GROWTH OF PASTURE SPECIES IN THE SHADE IN RELATION TO ALDER SILVO-PASTORAL SYSTEMS

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ABSTRACT

An increased understanding of the competitive interactions between tree species and understorey pastures is required for the development of deciduous tree based silvo-pastoral systems. In particular, the shade tolerance of pasture species likely to be used under trees in New Zealand needs to be determined. This thesis examines the effects of light intensity and quality on the growth of pasture species in a series of glasshouse experiments, and under the shade of alder trees pruned to different heights.

The shoot dry weight per plant of all grass and legume species examined showed a linear increase (P<0.0001) with % ambient photosynthetically active radiation (PAR). Highest shoot dry weight was at 73% and lowest was at 14% PAR (heavy shade). Shade also affected the tillering ability of pasture species. Under heavy shade, cocksfoot (*Dactylis glomerata* L.) produced more tillers per plant than the other grass species examined. Perennial ryegrass (*Lolium perenne* L.) had the lowest tillering in heavy shade. Under medium shade (43% ambient PAR), tiller number per plant for browntop (*Agrostis capillaris* L.) and Poa trivialis (*Poa trivialis* L.) was higher than other species. Lotus (*Lotus uliginosus* L.) produced a higher (P<0.0001) number of branches under heavy shade than white clover (*Trifolium repens* L.) and subterranean clover (*Trifolium subterraneum* L.).

Shade affected perennial ryegrass more than cocksfoot selections, especially at the lowest PAR level both in the glasshouse and the field experiment. For example, tillers per plant under tree shade, and also at the low PAR level in the glasshouse for perennial ryegrass were 18 compared with 28-29 (P<0.0001) for Wana cocksfoot and 24-27 for PG 74 cocksfoot. Leaf area per plant for perennial ryegrass was also significantly (P<0.0001) lower than for Wana cocksfoot. Cocksfoot selections were more tolerant of heavy shade than perennial ryegrass, and Wana was the most tolerant of the cocksfoot selections of heavy shade.

There were no effects of R:FR ratio (P>0.05) on the shoot dry weight production of the pasture species examined. Similarly, the interaction between PAR × R:FR and species was not significant (P>0.05) for most morphological characteristics when plants were not defoliated. Perennial ryegrass, Wana cocksfoot and Yorkshire fog (*Holcus lanatus* L.) at low PAR had similar yields, that higher than white clover and lotus, which were similar. However, when plants were defoliated weekly or three-weekly, Wana cocksfoot out produced Nui perennial ryegrass at low PAR/R:FR due to its ability to maintain higher leaf area and higher leaf dry weight, higher SLA, and more tillers per plant.

Herbage mass of swards in heavy and medium shade created by pruning alder trees was about 50% and 70%, respectively, of that of light shade (P<0.0001). Herbage mass was highest for cocksfoot either with lotus or white clover (P<0.0001), whereas values for perennial ryegrass and Yorkshire fog were lower and similar. Shade affected perennial ryegrass more than cocksfoot and Yorkshire fog, especially at the lowest PAR level. Cocksfoot in mixture with either white clover or lotus had the highest leaf expansion per tiller, which was in the order cocksfoot> Yorkshire fog>perennial ryegrass. There was no significant difference (P>0.05) between the pasture species in the total number of sheep grazing observations in 2 hours, but more sheep grazed in light shade than in heavy shade (P<0.05).

The research highlighted the importance of measuring shade tolerance of pasture species in terms of attributes that determined growth and persistence. As perennial pasture species are regularly defoliated they must be able to vegetatively reproduce in the shade as well as be productive. Shade tolerance of the pasture species examined varied greatly, but their relative shade tolerance was also sensitive to the level of shade. Although, cocksfoot was the most shade tolerant species in heavy shade (PAR level <200 μmoles photons m^{-2} s^{-1}) it was similar to other species in medium shade (PAR level ≥ 400 μmoles photons m^{-2} s^{-1} or more).

Light intensity was more important for growth and vegetative reproduction than light quality for pasture species under shade. Likewise, pruning trees was more important for pasture production under tree shade. The morphological attributes related to shade tolerance of New Zealand hill country pastoral plants were identified in this thesis as tiller number per plant, leaf area, specific leaf area (SLA), and leaf appearance interval.

For alder silvo-pastoral systems with high tree density and heavy shade (PAR level <200 μmoles photons m^{-2} s^{-1}) cocksfoot in combination with either lotus or white clover was the most productive pasture, while perennial ryegrass, or browntop, with white clover was as productive as cocksfoot if shade was maintained at a PAR level >200 μmoles photons m^{-2} s^{-1}). Additionally, cocksfoot and lotus are both tolerant of the low to medium soil fertility and seasonal dry periods likely to be encountered on the hill country where deciduous trees are also used to control soil erosion.

Shade had a marked effect on tillering as well as on shoot dry weight, and is the most significant factor determining the understorey pasture production. However, the decrease in pasture production due to shading can be managed by appropriate pruning practices and choice of appropriate pasture species.

GLOSSARY AND ABREVIATIONS OF TERMS USED

Agroforestry: it refers to silvo-pastoral systems oriented to timber production or soil erosion control. Agroforestry in New Zealand is often used synonymously with "farm forestry" i.e. farmers managing forest plantation on the farmland. Here, agroforestry is taken as an intensive land management practice using trees, pastures, and livestock on the same area of land at the same time.

AGR: absolute growth rate.

Agrosilviculture: a combination of crops plus trees.

Agrosilvopastoral: covers crops, pasture/animal and trees.

Breast height: breast height in New Zealand is 1.4 m above ground on the uphill side of the tree. Many other countries including Australia, use 1.3 m as breast height.

^{0}C: degree Celsius.

C: carbon.

C_3: photosynthetic pathway of carbon assimilation for most of the temperate pasture species.

C_4: photosynthetic pathway of carbon assimilation for most of the tropical pasture species.

Canopy: the part of a tree consisting of branches and foliage. " Canopy closure" is the stand age when the branches at neighbouring trees touch, or nearly so, thereby restricting light to the forest floor.

CP: crude protein.

Cultivar name: all species and cultivars are fully named in the materials and methods section of each chapter. Elsewhere they are presented in an abbreviated form e.g. 'Grasslands Wana' has been referred to as Wana.

DBH: tree diameter at breast height.

Deciduous tree: broad-leaved hardwood tree that sheds its leaves during autumn/winter and develops new leaves the following spring. Some deciduous trees like alder can also fix atmospheric nitrogen.

Defoliation: practice of clipping or removing aerial plant parts. Here, defoliation means cutting pasture plants at a specific height at specific intervals.

