5.2.1.3).

5.3.4 Results- experiment 4

5.3.4.1 Plant herbage mass

Total accumulated shoot masses were not significantly different between species at any harvest time (Table 5.61). At the first harvest (LAS1) treatment C had a significantly greater shoot mass than the other treatments, and in the other harvest periods treatment H had the lowest shoot mass between treatments, though the difference was not statistically significant at LAS3 (Table 5.62). The interaction of species x defoliation treatments was not significant for all harvests.

5.3.4.2 Tiller number and tiller weight

Both adjusted and unadjusted tiller number per plant differed between species. In both cases tall fescue had lower tiller numbers per plant than perennial ryegrass at all harvests (Tables 5.63 and 5.65). The differences between defoliation treatments were apparent after LAS3 when the adjusted tiller numbers per plant were lowest under treatment H (Table 5.64), and after LAS4 when treatment unadjusted tillers were lowest under treatments M and H (Table 5.66). The interactions of species x defoliation treatments for both adjusted and unadjusted tillers were not significant

Tall fescue plants produced larger tillers than perennial ryegrass at all harvests (Table 5.67). The effects of leaf defoliation treatments on tiller weight were not statistically significant at any harvests (Table 5.68). No interactions were observed for species x defoliation treatments at all harvests.

Table 5.61: Total accumulated shoot mass (g plant^{-1}) of perennial ryegrass and tall fescue.

Leaf appeareance sequence	Ryegrass	Fescue	SEM	F
LAS1	11.6	9.4	0.78	ns
LAS3	26.5	22.7	3.16	ns
LAS4	35.3	28.2	2.93	ns
LAS5	40.5	36.0	1.96	ns

Table 5.62: Total accumulated shoot mass (g plant^{-1}) of perennial ryegrass and tall fescue under different leaf defoliation treatments.

Leaf appeeance sequence	Ryegrass				Fescue					F values for		
	C	L	M	H	C	L	M	H	SEM	SP	TR	SPxTR
LAS1	16.6	9.7	12.1	8.3	11.5	8.2	8.6	9.2	1.56	ns	*	ns
LAS3	30.8	27.1	28.8	19.1	22.2	25.9	26.7	15.8	6.32	ns	ns	ns
LAS4	47.9	45.2	29.8	18.3	32.9	29.5	26.5	24.0	5.87	ns	*	ns
LAS5	52.8	40.3	37.5	31.5	40.3	36.9	38.2	28.7	3.93	ns	**	ns

Table 5.63: Tiller number per plant for perennial ryegrass and tall fescue (adjusted mean).

Leaf appearance sequence	Ryegrass	Fescue	SEM	F
LAS1	87	61	4.72	**
LAS3	99	78	6.14	*
LAS4	119	83	7.77	*
LAS5	141	95	8.80	**

Table 5.64: Effect of leaf defoliation treatments on mean tiller number per plant of perennial ryegrass and tall fescue (adjusted mean).

Leaf appearance sequence	Treatments					
	C	L	M	H	SEM	F
LAS1	74	71	75	77	5.80	ns
LAS3	91	86	101	75	6.15	*
LAS4	123	100	93	87	8.53	*
LAS5	129	138	107	98	9.46	*

Table 5.65: Tiller number per plant for perennial ryegrass and tall fescue (unadjusted mean).

Leaf appearance sequence	Ryegrass	Fescue	SEM	F
LAS1	98	51	5.84	***
LAS3	113	63	5.29	***
LAS4	132	70	6.79	***
LAS5	150	86	7.08	***

Table 5.66: Effect of leaf defoliation treatments on mean tiller number per plant of perennial ryegrass and tall fescue (unadjusted mean).

Leaf appearance sequence	Treatmeants					
	C	L	M	H	SEM	F
LAS1	75	67	73	83	8.26	ns
LAS3	84	86	107	77	7.49	ns
LAS4	125	104	87	87	9.61	*
LAS5	134	143	98	99	10.02	**

5.3.4.3 Water soluble carbohydrate

Water soluble carbohydrate concentrations in the stem bases of tall fescue plants were lower than in perennial ryegrass at the fourth and fifth harvests (Table 5.69). Water soluble carbohydrate concentrations were lowest under treatment H at all harvests, though the differences between treatments were not statistically significant at LAS1 (Table 5.70). There were no interaction of species x defoliation treatments at any harvests.

Table 5.67: Tiller weight (mg tiller^{-1}) of perennial ryegrass and tall fescue.

Leaf appearance sequence	Ryegrass	Fescue	SEM	F
LAS1	122	196	16.20	**
LAS3	233	362	40.81	*
LAS4	266	411	31.79	**
LAS5	282	433	26.57	**

Table 5.68: Effect of leaf defoliation treatments on tiller weight (mg tiller^{-1}) of perennial ryegrass and tall fescue.

Leaf appearance sequence	Ryegrass				Fescue				SEM	F values for		
	C	L	M	H	C	L	M	H		SP	TR	SPxTR
LAS1	165	109	131	83	258	185	166	175	32.56	**	ns	ns
LAS3	264	249	226	193	420	415	330	282	81.63	*	ns	ns
LAS4	332	310	259	164	325	493	438	387	63.59	**	ns	ns
LAS5	322	220	317	271	433	422	519	364	53.14	**	ns	ns

Table 5.69: Water soluble carbohydrate (mg g^{-1} dry weight) in the stem bases of perennial ryegrass and tall fescue.

Leaf appearance sequence	Ryegrass	Fescue	SEM	F
LAS0	148	146	8.2	ns
LAS1	114	95	14.8	ns
LAS3	198	176	20.8	ns
LAS4	221	119	15.3	***
LAS5	192	134	18.9	*

Table 5.70: Water soluble carbohydrate (mg g^{-1} dry weight) in stem bases of perennial ryegrass and tall fescue under different defoliation treatments.