GLM: general linear model of SAS.

HH: herbage harvested. The mass of herbage per unit area removed by mechanical means, usually expressed as g/m^2.

Hill country: all the land with slopes between 12 and 28^0, but low relief; typically 100 to 300m difference in elevation. Valley bottoms are usually narrow.

HM: herbage mass. The total dry weight of herbage per unit area of land, usually above ground level and at a defined reference level. Commonly expressed as g/m^2.

Intercepted PAR: is the difference between global PAR above a canopy and PAR transmitted through a canopy.

J: joule, unit of measurement.

K: potassium.

kg: kilogram, 1000gram.

LAI: leaf area index, leaf area per unit ground area.

LAR: leaf area ratio, ratio of leaf area to whole plant dry weight.

LPC: light compensation point for photosynthesis.

Lopping: cutting one or more branches off a woody plant; synonym to pruning.

nm: nanometer.

NZMF: New Zealand Ministry of Forestry.

PB: polythene bag used as a pot to grow pasture species in glasshouse conditions.

PGU: plant growth unit.

Shelterbelt: a long narrow strip of trees and/or shrubs intended to reduce wind flow, often for agricultural gain.

Silviculture: the procedure used in growing trees, especially pruning and thinning.

Silvo-pastoral system: which includes trees plus pasture/animals. Basically pasture production is emphasised under tree shade. Generally the term agroforestry also describes silvo-pastoral systems.

Stocking rate: the number of live trees per hectare, also known as “tree density”.

TDR: time domain reflectometry.

Tissue turnover: in a given period the net change in the weight of living shoot material of a species brought about by the formation of new tissue and the gross decrease caused either by senescence and decomposition of older tissue, or by herbage intake is commonly known as tissue turnover. It is commonly expressed in $g/m^2/day$.

Thinning: the removal of trees within a stand at some time before clear felling. If trees are left lying in the forest, it is “waste thinning”. If trees are extracted, it is “production thinning”.

Transmitted PAR: when shade is created with shade cloth, transmitted PAR is measured under the shade cloth. In the case of trees, transmitted PAR is measured under the canopy.

Abbreviations related to experimental treatments

ANOVA: analysis of variance.

CL: cocksfoot with lotus.

cm^2: square centimetre.

cv: cultivar.

CVA: canonical variate analysis.

CV: canonical variate.

CW: cocksfoot with white clover.

d.f.: degrees of freedom.

DM: dry matter.

Fig: figure.

g: gram.

GP: white clover growing points.

ha: hectare.

h: hours.

H/N: high natural, here denotes high PAR with natural R:FR.

L/N: low natural, here denotes low PAR with natural R:FR.

L/R: low reduced, here denotes low PAR with reduced R:FR.

LSD: least significant difference.

m^2: metre square area.

mg: milligram.

mm: millimetre.

N: nitrogen.

n: number.

na: data not available.

NA: data not taken.

NS: non-significant at P=0.05.

P: phosphorus.

P: probability.

PAR: photosynthetically active radiation. Measured in µmoles photons m^{-2} s^{-1}, 400-700nm.

R:FR: red to far red ratio. Ratio of photon irradiance between 655 and 665nm, and 725 and 735nm, respectively.

RGR: relative growth rate.

RW: perennial ryegrass with white clover.

s^{-1}: per second.

SEM: standard error of the mean.

SLA: specific leaf area, the area of leaf displayed per unit of leaf weight.

SU: site usage, expressed as tillers per leaf.

vs: versus.

W1: weekly defoliation.

W3: three- weekly defoliation.

YW: Yorkshire fog with white clover.

α: statistical significance.

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1. General Introduction and Objectives

1.1 Statement of the problem

Silvo-pastoral systems involve the use of timber or fodder trees with an understorey of pasture or range lands. The trees in silvo-pastoral systems also provide microclimate modification and soil protection or improvement (Gordon *et al.* 1997). Silvo-pastoral systems are a means of diversification and developing sustainable agricultural systems.

An increase in tree cover would help to achieve more sustainable management systems on many New Zealand farms (Thorrold *et al.* 1997). It is estimated that about 3.7 million ha or 33% of the North Island requires significant soil conservation measures in order to be able to physically sustain pastoral land use (Wall *et al.* 1997). Broad-leaved deciduous trees are preferred for silvo-pastoral systems due to their excellent root development (Hicks 1995; Guevara *et al.* 1997) that helps preserve or improve land quality, and due to their better understorey pasture production than under evergreen trees (Hawke and Knowles 1997).

In New Zealand most silvo-pastoral research has been conducted under agroforestry systems using *Pinus radiata* (Pollock *et al.* 1997; Wall *et al.* 1997; Hawke and Knowles 1997; Power *et al.* 1998) with little research involving the use of alternative tree species (Power *et al.* 1998). Studies on *Pinus radiata* indicated that understorey herbage yield decreases linearly as crown density increased (Anderson and Batini 1983; Pollock *et al.* 1994; Hawke and Knowles 1997). This same relationship does not appear to apply to broad-leaved deciduous trees. Also, the productivity of the pasture understorey is influenced by the species of the tree (Atta-Khrah 1993). Competitive interactions between broad-leaved deciduous trees and the understorey hill pastures include changes in microclimate, soil and water resources (Wall *et al.* 1997), but the impact of shading by broad-leaved deciduous trees on the productivity and persistence of hill pasture species has received little research attention (Hawke 1991; Knowles 1991; Pollock *et al.* 1994).

The development of a whole-farm package for the integration and management of deciduous tree based silvo-pastoral systems should be the objective of research in this area (Wall *et al.* 1997). An increased understanding of the competitive interactions between tree species and the pastures will be required for the development of appropriate management systems (Shelton *et al.* 1987; Wall *et al.* 1997). If land is to remain under sustainable pastoral use, a compatible mixture of pasture and trees needs to be identified (Clough and Hicks 1993).

This thesis is focused on determining which hill pasture species are the most productive and persistent under deciduous tree shade. The approach is to examine the growth of hill pasture species under a range of light intensities in the glasshouse and the field. The effects of light quality and defoliation on pasture species growing in shade are also examined. Finally, the preference for pasture species of sheep grazing under tree shade is evaluated.

1.2 Broad objectives

The main objectives of the nine experiments reported in this thesis were to:

(a) Screen hill pasture species for their growth and morphological responses to levels of shade.

(b) Evaluate the effect of the light intensity and quality, and selected defoliation regimes on the growth and re-growth of pastures species.

(c) Identify shade tolerant pasture species and understand their morphological attributes.

(d) Evaluate grazing preference of sheep for selected pasture species in a deciduous silvo-pastoral system.

1.3 Thesis organisation

This thesis is divided into nine chapters. Following the introductory chapter, current knowledge on growth of understorey pasture is reviewed in Chapter 2, mainly in terms of morphological attributes of pasture species with respect to effects of light, fertility and defoliation. Chapter 3 presents research on the screening of pasture species for shade tolerance at a range of light intensities. Available cocksfoot selections were compared with perennial ryegrass under different light intensities in a glasshouse and under tree shade in field conditions and the results are presented in Chapter 4. Chapter 5 describes the effects of intensity and quality of light on the commonly available pasture species used in Chapter 3 in terms of shoot dry weight, tillering and other morphological attributes. Chapter 6 presents the relative growth rate and also the effects of defoliation frequencies on selected heavy shade tolerant and intolerant pasture species. Chapters 7 and 8 present results of field experiments with selected grass and legume species carried out under three levels of alder tree shade created by pruning trees to different heights. In Chapter 7 cocksfoot, Yorkshire fog, and perennial ryegrass were compared in mixtures with white clover, and for cocksfoot also with lotus. At the end of the field experiment, diet selection by sheep was studied and presented in this Chapter. Chapter 8 examines the effects of tree shade on tissue turnover in perennial ryegrass/white clover, Yorkshire fog/white clover and cocksfoot/white clover pasture. The research site described in Chapter 4 (Experiment 4.2), Chapter 7, and Chapter 8 was the same one. General discussion, conclusions and research needs in relation to the shade tolerance attributes of pasture species are presented in Chapter 9.

Chapters 3-8 are presented as scientific papers but in thesis format. Except for Chapter 1, in which references are merged into the references of Chapter 2, the references related to individual chapters are included at the end of each Chapter. A Table of contents for all Chapters except Chapter 1 is presented at the beginning of each Chapter. Information about screening shade tolerant pasture species (Chapter 3) other than that included in the main text is presented in Appendix Tables 3.1-3.4. Appendix Tables 7.1a and b cover information on botanical composition as described in Chapter 7. Chapter 3, and part of Chapter 4 (Experiment 4.2) have been published in Proceedings Agronomy Society of New Zealand, Volumes 27 and 28, respectively.

2. Literature review

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2.1 Introduction

The simultaneous increase in numbers of ruminant animals and the human population has led to sharp competition between crops and animals, and has resulted in an increasing demand for forage resources (Blair 1991). Land management systems for producing herbaceous plants along with woody perennials are the result of searching for sound alternatives to grassland (Anderson 1991; Connor 1991; Bird *et al.* 1995). These systems have the potential to help check or reverse degradation of soil, forest, and pasture resources (Young 1989), and have a variety of other advantages, such as provision of shelter and lowering of water tables (Anderson 1991; McKenzie 1996). These systems are commonly termed agroforestry.

The interaction of trees, pastures and animals in agroforestry systems is complex (Bird *et al.* 1995), and there is a need for comprehensive knowledge about these components and their interactions if they are to be managed in a sustainable way.

In this chapter, a definition of agroforestry in the broader sense, and silvo-pastoral systems in the context of New Zealand are covered. The review also focuses on current trends in agroforestry systems in New Zealand, with an emphasis on the role of broad leaf trees in the silvo-pastoral system (section 2.2), together with the interrelationships between trees, pasture and animal components.

The current knowledge on production and persistence of understorey pasture is reviewed (Section 2.3) in relation to morphological adaptations and effects of light, fertilizer and defoliation. The final section (2.4) reviews the pasture species that were used in the thesis with emphasis on their characteristics, and their potential for growth in a shaded environment.

2.2 Agroforestry systems

2.2.1 Definition of agroforestry

Agroforestry systems are described as the land use systems and technologies where woody perennials are deliberately used on the same land management unit as agricultural crops and/or animals, in either a spatial arrangement, or a temporal sequence, there being both ecological and economic interactions between the different components (Came and Prinsely 1992). In this sense, agroforestry is the land-use science which deals with the interactions between trees and crops, and of both with animals in the same unit of land (Wood 1990). Agroforestry involves the coexistence of trees with agriculture, both in time and space, and has been practised on an informal basis ever since humans began to till the soil and herd animals (Churchill 1993).

Agroforestry systems have been classified according to various criteria such as their structure, function, socio-economic aspects and ecological spread. The primary classification is on the basis of their structure. As Nair (1987) stated, this gives three basic types: (a) *agrosilvicultural,* a combination of crops plus trees. (b) *silvo-pastoral,* which includes trees plus pasture/animals, and (c) *agrosilvo-pastoral*, which covers crops, pasture/animals and trees. All these types of agroforestry systems are commonly in practice (Nair 1987). Generally, the term agroforestry describes all three system types. Agroforestry in New Zealand is, however, dominated by silvo-pastoralism (Hawke 1991).

Trees, as a component of pasture systems, can be seen from two perspectives. The first involves the integration of pasture species (mainly grass and herbaceous legumes) into tree crop plantations. Thus, pasture is introduced as an additional element into the tree crop. The second perspective is where the tree is considered as an element of the pasture (Atta-Krah 1993). In either case, it can be argued that the productivity of the understorey is influenced by the species of the tree, as well as the tree population and canopy cover (Atta-Krah 1993). The tree can alter micro-climates and subsequently bring changes to the environment (Costello *et al.* 1996). Moreover, tree crops could play a role in diversifying farm production, promoting soil stability and ameliorating the microclimate, while maintaining an acceptable stock carrying capacity (Tustin *et al.* 1979).

Research on agroforestry has increased since 1983, and a scientific framework for the quantitative analysis of agroforestry systems is gradually developing (Ong 1996). Agroforestry systems, which use trees in farming systems are in one sense ancient, but in another, still at the stage of laying methodological foundations (Carruthers 1990).

2.2.2 Overview of silvo-pastoralism in New Zealand

2.2.2.1 Concept and current practices

The development of agroforestry in New Zealand commenced in the late 1960s, with several co-operative studies involving the Ministry of Agriculture and Fisheries and the Forest Research Institute (Hawke 1991). Silvo-pastoral systems were first considered in New Zealand in 1969, as a result of developments in plantation forestry, with 'direct sawlog' regimes for radiata pine (Knowles 1991). Broadleaved trees, however, have been used (Thompson and Luckman 1993; Anonymous 1995; Wall *et al.* 1997) as an important component in erosion prevention and control in New Zealand hill pastoral systems since the beginning of the twentieth century (Miller *et al.* 1996). Three distinct types of agroforestry are being practised in New Zealand: (a) widely spaced trees planted into permanent pastures, (b) grazing of forests under-sown with a leguminous based sward, and (c) timber belts (Hawke 1991).