Leaf appearance sequence	Ryegrass				Fescue				SEM	F values for		
	C	L	M	H	C	L	M	H		SP	TR	SPxTR
LAS1	155	101	117	84	112	120	81	66	29.6	ns	ns	ns
LAS3	289	248	173	83	204	253	166	80	41.5	ns	**	ns
LAS4	322	268	166	130	148	149	99	80	30.7	***	**	ns
LAS5	322	166	187	91	190	170	113	60	37.8	*	**	ns

5.4 Discussion

Experiments at the level of the single plant have been relatively few, although this approach provides valuable information about the physiological principles underlying the response of plants to defoliation. The response of reed canarygrass (*Phalaris arundinacea*)(Begg & Wright, 1964), cocksfoot (Davidson & Milthorpe, 1966a) and perennial ryegrass (Davies, 1974) plants stripped of one or more leaf laminae were examined after a single defoliation. Ryle and Powell (1975) determined the effect of older leaves on regrowth of uniculm barley by removing younger leaves. The current study was concerned with the relative effectiveness of each individual leaf to the regrowth of the plant under continuous defoliation by repeated removal of older leaves on a tiller axis. Under continuous stocking the proportion of young leaves in the sward increases as the intensity of grazing increases (Parsons *et al.*, 1988). So, it is important to understand how much each individual leaf contributes to the carbon economy of the plant, and the influence of leaf structure on the fate of a sward. Use of this defoliation technique made it possible to establish consistent conditions to examine the role of each individual leaf to plant regrowth, and provide information about sink and source relationships under continuous defoliation.

Up to a point repeated removal of older leaves (L3 and L4) had little effect on tiller production, tiller weight, leaf growth per unit leaf weight and consequently total accumulated shoot and root mass, and mean shoot and root relative growth rates. Removal of all fully expanded leaves (L2,L3 and L4) resulted in significant reduction in the above components, though hard defoliation had little effect on leaf elongation rate.

Because of different development in the vegetative and the reproductive phases of the plants, defoliation was on different tillers in the reproductive phase, whereas in the vegetative phase one tiller was treated all the time. The two species had larger tillers during reproductive development through longer regrowth, but tillering was lower. Defoliation had a similar effect on plants in both the reproductive and vegetative phases of development.

Tall fescue produced larger tillers with longer leaves and had a longer leaf life-span than perennial ryegrass, but it had slower leaf growth and leaf appearance, and produced fewer tillers per plant which resulted in lower regrowth compared with perennial ryegrass in most cases. The slower leaf appearance of tall fescue influenced frequency of defoliation and resulted in less frequent defoliation relative to perennial ryegrass.

Tillering rate depends on the rate of leaf appearance, which controls the production of potential tiller sites, and on the percentage of sites which actually produce tillers (site usage) (Davies & Thomas, 1983; Hume, 1990b; Skinner & Nelson, 1992). Low leaf appearance rates and low site filling were the causes of low tiller numbers per plant in tall fescue relative to perennial ryegrass. The larger leaf of tall fescue increased the duration of leaf elongation and so decreased leaf appearance rate (Skinner, 1991). Lower tillering activity results in lower plant regeneration (Jewiss, 1972) which could be a disadvantageous characteristic of tall fescue under hard defoliation, especially when grown with faster tillering species like perennial ryegrass.

In contrast, lower tillering rates in perennial ryegrass than in tall fescue in experiment 1 were partly due to the plant entering the reproductive stage while all tillers of tall fescue were still in the vegetative stage. Also, Skinner and Nelson (1992) suggested a decrease in leaf appearance rate with an increasing number of leaves above the youngest primary tiller at its appearance. So, in the case of perennial ryegrass, faster leaf appearance may increase the leaf numbers above the primary tiller and result in an earlier reduction in leaf appearance rate and consequently tillering rates.

Leaf elongation rate is correlated positively with the yield of tall fescue (Horst *et al.*, 1978) , but Penning de Vries *et al.*, (1979) suggested that leaf elongation rate was not a good indicator of yield of ryegrass. In this study, tall fescue often had lower leaf elongation rates and leaf lamina growth rates relative to perennial ryegrass. The results of Butler and Hodgson (1993) also indicated lower leaf elongation rates for tall fescue than for perennial ryegrass under continuous stocking. Generally, producing thinner leaves (higher SLA) in response to increased intensity of defoliation resulted in decreased leaf growth rate as severity of defoliation increased. These results indicated that leaf growth rate could be a better criterion for evaluating regrowth after defoliation than leaf elongation rate.

In both species the rate of photosynthesis of individual leaves reached the maximum at full leaf expansion and then decreased as the leaves aged, as found previously by other workers (e.g. Woledge, 1971; Chapman & Robson, 1988). Both species had similar photosynthetic rates per unit leaf area under the conditions of the experiments, but tall fescue often had lower leaf photosynthetic rates per unit leaf weight than perennial ryegrass due to higher specific leaf weight. Photosynthetic rates of leaves of vegetative and reproductive tillers were similar. Under field conditions differences in illumination during leaf development causes differences in photosynthetic capacity between leaves of vegetative and reproductive swards (Woledge, 1977; Parsons & Robson, 1981, 1982; Robson *et al.*, 1988), but in the current experiments individual plants received relatively the same illumination at both vegetative and reproductive stages.

Tall fescue leaves with a longer leaf life-span than perennial ryegrass leaves photosynthesized for a longer period of time. This characteristic may be of benefit to tall fescue under laxer defoliation, whereas under hard defoliation it could be a disadvantage as plants may be grazed at the time of highest photosynthetic rate or before reaching this level. In contrast, under hard defoliation perennial ryegrass may have the advantage over tall fescue due its faster leaf turnover and reestablishment of high photosynthetic area, but it is a disadvantage to perennial ryegrass under lax defoliation by producing more senescent leaf than tall fescue.

Relative growth rate is positively related to LAR, SLA and leaf N mass, and negatively related to root mass ratio (Reich & Walters, 1992; Lambers and Poorter, 1992), and leaf N concentration is negatively related to leaf life-span (Reich & Walters, 1992). The lower mean RGR for vegetative tall fescue than perennial ryegrass can be explained by lower LAR and SLA, and higher proportion of root to shoot mass of tall fescue relative to perennial ryegrass.