The plantation forest estate in New Zealand covers more than 1.2 million ha (4.4% of the total land area), of which 88% is planted in *Pinus radiata* D. Don, commonly known as Monterey or radiata pine (Knowles 1991; Knowles *et al.* 1991). Grazing in saw log *Pinus radiata* plantation forests is common in New Zealand (Knowles 1991), and many such plantations have had a history of understorey grazing by cattle and sheep over the last 20 years. Initially seen as a supplementary feed during winter or drought, grazing has increasingly become accepted as a routine silvicultural tool (Knowles 1991).

High or low density planting of trees by farmers has become a common land use practice in recent years as a means of income diversification and/or erosion control (Pollock *et al.* 1994). Planting widely spaced trees has led to the establishment of several trials to evaluate the value of such silvo-pastoral systems (Yunusa *et al.* 1995). Forestry earnings have increased, with timber production predicted to reach 25 million cubic metres by 2015 (Pottinger 1993). Farm forestry in New Zealand is often more profitable than farming or forestry alone (Knowles 1991).

There are several published reviews on agroforestry which provide an array of information on tree-crop systems (Wolters 1982; Cameron *et al.* 1989; Nair and Dagar 1991; Stür and Shelton 1991; Wilson and Ludlow 1991; Bird *et al.* 1992; Atta-Krah 1993; Ong 1996). However, very few studies have looked at overall pasture production under tree plantations and in shelterbelts (Gregory 1995). Knowledge of interactions in tree-pasture systems that may help to maintain sound and sustained pasture production under trees is limited. Likewise, knowledge on the impact of land use changes from pasture to exotic forest plantations on soil properties, fertility, and water quality is also limited (Parfitt *et al.* 1997).

Most of the information in New Zealand is associated with *Pinus radiata* based systems (Knowles *et al.* 1991). Studies on *Pinus radiata* indicated that understorey herbage yield decreased as crown density increased (Anderson and Batini 1983; Pollock *et al.* 1994; Hawke and Knowles 1997). Long-term research at Tikitere, New Zealand, about the effect of *Pinus radiata* on pasture production also revealed an increased loss of pasture production associated with increased density, age and slash of trees (Knowles *et al.* 1995; Hawke and Knowles 1997).

Pasture production is also reduced under deciduous trees (Ditschal *et al.* 1997), but in contrast to *Pinus radiata* plantations this can be improved by pruning trees, by shortening rotations, and through coppice management (New 1985). Pasture production under deciduous tree is considerably higher than on equivalent spaced *Pinus species* (Miller *et al.* 1996). Most importantly, deciduous trees have considerable potential for use in agroforestry systems as they use growth resources for only part of the year, thus reducing competition with pastures or crops (Newman 1997). Moreover, deciduous trees also provide pastoral farms with greater resilience to drought (Treeby 1978).

Soil erosion is common in New Zealand soils (Kelliher *et al.* 1995), mostly as a consequence of forest clearing for agriculture (Trustrum and Blaschke 1992). Besides *Pinus radiata*, broadleaved tree species like poplars have been used in erosion control (NZMF 1995; Maclaren 1993). Studies on broadleaved trees, (e.g. poplars) revealed that they increased soil organic matter and nutrient status of the soil as well as helping to increase the population of earthworms (Bowersox and Ward 1977; Jaswal *et al.* 1993; Thevathasan and Gordon 1997). There is little detailed information associated with the role of deciduous trees in understorey pasture production (Wall *et al.* 1997). This emphasizes the need to study the effect of management practices on deciduous based tree-pasture systems.

2.2.3 Relationships between trees, pastures, and animal components

Trees and their associated pasture understorey will compete for light, water and mineral nutrients, and livestock will have an impact on both the trees and pastures (Cameron *et al.* 1989).

Relationships between trees, pastures, and animals on farmland have been studied in various research works (Hay 1987; Richardson *et al.* 1993). The relationships are dependent on tree density (Hawke 1991; Eason *et al.* 1997) and the trees, pasture and animal species involved (Fraser and Rowarth 1994; Casler *et al.* 1998).

Work by Hawke (1991) with pine agroforestry in New Zealand revealed that lower tree density allowed pasture production to occur well into the rotation (tree age 15 years) to the extent that at 100 stems/ha, pasture growth was 32% that of open pasture (no trees). Higher tree density, such as 400-600 stems per hectare reduced pasture production as well as sheep carrying capacity compared to open sward (Pollock *et al.* 1997). Bird *et al.* (1995) reported that nutritive value of pasture under *Pinus* agroforestry systems decreased along with animal production. This could be due to a number of factors including: increased shading resulting in reduced pasture production, changing species composition, accumulation of decaying pine needles, and the addition of a relatively indigestible component to the diet (i.e. pine needles).

In the United Kingdom, under 100-400 stems/ha of sycamore and hybrid larch, there was no reduction in animal production even after eight years, despite interception of up to 10% of total PAR by the developing canopy (Eason *et al.* 1997). In fact, pruned canopies result in more herbage production (Sibbald *et al.* 1991). This shows that performance of grazing animals under forestry could depend on the species of tree. It may be advantageous to use broadleaved species for long term grazing. Calzadilla *et al.* (1992) concluded from research about performance of sheep with controlled grazing under a pole stage broadleaved plantation, that after 6 years of forest pasture the grazing was still economic but was approaching the end of its efficiency. Thinning affects cover and species composition, but the response could be related to the individual species involved (Papanastasis *et al.* 1995).

Apart from direct grazing activity under the trees, trees may provide environmental and nutritional advantages for animals. Agroforestry has scope to alleviate adverse climatic effects on livestock through the provision of both shelter and pasture (Djimde *et al.* 1989). Shade, windbreaks, shelterbelts, and trees in pasture all have potential for alleviating climatic stress on animals and increasing pasture production (Radcliffe 1983; 1985; Djimde *et al.* 1989; Gregory 1995) as well as improving milk yield, milk fat, freedom from mastitis, and conception rates in dairy cattle, and growth rate in fattening cattle (Gregory 1995). Thus, Sturrock (1982; 1990) suggested the research direction for, and possible improvements of, shelter trees in New Zealand.

Performance of grazing animals under agroforestry in general declines over time (Percival *et al.* 1984a; 1984b; Hawke 1991). Generally, herbaceous yield decreases as tree basal area increases (Scanlan and Burrows 1990) which affects the quality (Percival *et al.* 1984a) and quantity of feeds, voluntary feed intake (Samarakoon *et al.* 1990a), and animal performance. Specific edapho-climatic conditions and the growth rate of trees are the factors determining the point at which herbage production starts to decline sharply (Sibbald *et al.* 1991; Papanastasis *et al.* 1995). The effect of these factors on animal performance will vary according to the nature of tree species, and species of animal involved. However, increased production of pastures under trees in the summer and autumn which could sometimes be higher in crude protein level and dry matter digestibility as well depending on season (Rhodes and Sharrow 1990), can be used to advantage in fitting pasture availability to animal requirements (Hawke 1991).

2.2.4 Tree pasture interactions

Vandenbeldt *et al.* (1990) critically examined three types of tree/crop interactions: positive, negative, and complex, and recommended the study of the processes and mechanisms involved in tree/crop interactions. Out of the several mechanisms, inter-root competition is likely to have the major effect on plant production (Campbell 1989). According to Callaway *et al.* (1991) positive effects elicited by litterfall and negative effects of shallow roots could vary according to tree species and may affect understorey productivity. Under competitive conditions, only understory species which are best equipped to capture resources and maximize production can prevail (Al-Mufti *et al.* 1977). Forage production is a function of tree density and light penetration, with light penetration decreasing with increasing tree density (Acciaresi *et al.* 1994).

The level of interaction between trees and the productivity of grass understorey is influenced by the species of tree (Stuart-Hill and Tainton 1989; Shelton *et al.* 1991), canopy cover (Atta-Krah 1993), and distance from the tree (Hawke and Tombleson 1993) as well as limiting environmental factors and their interrelationship in the system (Cameron *et al.* 1989). The tree species and seasonal variation also exhibit an interaction, as pasture growth was significantly depressed near broad-leaved poplars and willows during spring and summer in New Zealand (Gilchrist *et al.* 1993). Suppression of grass, clover and lotus yield near planted broad-leaved trees was estimated to be up to 12-23% during summer in New Zealand (Christ *et al.* 1993).

Several research reports from Australia and elsewhere in the world suggest that leguminous trees may be beneficial to understorey herbage and this type of effect could be species and ecosystem specific (Wilson *et al.* 1990). Type of tree also plays a significant interactive role with understorey crops (Dhukia *et al.* 1989). Shading by *Salix* had a weak influence on vegetation cover, and the zones of this effect did not coincide with the crown outline (Yastrebov 1989). Eucalypts appear to depress pasture growth under their canopy more than poplars and willows (Christ *et al.* 1993). Savanna trees competed more intensely with understorey plants at wetter sites, where their roots terminated in or near crown zones, than at drier sites, where their roots extended farther into open grassland (Belsky 1994).

Differences in the density of the tree cover are likely to be the main source of variation in pasture production (Eastham *et al.* 1990; Robinson, 1991; Lee *et al.* 1992; Kellas *et al.* 1995). Tree density in agroforestry affects water use efficiency of both tree and pasture components, reducing evaporation by pasture in densely planted trees. Therefore, pasture production could be higher at the intermediate tree densities (Eastham *et al.* 1990).

Likewise, length of the pasture measurement periods, shade tolerance of pasture species, (Gadgil *et al.* 1988; Robinson 1991), differences in growth season (Shelton *et al.* 1991; Gilchrist *et al.* 1993), differences in soil moisture and fertility of soils as well as species mixture (West *et al.* 1988; Campbell 1989; Shelton *et al.* 1991; Wild *et al.* 1993; Farnham and George 1994; Reategui *et al.* 1995), the nature of below ground interaction of the tree and crops (Ong *et al.* 1991), the stage of development of the silvo-pastoral system (Qarro and Montard 1989; Stuart-Hill and Tainton 1989; Campbell *et al.* 1994; Dunn *et al.*1994), and effects of silvopastoral practices like thinning and pruning (Kellas *et al.*1995) may all affect pasture performance. Established grasses also affect growth of companion legumes by reducing light along with competing for water and nutrients (Dear *et al.* 1998).

Management strategies such as fertilizer application and different cutting and grazing regimes may also be designed to alter the competitive balance (Campbell 1989), which also depends on the level of tree and pasture interactions (Sukanten *et al.* 1993). Having the correct tree species coupled with appropriate density and management is essential for a highly productive tree-pasture system (Atta-Krah 1993).

2.3 Production and persistence of understorey pasture

Since herbage production is inversely related to tree density, maximum yields of herbage would necessitate thinning of trees (Beale 1973). Therefore, this review of production and persistence of understorey pasture is mostly focused on the role of light (Everson *et al.* 1988; Wilson 1997). This is because understanding the differences in whole plant carbon gain, growth and reproduction success (Givnish 1988) and the effect of light environment on leaf area, tillers, and frequency of species (Garnier and Roy 1988) could be helpful in understanding the adaptations and persistence of species in shaded environments.

2.3.1 Pasture species and shade tolerance

Shade tolerance and avoidance are the alternative strategies plants use to adapt to shade. Shade avoiders respond to shade by stem extension at the cost of leaf development. Tolerators concentrate mainly on leaf development, perceive mainly light quantity and increase their photosynthetic efficiency upon shading (Smith 1981). For plants to survive in low light, leaves must be capable of trapping the available light and converting it into energy with the highest possible efficiency (Ninemets 1997).

Plants respond to shading in general by partitioning dry matter to maintain or increase leaf area and stem length (Kephart and Buxton 1993; Grubb *et al.* 1996), by decreasing leaf thickness (Kephart and Buxton 1993), and decreasing dry matter partitioning for root growth (Grubb *et al.* 1996). Likewise, high photosynthetic efficiency through maximum interception of radiation, regeneration of a large leaf area (Wilson and Wild 1991; Walters and Reich 1996), and lower respiration rates (Björkman 1981; Teskey and Shrestha 1985) under low light are common processes for the success of plants under shade. Moreover, responses of plant characters to shade change as the plant grows (Taylor *et al.* 1968).

More than 29 pasture species are available to farmers in New Zealand (Charlton and Belgrave 1992), but these species perform differently under shade (Hunt and Easton 1989). For example, forage production under *Pinus radiata* trees at 400-600 stems/ha, aged 4-6 years in New Zealand (Pollock *et al.* 1997) was highest for lucerne (24.6 t DM/ha) followed by phalaris/clover (22.8 t DM/ha) and cocksfoot/clover (21.3 t DM/ha), and least for perennial ryegrass/clover (17.8 t DM/ha) and perennial ryegrass only pasture (Pollock *et al.* 1997). Research results also showed good persistence of lotus in *Pinus radiata* agroforests (Gadgil *et al.* 1986). Perennial ryegrass has reduced photosynthesis in shade than in the open (Woledge 1972), and Ong and Marshall (1979) reported that its tillers can not withstand shade for more than 5 weeks.