Plants responded to hard defoliation by reducing leaf width, length, area and weight and producing thinner leaves, corresponding with results obtained by other workers (e.g. Davies, 1974; Ollerenshaw & Incoll, 1979; Bircham & Hodgson, 1983; Brock & Fletcher, 1993; Chapman & Robson, 1988) in perennial ryegrass and white clover.

Leaf appearance rate in vegetative plants was not affected by leaf defoliation in this study. These results were in contrast to the results of Davies (1974) and Hume (1991a) in perennial ryegrass and prairie grass who found leaf appearance rate reduced with increasing cutting severity and frequency. But Tallowin *et al.* (1989), Parsons *et al.* (1983) and Xia (1991) observed similar leaf appearance rates for perennial ryegrass under different grazing intensities. Recently, Chapman and Lemaire (1993) suggested that leaf appearance rate is genetically determined, but further modified by variation in temperature, nitrogen nutrition, water status, or other factors.

Increases in the photosynthetic capacity of leaves after defoliation have been observed for many species. For example, *Festuca ovina* (Atkinson, 1986), *Lolium multiflorum* (Gifford & Marshall, 1973) and *Lolium perenne* (Woledge, 1977) have shown increased rates of photosynthesis following partial defoliation relative to similar aged leaves of undefoliated plants. The results of the present experiment indicated no differences between the photosynthetic and respiration rates of leaves per unit leaf area of defoliated and undefoliated plants either for tall fescue or for perennial ryegrass. Leaves developed in low irradiance (30% of full sun) had lower photosynthetic capacity compared with leaves grown at high irradiance (1500 µmol m^{-2} s^{-1}) (Allard *et al.*, 1991). Woledge (1977) suggested that the changes in photosynthetic capacity in grass swards are the consequence of changes in light intensity after defoliation rather than changes in demand for assimilates or growth substance supply. In these experiments leaves of the same age were placed in the same position because the leaves were removed from the bottom of tiller, and so little change in light intensity would be expected. Photosynthetic rate of leaves per unit leaf weight of defoliated and undefoliated plants was initially similar, but repeated defoliation of plants decreased SLW and resulted in increased photosynthetic rate per unit leaf weight of defoliated plants relative to undefoliated plants.

Reduction in the total nonstructural carbohydrates (TNC) of the root and remaining shoot occurs after defoliation. For example, Volenec (1986) reported that the amount of TNC in the stem bases of tall fescue decreased to about 50% of the value before defoliation by day 4 and then returned to the original concentration by day 25 after defoliation. In perennial ryegrass WSC was depleted to about 5% of the dry matter 0-6 days after defoliation and then returned to original levels (22%) by day 28 (Gonzalez *et al.*, 1989). Depletion in water soluble carbohydrate concentrations in the stem bases of plants in the present study occurred in the plants subjected to defoliation. The magnitude of the reduction was related to the severity of defoliation, and was greater in tall fescue than in perennial ryegrass. The low levels of WSC (maximum 9% in stem bases) in plants defoliated to leave only one leaf per tiller indicated that the photosynthetic area and the capacity of the expanding leaf was not sufficient to provide assimilate for maintenance, for synthesis of new tissue and for restoration of carbohydrate reserves to the same level as the other treatments. Whereas, plants defoliated to retain two leaves per tiller maintained a higher level of WSC and were as productive as the laxly defoliated and control plants.

The results of the current study agree with Mitchell and Coles (1955), Matches (1966), and Davies (1974) from indoor studies and Bircham and Hodgson (1983) and Grant *et al.*(1983) from outdoor studies in showing reduction in tiller weight and tiller production under severe defoliation.

Regular severe defoliation of plants resulted in gradual depletion of carbohydrate reserves which along with the decreased SLW, could be regarded as the cause of reduction in tiller weight. The decrease in tiller weight of plants under severe defoliation was progressive with subsequent defoliations and was in accord with the reduction in carbohydrate reserves in the stem bases of the tillers (see results of tiller weight and WSC of experiments 1,2,3 and 4). Tiller weight of tall fescue was affected more under severe defoliation than tiller weight of perennial ryegrass.

Overall, the tillering rate of the plants in all the treatments declined over time. Similar results were reported for perennial ryegrass (Davies & Thomas, 1983) and for tall fescue (Zarrough *et al.*, 1984; Skinner & Nelson, 1992). As a consequence of canopy closure shading the base of the tillers, tiller production is inhibited (Casal *et al.*, 1985; Skinner & Nelson 1992; Davies pers. comm.). Basal crowding may also have inhibited the emergence of new tillers in the pot experiments, whereas under natural grazing or cutting conditions, disturbance and damage to established tillers may facilitate the initiation of new tillers. The leaf appearance rates, and therefore the creation of potential buds, were the same in all treatments, but when plants were defoliated to one expanding leaf, the development of new tiller buds appeared to be inhibited. This inhibition of new tillers was likely to be due to substrate limitation, resulting from low current assimilate supplies (due to low photosynthetic area with low photosynthetic capacity) and low carbohydrate reserves, which resulted in reduced site usage.

Among successive generations of tillers, photoassimilates or nutrients from parent tillers affect the growth rates of axillary tillers (Davidson &

Milthorpe, 1966b; Ong, 1978; Carman & Briske, 1982; Zarrough *et al.*, 1983b). Under stress conditions when carbohydrate reserves and nitrogen are in short supply, they are increasingly monopolised by the main shoots (Ong *et al.*, 1978; Gu & Marshall, 1988). Preferential partitioning of assimilates to the developing leaf tissue reduces production of new tillers under low irradiance (Schnyder & Nelson, 1989). Ryle (1972) suggested that most of the assimilate generated in the growing leaf is utilized in its own basal meristem, where new leaf or sheath tissue is being laid down, but a little passes through the zone of meristematic activity and is exported to other meristems.

Tillering rate during the reproductive stage was lower than during the vegetative stage. This could also be counted as a further cause of source limitation since the demands of the rapidly elongating stems and developing seeds would affect the availability of carbohydrate elsewhere (Jewiss 1972).