Responses of plants to shade could vary according to the heterogeneity of the soil. Cui and Caldwell (1997) reported that effects of shade were most pronounced if species were foraging for nutrients such as phosphorus, in heterogeneous soils.

Genetic variation may also affect the production potential of species under shade. Bretagnolle and Thompson (1996) reported that diploid cocksfoot (2n=2x=14) produced more leaves more rapidly during winter than tetraploid species (2n=4x=28) under 25% shaded and unfertilized conditions. Since leaf production is correlated with tiller production, diploid plants could be more productive than tetraploid in the winter (Bretagnolle and Thompson 1996), though this may equally depend on the habitat of the species. The authors further indicated that diploids are mainly confined to the forest floors, whereas tetraploids also occur in open fields.

Response of pasture species to shade could also be discussed in relation to the different photosynthetic pathways. For example, C_4 grasses have greater light-saturated photosynthetic rates, and are prone to reduced assimilation even with minimal shading while C_3 plants have lower light-saturated photosynthetic rates with a lower conversion coefficient for water (4 kg mm^{-1} Kpa^{-1} for C_3 compared with 8 for C_4) (Squire 1990).

This indicates that C_3 plants are more likely to tolerate a shaded environment than C_4 plants.

2.3.1.1 Intensity of light and pasture productivity

Light provides the energy for photosynthesis, and hence for plant growth (Cooper and Tainton 1968; Monteith 1981), but the effect of a particular energy input will be influenced by both its intensity and duration (Cooper and Tainton 1968). Effects of light intensity on growth, anatomy and quality of grasses have been widely discussed (Deinum *et al.* 1996).

Solar radiation is transmitted by most leaves and is absorbed in the uppermost part of the canopy (Caldwell 1987). Light availability under the canopy is estimated by measuring intercepted photosynthetically active radiation (PAR). Measuring transmitted PAR accurately is difficult, as the intensity of transmitted light is highly variable (Moss 1992) due to differences in the canopy and available sunlight. Table (2.1) shows the variation in available total photons (400-800nm) and R:FR in nature (derived from Smith 1982).

Table 2.1 Total photons (400-800 nm) and R:FR in nature.

	μmoles photons m^{-2} s^{-1}	R:FR
Daylight	1900	1.19
Sunset	26.6	0.96
Moonlight	0.005	0.94
North aspect	480	1.3
Ivy canopy	17.7	0.13

Grassland production is based on the conversion of solar energy, CO_2, soil nutrients, and water into herbage. The basic climatic factor limiting production, however, is the input of solar energy (Cooper and Tainton 1968; Saeb∅ and Mortensen 1995).

The influence of light intensity on growth rate has often been examined by using natural daylight modified by shading. In general, all components of growth are depressed by a low energy input, but root growth and tillering are particularly dependent on carbohydrate supply (Cooper and Tainton 1968).

The development of the photosynthetic area is influenced by both light intensity (Henderson and Robinson 1982) and photoperiod (Solhaug 1991). Leaf area ratio and leaf weight ratio of temperate pasture species, for example perennial ryegrass and cocksfoot, are decreased at high light intensities. At the same time, leaf length and specific leaf area are also reduced. Chlorophyll content per unit area of leaf increases, as the light intensity is raised (Cooper and Tainton 1968).

Decreased dry matter production under reduced light intensity has been reported in many grass and legume species (Ludlow *et al.* 1974; Deinum *et al.* 1996). The magnitude of the effect on growth depends on the stage of growth, on concurrent temperature, moisture, nutrient stresses (Eriksen *et al.* 1981), and season and age of the plant (Davis and Evans 1990). Low intensity of light (Shade) has a marked effect on the productive performance of both temperate (Hawke 1991; Kephart *et al.*1992) and tropical pasture species (Senanayake 1995). The response to low-light stress is generally an increase in leaf area, and changes in physiological processes (Sanderson *et al.* 1997), to a greater extent than those caused by defoliation (Havstad 1997). There are also effects on nutritive value and chemical composition (Deinum *et al.* 1968). Decrease in PAR does not always result in a proportionate decrease in growth because of the compensatory changes in plant development. For example, a change in specific leaf area (Mitchell and Woodward 1988), which normally increases with reduced light intensity, is a commonly known adaptive mechanism by plants in shade. Nevertheless, intensity of light is one of the most critical factors determining production and persistence of pasture under a shaded environment.

2.3.1.2 Morphological adaptation of plants to shade (low light)

Plants respond to under shade by showing typical morphological responses, a phenomenon commonly known as phenotypic plasticity (Abrams 1994). For example, under shade orthotropic plants respond in the length of the inter-node of the shoots, in contrast to plagiotropic plants which adapt more in the length of the petiole (Huber and Hutchings 1997). This indicates that plants which grow vertically could have a higher degree of shade-induced plasticity than those which spread horizontally (Huber 1996; Huber and Hutchings 1997).

Common morphological responses of grasses to shade include: increased leaf-area ratio, increased shoot-to-root ratio (Cooper and Tainton 1968; Stür 1991; Kephart *et al.*1992) increased specific leaf area (SLA) (Grubb *et al.* 1996), and increased plant height and reduction in vegetative shoots (Park *et al.* 1988). Likewise, morphological responses of grasses that include decreased specific leaf weight, leaf blade thickness and shoot dry weight (Cooper and Tainton 1968; Stür 1991; Kephart *et al.*1992), etiolation of shoots and lower shoot densities (Iason and Hester 1993) have also been reported. Some of the characteristic differences between plants adapted to sun and shade environments are been summarised in Table 2.2.

Table 2.2 Characteristic differences between plants adapted or acclimated to sunny *v*. shady extremes in irradiance level (derived from Givnish 1988).

Trait	Sun	Shade
Leaf-level		
Photosynthetic light response		
Light-saturated rate	High	Low
Compensation irradiance	High	Low
Saturation irradiance	High	Low
Biochemistry		
N, Rubisco, and soluble protein/mass	High	Slightly lower
Chlorophyll a: chlorophyll b ratio	High	Low
Morphology		
Leaf mass/area	High	Low
Leaf thickness	High	Low
Leaf orientation	Erect	Horizontal
Stomatal density	High	Low
Canopy-level		
Leaf area index	High to low	Low
Asymmetric leaf bases	Very low	Infrequent
Plant-level		
Fractional allocation to leaves	Low	High
Fractional allocation to roots	High	Low
Reproductive effort	High	Low

Morphological adaptations of tropical grasses to shading such as stem elongation, and increased allocation of dry matter to shoots have also been reported (Wong *et al.* 1985). Leaf area of shaded leaf blades is maintained or increased at the expense of leaf thickness, producing thinner leaf blades. Thinning of leaf blades may result due to the reduction in cell size (Cooper and Tainton 1968; Kephart *et al* 1992; Kephart and Buxton 1993). However, increased leaf area expansion may allow limited photosynthate for growth of secondary cell walls, which may cause lower cell wall concentration and increased forage quality (Kephart *et al.* 1992).

2.3.1.3 Persistency of pasture under shade

Decreasing irradiance reduces the growth of pasture species and influences production under plantations (Shelton *et al.* 1987), as well as modified forest canopies (Chen 1993). Very few high yielding grass species have the potential to grow under shade, and with few exceptions, they do not persist well under shading and grazing, and are usually replaced by naturalized species as well as broad leaf weeds (Shelton *et al.* 1987). This raises the question about the relationship between growth and persistence of plant species under shade. Factors affecting the persistence of pastures are discussed in a following section (section 2.3.1.5).

2.3.1.4 Light quality in relation to survival and persistency of shaded plants

The quality of light also affects herbage performance. Holmes (1981) reviewed in detail the effects of light quality and quantity on plant performance, and commented on the role of green leaf canopies in reducing the quantity of radiation penetrating to ground level, and in modifying the spectral quality of light as well (Holmes 1981).

Within the solar spectrum, radiation between 350 and 730nm is photosynthetically effective, and several wavebands like blue (400-500nm), red (550-700nm) and far-red (700-800nm) are biologically active. It is known that red and far-red controls photo conversion of phytochrome, and the red:far-red (R:FR) ratio, which is the ratio of photon flux density in 10nm wavebands between 660 and 730nm, is considered a relevant parameter for plant physiology (Pontailler and Genty 1996). Red:far-red (R:FR) transmittance ratio was relatively unchanged during summer and autumn under an oak canopy (McCree 1981; Hughes *et al.* 1985).

The effect of R:FR ratio on vegetation canopies has been widely reviewed (Smith 1982; Deregibus *et al.*1983; Casal *et al.* 1985; Casal *et al.* 1987a; Casal *et al.* 1990; Arnone III and Korner 1993; Murphy and Briske 1994; Warringa and Kreuzer 1996; Jefferson and Muri 1997; Hay *et al.*1997). Keating and Carberry (1993) suggested that changes in light quality can change plant form, especially an increase in the FR:R ratio, particularly in shaded regions and at low solar elevation angles. Common effects are reduced branching and leaf production. Adjustments in leaf structure can result in thinner leaves with a more horizontal orientation. Photosynthetic rate per unit area of such leaves is lower under high light but greater under low light (Keating and Carberry 1993).

Reduction in the R:FR ratio under tree canopies may affect the understorey independently of the effects of reduced PAR (Arnone III and Korner 1993), but defoliation of pasture may help to increase the supply of red light and thereby the growth of young branches and buds of pasture plants (Teuber and Laidlaw 1996).

Longer leaves and shoots of grasses developed due to end of day R:FR, or low R:FR, while increased R:FR also increased in tiller extension (Deregibus *et al.* 1983; Casal *et al.* 1987a,1987b; Jefferson and Muri 1997). Low R:FR reduced tillering in *Lolium multiflorum* (Casal *et al.* 1985; Casal *et al.* 1986), but plant dry weight was unaffected (Casal *et al.* 1985). Low R:FR might preclude morphogenic responses to the density of species (Casal *et al.* 1986) as well.

Reduction in stolon growth and increased elongation of petioles of white clover in dense canopies (Thompson 1993) suggests that the stolon is the primary sensor of radiation, although white clover clones could differ in their responses to PAR and light quality (Solangaarachchi and Harper 1987). Delayed outgrowth of axillary buds of white clover by 0.5 plastochrons due to reduced R:FR light (minimum 0.27) at the apical bud indicates that legumes can also initiate localised responses to a heterogeneous light environment (Hay *et al.* 1997).

2.3.1.5 Factors affecting persistence of pasture under shade

The persistence of pastures under tree crops varies according to environmental conditions, and tree species and densities (Percival *et al.* 1984a; Pineiro and Perez 1988).

Density of tree plantation can affect the persistence of pastures (see Section 2.2.3). Research results show that perennial ryegrass and white clover established poorly and their yield declined with increasing tree densities of *Pinus radiata* over time (Percival *et al.* 1984a). Similarly lotus cv. 'Grasslands Maku' as a forest understorey, changed in composition to a mixture of Maku and lower fertility demanding grass such as Yorkshire fog and flat weeds (West *et al.* 1991). Sharrow (1991) reported a strong interaction between density and planting pattern of trees, with highly aggregated plantations better able to maintain forage production even at high tree density.

Sensitivity to the slash from silvicultural operations could be one factor that affects persistency of pasture. West *et al.* (1991) reported that slash had much less effect on forage availability on lotus based swards than on white clover based swards. In fact, Maku lotus had good growth and could persist at least for 8 years with or without cattle grazing (West *et al.* 1991). The success of perennial lotus species could also be related to their relative unpalatability compared with red and white clover, and their ability to compete with the resident weed population (Gadgil *et al.* 1986; 1988).

Seo *et al.* (1989) concluded that certain levels of shade (45%) and fertilizers could be used to sustain fodder production in woodland pastures for species like cocksfoot. This indicates the role of management practices in sustaining production of pasture under shade. Likewise, choice of suitable legumes in a mixture could be one way to cope with shade from companion grass species, in order to have better persistency. Hopkins *et al.* (1996) reported that lotus can be an alternative legume to white clover, especially for low soil nutrient.

2.3.1.6 Positive effects of shade on the understorey pastures

Shade can contribute positively to understorey pastures, especially in the tropical environments (Wilson *et al.* 1986), which are more likely to be driven by increasing mineralisation rates (Wilson and Wild 1991).

Cameron *et al.* (1989) reported that pasture production was not reduced under widely spaced eucalyptus trees. Belsky (1994) in a study of the influences of trees on Savanna productivity, reported that effects of shade could also be positive, depending on the nature of the limiting factors. Moreover, Belsky (1992) noted that in Savannas, trees increase the availability of nutrients in the herbaceous forage, due to improved nutrient cycling (Shelton *et al.* 1991). Similarly, soil under deciduous blue oak canopies had higher nitrogen turnover and inorganic nitrogen availability than open grassland (Jackson *et al.* 1990).

Tree shade can possibly conserve soil moisture, allowing better growth of the understorey through reducing evaporation. Ella *et al.* (1991) in agroforestry research of *Sesbania grandiflora, Calliandra calothyrsus, Gliricidia, and Leucaena with Digiteria, Panicum, Pennisetum purpureum, and P. clandistenum* under different cutting frequencies concluded that any factor that resulted in conservation of water contributed to increased plant productivity.