Regulation of tillering by hormones (Jewiss 1972) is another possibility which should be taken into consideration. Chapman *et al.* (1991) suggested that leaf meristems become a stronger sink for assimilate in white clover under defoliation stress. Defoliation and root pruning of *Lolium multiflorum* showed that expanding leaves were able to compete successfully for assimilate, probably through the production of substances capable of mobilizing supply (Clifford & Langer, 1975). The role of hormones in the control of tillering was not measured in the present study, but a substantial change in root:shoot and leaf:shoot ratios under hard defoliation might have changed the hormonal balance (Clifford & Langer, 1975) and resulted in low tiller production in this treatment.

Leaf elongation rates declined over time, which corresponds with the findings of Davies *et al.* (1989) for perennial ryegrass and Moser *et al.* (1982) and Skinner and Nelson (1992) for tall fescue. Leaf defoliation had no substantial effect on leaf elongation rates even with removal of all the expanded leaves. Davidson & Milthorpe (1966a) also found that in cocksfoot expansion of new leaf tissue was not greatly affected by removal of expanded leaves. It was suggested that plants respond to defoliation by preferential allocation of assimilates to leaf meristematic tissue for re-establishment of photosynthetic tissues (Ryle & Powell, 1972; 1975; Whilhelm & Nelson, 1978; Schnyder & Nelson, 1989). A substantial increase in the proportion of leaf to shoot mass corresponds with this response. Bucher *et al.* (1987a,b) showed that the leaf elongation zone of *Festuca pratensis* is a much more competitive sink for the assimilates produced by the subtending leaf laminae than is the sheath that connects the tissue.

A significant reduction in root mass occurred as the result of removal of all fully expanded leaves, and resulted in a substantial reduction in the root to shoot ratio. In agreement with this result, a single defoliation removing 50% or more of the shoot volume retarded root growth for 6-18 days in seven of eight perennial grasses investigated by Crider (1955). A single defoliation removing 80% and 90% of shoot volume stopped root growth for 12 and 17 days, respectively. Multiple defoliations of plants to 70% shoot volume for three subsequent clippings per week stopped root growth for the entire 33-day investigation in all three species subjected to multiple defoliations (Crider, 1955). Cessation of root growth has been observed to occur within hours after defoliation (Davidson & Miltorpe 1966b; Hodgkinson & Baas Becking, 1977). Shortage of water soluble carbohydrate and greater allocation of current assimilates to shoot meristems (Marshall & Sagar, 1965; Ryle & Powell, 1975) resulted in reduction of root growth under hard defoliation. Severe reduction in root growth may influence plant regrowth by reducing water and nutrient uptake (Evans, 1971).

The consequences of the physiological and morphological responses of tall fescue and perennial ryegrass plants under hard defoliation were a dramatic change in root to shoot, and leaf to shoot ratios, and the production of less accumulated shoot and root mass. Also, shoot and root relative growth rates were lower in the treatment with only one live leaf per tiller compared with treatments in which two or more leaves remained on each tiller after defoliation. Similar responses to defoliation have also been described in other studies (e.g. Begg and Wright 1964; Matches, 1966; Brown *et al.*, 1966; Davidson and Milthorpe, 1966a; Davies 1974, Wilson, 1988) for cocksfoot, perennial ryegrass and tall fescue.

Generally, tall fescue and perennial ryegrass plants responded similarly to leaf defoliation at both vegetative and reproductive stages. The response was progressive by repeated defoliation. For example, in experiment 4 up to three or four times of leaf defoliation had no significant effect on tiller production, tiller weight or levels of WSC of plants in a defoliation treatment. The differences between treatments became more obvious after applying six or seven defoliations in the later experiments. This result indicated that plants can be defoliated severely as long as they are given a long enough time in which to recover. Conversely, they can be defoliated to leave more leaves if they are defoliated more frequently. However, repeated severe defoliation at short time intervals may prevent full recovery and result in poor regrowth or even death.

However, both species often behaved similarly under the same defoliation intensities, but tall fescue was defoliated less frequently than perennial ryegrass due to its longer leaf appearance intervals. Less frequent defoliation allowed tall fescue to produce sites for tillering, reaching the same photosynthetic capacity as perennial ryegrass by end of each leaf appearance interval. Therefore, the greater sensitivity of tall fescue to hard defoliation would be expected if tall fescue and perennial ryegrass were defoliated with the same intensity and frequency.

5.5 Summary

Tall fescue had slower leaf turnover, lower leaf appearance rate and less tillering capacity than perennial ryegrass, but produced larger tillers. The two species showed similar leaf photosynthetic rates per unit area but different leaf life-spans which allowed tall fescue leaves to photosynthesize for longer periods of time. Tall fescue often produced less herbage mass than perennial ryegrass due to lower tiller production and leaf growth.

Overall, the plants responded to hard defoliation by reduction in tiller production, tiller weight and leaf lamina growth rate, but not necessarily a decrease in leaf elongation rate. Tall fescue tiller weight was affected more by defoliation intensity than perennial ryegrass. Leaf defoliation resulted in changes in leaf morphology; plants produced shorter and narrower leaves with smaller leaf areas and leaf weights under hard defoliation. Leaves became thinner with increasing severity of defoliation, but leaf appearance rate was not affected by leaf defoliation.

The physiological response to defoliation of perennial ryegrass and especially tall fescue was to decrease water soluble carbohydrate concentrations in stem bases of the plants as the severity of defoliation increased, but photosynthetic rate per unit leaf area was not influenced by leaf defoliation intensity.

The consequence of hard defoliation was to change the proportion of root mass to shoot mass, leaf mass to shoot mass and to reduce shoot and root regrowth. Possibly, lower leaf area per tiller, lower life-span of leaf area and lower photosynthetic efficiency, and a shortage of water soluble carbohydrate were responsible for the lower regrowth of plants under hard defoliation.

CHAPTER 6: General discussion and conclusion

6.1: General discussion

The underlying aims of this study were to provide further information on the responses of tall fescue to defoliation in terms of regrowth and competition with other species, and also to determine which physiological and morphological factors are important for regrowth of tall fescue and perennial ryegrass (as a standard species) under continuous defoliation. To cover these concepts, the responses of plants to defoliation were examined in the field (Chapter 3), in the glasshouse (Chapter 4) and under controlled environment conditions (Chapter 5). In this Chapter, the general results are considered in the form of an integrated discussion. In this discussion the main results of the three experimental programmes are highlighted first. The differences between species are discussed in terms of tillering activity and energy investment for production of tillers, leaf growth potential and its role in plant regrowth, plasticity in changing tiller population and tiller weight under different defoliation managements, and the role of leaf life-span in management of species. Then causes of response to defoliation are considered for both species. Finally, conclusions are drawn based on the general results obtained in this study.

Under the field conditions, tall fescue showed sensitivity to hard grazing management by maintaining low tiller population density, tiller weight and leaf growth (Tables 3.5 & 3.9) and consequently low growth and productivity. Tall fescue was more sensitive to competition by volunteer grasses (especially perennial ryegrass) than white clover (Section 3.3.2).

Under cutting management (Chapter 4) tall fescue was less productive than perennial ryegrass due to less tiller production and leaf growth. The larger tillers of tall fescue did not compensate for the lower tiller production. The consequence of repeated cutting was to decrease tiller production, tiller weight, leaf growth and root growth with increasing severity of defoliation in both species.

The general results of the four experiments under controlled environment conditions (Chapter 5) confirmed the superiority of perennial ryegrass to tall fescue in terms of tiller production and leaf growth. The results distinguished the factors responsible for differences between the species in the response to defoliation.

Tall fescue often showed lower tillering activity relative to perennial ryegrass (Sections 4.3.2, 5.2.4.3, 5.3.2.2). Lower leaf appearance rates and site filling (Table 5.29) were the causes of lower tiller production in tall fescue. Tall fescue produced larger tillers with longer leaves than perennial ryegrass (Tables 4.7, 5.9, 5.28, 5.51, 5.67). This means that tall fescue invested more energy in the production of larger tillers and leaves compared to perennial ryegrass, which had more and smaller tillers. Chapman and Lemaire (1993) suggested that investment of growth resources for producing larger organs (e.g. larger leaves) accompanied the production of less sites for branching. They concluded that a less-branched plant structure would not be a profitable strategy under intensive grazing because additional investment in new growth (for example larger leaves) cannot be fully recouped by the plant since leaves are usually removed long before they would die naturally. In contrast, plants characterized by a small number of large leaves are more competitive in environments with dense canopies (Briske, 1991). The compatibility of tall fescue with perennial ryegrass improved under less intensive grazing (Figures 3.1, 3.2) which is consistent with results of other workers (e.g. Bell, 1985; Sato *et al.*, 1990). From the above results it can be concluded that under lax defoliation taller plants (e.g. tall fescue) may be capable of shading shorter plants (e.g. perennial ryegrass) and producing less efficient leaves in terms of photosynthetic activity (Woledge, 1977). Under hard defoliation other morphological or physiological features such as leaf positioning, leaf growth, tillering activity, branching angle and so on (Briske, 1991; Korner, 1991) become growth determinants under competitive conditions.

Leaf growth was often lower in tall fescue than perennial ryegrass (Figure 4.3 & Tables 5.12, 5.31, 5.33, 5.52) despite tiller weight usually being higher in tall fescue. The higher ratio of root mass to shoot mass (Figure 5.4) in tall fescue indicated investment of more assimilate for root growth and maintenance. Also, tall fescue had a longer leaf life-span with thicker leaves (Tables 5.16, 5.35, 5.56) than perennial ryegrass, which increased the cost of growth and maintenance for longer-lived leaves as a consequence of a greater degree of lignification (Mooney & Gulmon, 1982). It has been suggested that the degree of movement of nitrogen from old leaves depends on growth rate (Chapin, 1980). Species with high growth rates (e.g. perennial ryegrass) recover a high percentage of nitrogen from senescing leaves. Therefore, the lower leaf growth and tillering activity and consequently lower shoot growth in tall fescue relative to perennial ryegrass may be explained by the lower rate of photosynthesis per unit leaf weight (Tables 5.18, 5.38, 5.58), the higher energy cost for maintenance of longer lived leaves and the growth and maintenance of a higher proportion of root, and also lower nitrogen mobilization for new growth.

Species that rapidly replace photosynthetic surface gain a competitive advantage over associated species that grow more slowly following defoliation (Briske, 1991). The slower leaf growth in tall fescue relative to perennial ryegrass is a disadvantageous characteristic under intense defoliation because photosynthetic surface can not be reestablished as quickly as in perennial ryegrass. So, less leaf growth in tall fescue may be counted as one reason for the reduced competition of this species with perennial ryegrass under hard grazing (Figure 3.1, 3.2).

Plasticity in changing tiller population density and tiller size is an important feature determining regrowth after defoliation. Under continuous stocking, tall fescue showed little scope for compensation of decreasing tiller weight under increased grazing intensity by increasing tiller density (Figure 6.1). Under the same management perennial ryegrass and Yorkshire Fog exhibited a wider range of compensatory behaviour in changing tiller population density and tiller weight (Figure 6.2 after Butler, 1993). In another study (Chapman & Lemaire, 1993) a tall fescue sward defoliated each week to 30 mm height failed to increase tiller density in response to decreased tiller weight under repeated defoliation, whereas both cocksfoot and perennial ryegrass were able to do so. The limited plasticity in changing tiller population density for tall fescue and high plasticity for perennial ryegrass have also been observed by other researchers (Hart *et al.*, 1971; Hodgson *et al.*, 1981; Bircham & Hodgson, 1983; Grant *et al.*, 1981b, Zarrough *et al.*, 1983a,b). The poor relationship between tiller weight and tiller population density for tall fescue may be explained as poor adaptability of this species to hard grazing. Therefore, less regrowth of tall fescue under hard grazing (Chapter 3) can be partly attributed to the low plasticity of this plant to increase its tiller density in response to a decrease in tiller weight. The consequence of this response was inadequate leaf area per tiller and per unit area for light interception and photosynthesis, and therefore, less pasture regrowth.

Differences between leaf life-span of perennial ryegrass and tall fescue may result in differences in response to defoliation. Plants with longer leaf life-span (e.g. tall fescue) need more time to reach maximum photosynthetic capacity than shorter leaf life-span plants (e.g. perennial ryegrass). Under more intense defoliation the leaves may be removed in the former species before they reach maximum photosynthetic capacity, resulting in less contribution of these leaves to the carbon economy of the plant. Under less intense defoliation longer lived leaves have the opportunity to photosynthesise for longer periods relative to short lived leaves, which may accumulate a higher mass of senescent leaf. This characteristic may be regarded as another reason for the poor regrowth and competition of tall fescue under hard grazing management.

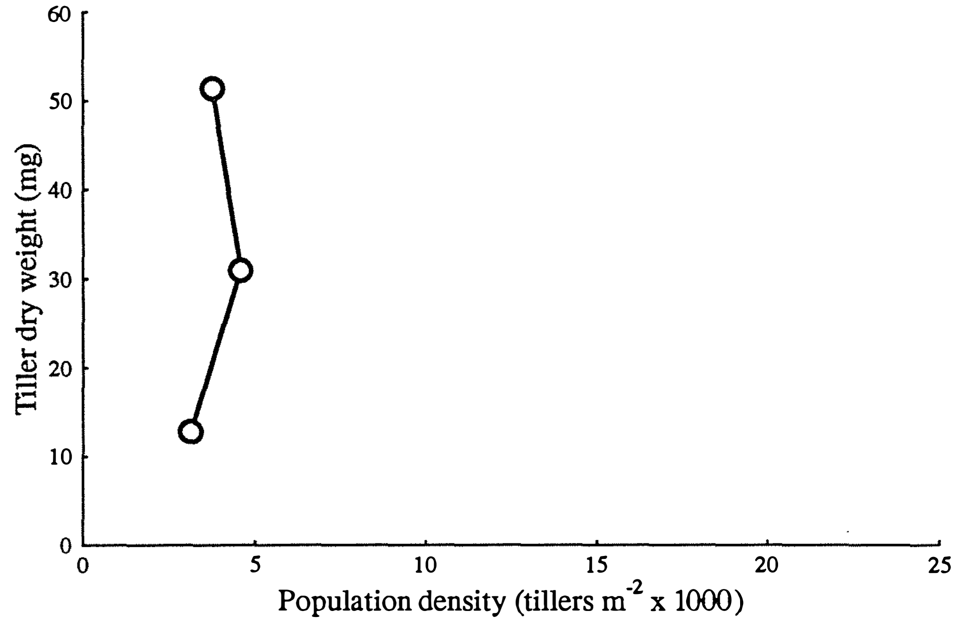

Figure 6.1: Relationship between tiller weight and population density of tall fescue under set stocking management.

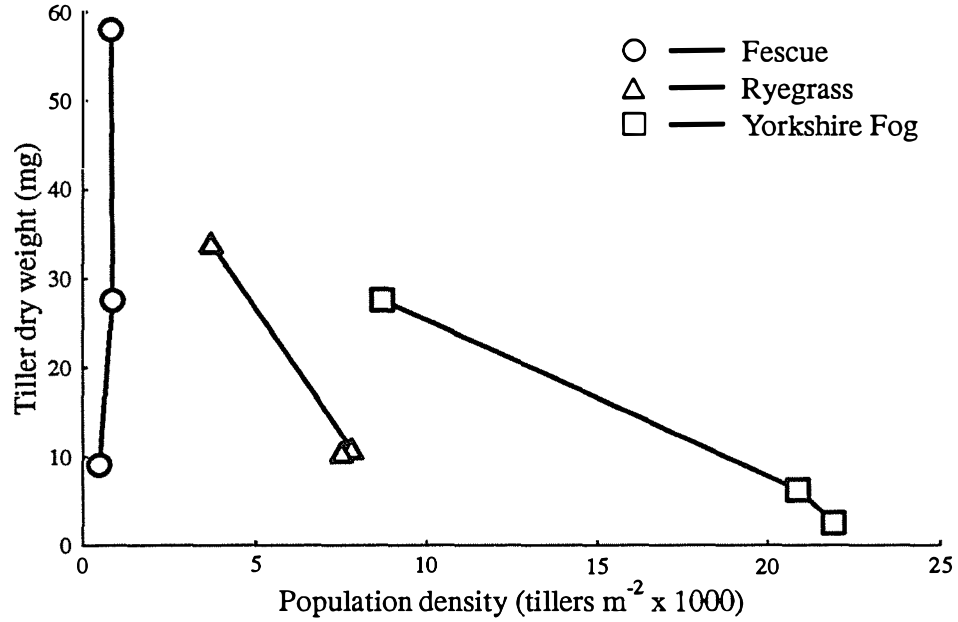

Figure 6.2: Relationship between tiller weight and population density of tall fescue, perennial ryegrass and Yorkshire Fog under set stocking management (Data from Butler, pers. comm.).

The speed and amount of regrowth after defoliation depends on how much top growth is left and also on the general energy reserves of the plant (Booysen & Nelson, 1975). Regrowth of plants was severely affected when they were repeatedly defoliated to 30-40 mm surface height (Chapter 3 & 4) and where all fully expanded leaves were removed (Chapter 5). Under these conditions plants showed less regrowth, productivity and persistency.

Under hard defoliation plants responded by reduction in tillering activity and by producing small tillers with short leaves of small surface area. All of these factors resulted in a decrease in photosynthetic surface (Tables 3.7 , 5.23) and consequently less effective light interception and assimilate production. On the other hand, under hard grazing, leaves have more chance of removal before they become fully expanded. Expanding leaves have less photosynthetic capacity than fully expanded leaves (Section 5.2.4.7), and may act more as a sink (Davidson & Milthorpe, 1966b; Atkinson, 1986; Allard, 1991) for assimilate and remain in negative carbon balance in the early stages of development even during daylight (Caldwell, 1984). For example, under hard defoliation (Chapter 5) there was a decrease in the proportion of root mass to shoot mass and an increase in the proportion of leaf mass to shoot mass, indicating less contribution of expanding leaves to the carbon economy of the other plant parts. Under these circumstances plants become less efficient in terms of providing assimilate through photosynthesis for growth and maintenance, and may use carbohydrate reserve for new growth. The severe depletion in water soluble carbohydrate concentration in the stem bases of plants under hard defoliation (Tables 5.20, 5.41, 5.60, 5.70) indicated limitations in current assimilate and the use of this stored assimilate for growth and maintenance of the plant. On the other hand, when plants under treatment M (Chapter 5) were allowed to maintain an expanded leaf per tiller for about one leaf appearance interval they continued to photosynthesise with high capacity, and produced as much shoot dry weight as treatments L and C. The expanding leaves and the youngest fully expanded leaves together contribute more than 75% to the total photosynthesis of the canopy(Parsons *et al.*, 1983).

Therefore, repeated removal of photosynthetic surface, which reduces carbon assimilation and carbohydrate reserves in the stem bases, results in plants of short assimilate supply and reduction in tillering activity, tiller weight, leaf and root growth.

Reduction in tillering activity limits pasture regeneration (Jewiss, 1972) and causes the sward to open-up in response to continuing defoliation pressure. Reduced leaf growth limits assimilate production and results in depletion of stored reserves, and eventually may result in pasture deterioration. Lack of root function affects regrowth because of reduced mineral and water uptake (Davidson & Miltorpe, 1966b; Evans, 1971; Richards, 1993). Possibly, all of these effects contributed to the reduced regrowth and productivity of tall fescue and perennial ryegrass under hard defoliation.

6.2 Comment and conclusion

Under continuous stocking tall fescue showed sensitivity to hard defoliation by reduction in tiller population density, tiller weight and leaf growth. This resulted in poor regrowth of tall fescue and invasion by associated species, especially perennial ryegrass. The main effect of hard defoliation was primarily decreased tillering activity and then decreased leaf growth.

Lack of plasticity in the balance between tiller population density and tiller weight, reflected the low tillering potential and slower leaf growth in tall fescue than in perennial ryegrass. This lack of plasticity contributed to the poor behaviour of tall fescue under hard grazing. Producing large tillers, maintaining longer-lived leaves, and growth and maintenance of a higher proportion of root mass requires energy, and may limit tillering and leaf growth. In contrast, perennial ryegrass, with higher tillering potential and faster leaf growth, is able to produce faster and greater photosynthetic area, intercept greater amounts of solar energy, and assimilate a greater amount of energy; this enhances its competitive ability over tall fescue under hard defoliation.

The results of experiments at the level of the single plant highlighted some physiological and morphological causes of poor regrowth of tall fescue plants. Plants responded to defoliation similarly in both the vegetative and reproductive phases. Under hard defoliation reduction in leaf area per tiller, leaf area duration and photosynthetic efficiency, and a consequent shortage of carbohydrate reserves were the cause of poor plant regrowth through reduction in tiller production, tiller weight, leaf, root and shoot growth. Reduced tillering activity affects plant regeneration, and reduced root growth may reduce water and nutrient uptake.

Overall, the results indicated that tall fescue plants can be defoliated frequently when there is sufficient photosynthetic area after defoliation. Conversely, plants need a longer time for recovery from defoliation when a high proportion of leaves is removed at each defoliation. Repeated removal of most of the photosynthetic area would be detrimental to sustained production and persistence. Under continuous stocking tall fescue should not be grazed closer than 5-10 cm above ground level to ensure good production and longevity of the stand.

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APPENDICES

Appendix 3.1: Summary of rainfall, temperature and sunshine from November 1990 to March 1991,at the CRI climate station at the trial site (40°23'S 175°37'E,34m asl).

Month	Total rainfall (mm)	Air temperature °C			Sunshine hours
		Max	Min	Mean	
NOV.	98	18.8	10.9	14.9	167
DEC.	51	20.5	12.3	16.4	207
JAN.	120	22.2	12.9	17.6	186
FEB.	132	21.7	13.1	17.4	152
MAR.	29	21.0	12.4	16.7	198
APR.	163	17.3	8.7	13.0	128

Appendix 3.2: Number of sheep in each plot over trial period.

Dates	Sheep number		
	Lax	Medium	Hard
26/10/90	12	8	14
30/10/90	8	6	10
08/11/90	0	0	0
12/11/90	8	8	12
13/11/90	8	10	14
16/11/90	10	15	12
20/11/90	10	10	12
04/12/90	8	10	12
07/12/90	8	5	7
11/12/90	6	5	8
14/12/90	7	5	8
19/12/90	0	0	0
20/12/90	7	5	6
21/12/90	7	5	5
01/01/91	7	3	5
08/01/91	3	3	5
11/01/91	1	0	2
18/01/91	1	4	4
23/01/91	1	3	4
25/01/91	1	6	6
28/01/91	0	0	0
30/01/91	0	8	10
01/02/91	2	8	10
04/02/91	6	8	10
07/02/91	10	8	10
11/02/91	20	8	10
15/02/91	14	8	10
19/02/91	6	8	10
22/02/91	3	8	10
26/02/91	3	8	6
04/03/91	3	6	4
06/03/91	0	0	0
08/03/91	6	5	4
15/03/91	10	5	4
22/03/91	10	5	6
26/03/91	6	3	6
28/03/91	4	3	6
05/04/91	4	5	6
12/04/91	4	3	6
15/04/91	4	4	6
19/04/91	2	2	6
20/05/91	2	2	6

Appendix 3.3: Analysis of variance of tall fescue herbage mass with three grazing regimes and with and without clover.

Source	DF	MS	F	Pr >F
Grazing	2	361944	24.5	0.0001
Block(Grazing)	9	54451	0.82	0.5998
Clover	1	55528	7.52	0.0070
Grazing x Clover	2	69015	4.67	0.0111
Block x Clover(Grazing)	9	29855	0.45	0.9054
Error	120	1457270		

Appendix 4.1: Analysis of variance of herbage harvested for perennial ryegrass and tall fescue under different cutting treatments over time.

Source	DF	MS	F	Pr >F
Block	3	2671	0.23	0.8734
Species	1	49476	4.29	0.0509
Cutting Treatments	3	689983	59.79	0.0001
Species x Cutting	3	19966	1.73	0.1915
Error	21	11540		
Time x Block	24	423	0.61	0.9239
Time x Species	8	11416	16.40	0.0001
Time x Cutting	24	18423	26.47	0.0001
Time x Species x Cutting	24	5124	7.36	0.0001
Error	168	696		

Appendix 4.2: Effect of cutting heights on herbage harvested per plant (mg/plant) of perennial ryegrass and tall fescue over time.

Cutting	Ryegrass				Fescue				SEM	F values for		
	L	M	H1	H2	L	M	H1	H2		SP	TR	SPxTR
C1	96.6	65.4	40.5	18.8	120.0	84.2	61.7	27.4	13.7	ns	***	ns
C2	95.3	68.3	43.7	22.4	119.4	82.8	34.6	13.7	12.8	ns	***	ns
C3	159.4	111.8	26.8	18.6	152.4	91.8	26.7	12.9	26.5	ns	***	ns
C4	163.6	95.6	15.1	15.3	186.1	95.7	22.8	8.6	26.3	ns	***	ns
C5	231.1	113.1	15.4	9.7	208.1	85.3	21.6	7.5	27.7	ns	***	ns
C6	376.1	175.5	18.6	10.7	196.8	73.5	9.2	11.0	17.6	***	***	***
C7	480.8	166.7	15.5	8.8	197.6	92.5	10.6	1.3	22.2	***	***	***
C8	373.4	140.6	7.0	5.0	271.3	82.6	6.5	0.9	21.9	*	***	ns
C9	352.5	110.1	7.4	4.7	235.0	78.8	5.4	0.4	22.0	*	***	ns

Appendix 4.3: Effect of cutting heights on tiller number per plant of perennial ryegrass and tall fescue over time.

Cutting	Ryegrass				Fescue				SEM	F values for		
	L	M	H1	H2	L	M	H1	H2		SP	TR	SPxTR
C1	10.0	10.0	10.3	6.3	9.8	10.3	10.5	6.0	1.04	ns	**	ns
C2	14.8	14.8	11.8	6.8	11.5	12.8	13.0	7.0	1.48	ns	***	ns
C3	19.0	17.0	12.0	7.5	15.3	16.3	13.8	7.3	2.04	ns	***	ns
C4	26.0	21.5	12.5	7.5	18.8	17.8	13.8	6.0	2.77	ns	***	ns
C5	31.5	24.5	12.5	7.5	24.0	23.5	13.8	6.0	3.61	ns	***	ns
C6	43.3	29.5	10.5	7.5	29.3	26.3	14.5	6.0	4.24	ns	***	ns
C7	59.8	36.0	9.3	7.5	33.3	28.3	12.5	3.8	4.94	*	***	*
C8	68.3	43.3	9.5	6.5	36.5	31.5	12.5	1.8	5.93	*	***	*
C9	77.3	45.5	9.0	5.8	40.5	34.0	9.5	1.8	6.61	*	***	*
C10	82.8	46.8	7.5	4.8	47.5	37.5	4.0	1.5	6.47	*	***	ns

Appendix 5.1: PAHBAH regent.

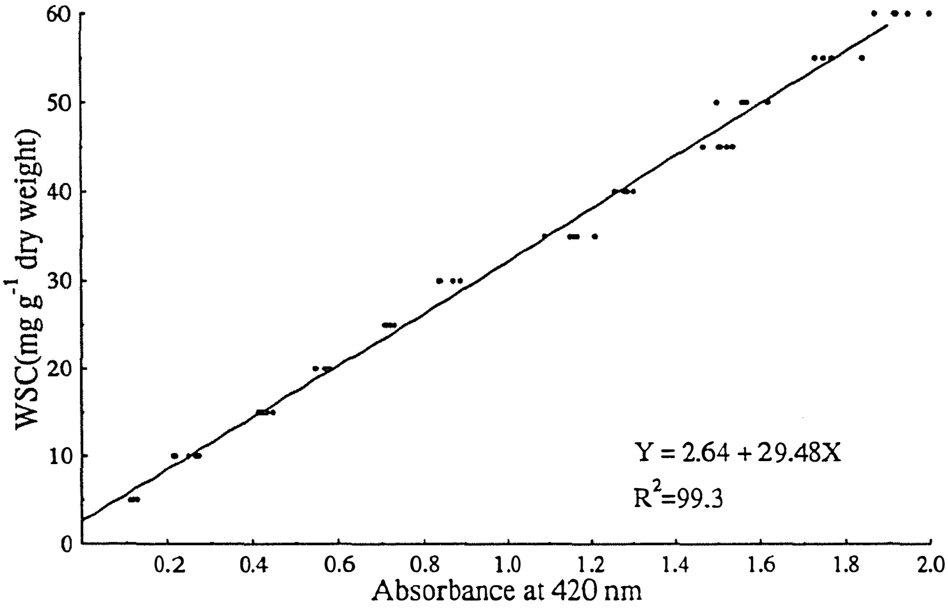
(1) Alkaline diluent

Trisodium citrate	14.704 g L^{-1}
Calcium chloride	1.47 g L^{-1}
NaOH	20.0 g L^{-1}

Dissolved trisodium citrate and $CaCl_2$ separately, mixed and added NaOH.

(2) PAHBAH regent

5 g solid PAHBAH + 1 litre alkaline diluent.



Appendix 5.2: Standard curve for determination of water soluble carbohydrate concentrations (WSC).