Certain species naturally may perform better in shade than others due to better ecotypes. Dry matter yields of *Paspalum pilosum* and *Stenotaphrum secundatum* (Toledo *et al.* 1989), and *Stenotaphrum secundatum* and *Axonopus compressus* were increased under low light transmission (Samarakoon *et al.* 1990b), the latter without reduction in nutritive quality. Both *S. secundatum* and *A. compressus* had a strong stoloniferous habit, with less culm elongation and stem development in tops resulting in better growth response under shade.

The concurrent decrease in cell wall content of *Panicum spp.* (Wilson and Wong 1982), and higher digestible organic matter of the whole crop at lower light intensity (Deinum *et al.* 1996), indicated that light intensity may affect forage quality. Moreover, Wilson *et al.* (1990), in their study with *Paspalum* under shade of *Eucalyptus grandis,* found that grass under the trees had a greater proportion of green leaf, greater concentration of N and K, and greater moisture content than grass in full sun. Similarly, higher dry matter yield of *Paspalum notatum* (Wilson *et al.* 1990), and green panic, Rhodes grass and speargrass under trees in a subtropical environment (Wilson 1996) than in open pasture, and adaptations of legumes like *Galactia elliottii* for higher production in shaded environments (Muire and Pitman 1989), indicate that shade can also stimulate pasture growth. Belsky (1994) under tropical conditions found trees increased understorey productivity by adding nutrients to the nutrient-limited systems, whereas shade increased productivity by reducing the temperature, evapo-transpiration, and conductance in species growing below tree crowns. Under certain tree species, the positive effects of soil enrichment and improved plant water relations will be greater than the negative effects of competition. However, Connor *et al.* (1989) reported that there was a marked drying under *Pinus radiata* indicating that improvement in soil moisture under trees does not always occurr.

2.3.1.7 Negative effects of shade on understorey pastures

Shading can also have a negative impact on the understorey pastures (Sections 2.2: 2.2.3, 2.2.4). For example, under *Pinus radiata* agroforestry systems, trees have a marked impact on the pasture by the age of 13 years (Bird *et al.* 1995). Those impacts are mostly due to changing pasture species composition, accumulation of decaying pine needles, and subsequent reduction in yields (Bird *et al.* 1995). Shading was the dominant factor responsible for decreased subterranean clover pasture growth under 15 years old pine trees (Anderson and Batini 1983).

Studies of grassland in a Korean forest also revealed that annual dry matter yield of *Dactylis glomerata*, *Phleum pratense*, *Lolium perenne* and *Trifolium repens* or a mixture dominated by *Dactylis glomerata* decreased by about 28-35% and 44-60% with 50% and 75% shade respectively (Park *et al.* 1987). Likewise, yield of *Axonopus* *affinis* and *Paspalum conjugatum* was reduced by about 38% and 27% respectively under shade (Toledo *et al.* 1989).

Shade also affects the nitrogen fixing ability of legumes. Sugawara *et al.* (1997) reported that nitrogen fixation by white clover was decreased considerably with shading (relative shading of 40% and 60%), through reduced nitrogen fixation and photosynthesis (Sugawara *et al.* 1997). Goh *et al.* (1996) reported that the nitrogen fixing capacity of pasture species altered under shade in an agroforestry trial in New Zealand. White clover in a perennial ryegrass and white clover pasture mix fixed more N under shade than other grass and clover pasture mixtures. However, differences in the rate of N fixation by clover under shade are not consistent.

2.3.1.8 Pruning of trees in relation to pasture production

The effective management of natural vegetation presupposes an understanding of the responses of the vegetation components to applied treatments (Walker *et al.* 1986). Thinning and pruning of trees is critical from the pasture productivity point of view, and varies according to species and the conditions applied. For example, according to Schacht *et al.* (1988), thinned stands of *Caatinga* could allow for high levels of forage production while maintaining moderate to high levels of wood production.

In general, pruning of trees allows penetration of more light to the pasture component. It can equally reduce competition with pastures in terms of other resources like water and nutrients. Pruning of branches may also reduce underground root competition with pastures. This situation varies with the nature of the tree species, and the stage, level, and severity of pruning. Very few such studies have been carried out (Walker *et al.* 1986) to determine the effects of tree pruning, and most available results are related only to the silvo-pastoral works of thinning stocks.

2.3.2 Fertilizer

Since pastures and trees are grown in association, they will compete for available nutrients, along with light and moisture. Thus improving soil fertility is important to enhance pasture establishment under trees, especially for poor fertility soils (Hunt and Easton 1989; Pinto *et al.* 1997).

Fertilizer application, especially nitrogen, has increased the nutritive value (Hight *et al.* 1968) as well as dry matter content of pasture (Steele *et al.* 1984). The differential effect of N deficiency on leaf extension rate and leaf appearance rate modifies sward structural characteristics (Belanger 1998). Application of nitrogen fertilizer can increase nitrogen content of grasses (Hight *et al.* 1968). Stopping nitrogen application can decrease tiller density and assimilate allocation to shoots (Van Loo *et al.* 1992). There could be a relationship between nitrogen concentration and soluble carbohydrate content as well (Alberda 1965).

In grassland development studies in a forest designed to investigate the effect of nitrogen fertilization, Seo *et al.* (1990) found highest dry matter yields of grasses (cocksfoot, perennial ryegrass, tall fescue, and kentucky bluegrass) at 240 kg N/ha. Earlier, Lee and Yun (1988) under similar conditions, with cocksfoot and tall fescue dominated pastures, under 80, 60, and 20% light, and low to high rates of nitrogen, phosphorus, and potassic fertilizers (100-350 kg/hectare each), reported increased tiller density, dry matter, and in-vitro digestibility, but found decreasing tiller density associated with increased level of shading. Lee (1991) in his study on the effects of shade and nitrogen fertilizer on cocksfoot reported that crude protein and nitrate-N contents were increased with shading and N application, while water soluble carbohydrate content was lowest with 70% shading and 300 kg N/ha. Likewise, Han *et al.* (1985) in their studies on the effects of fertilization on grass/clover mixtures under pines tree reported that plant height, chlorophyll content, and regrowth after the first cut were similar, but rate of leaf decay tended to increase and the proportion of prostrate plants in the sward increased markedly with increasing N rate, with the highest economic returns from 210-280 kg N, 100-150 kg P_2O_5, and 120-180 k_2O /ha.

2.3.2.1 Fertilizer responses of pasture species

Grasses preferentially take up soil nitrogen (Hight *et al.* 1968) but this may differ for pastures under shade (Campbell *et al.* 1994). This is because the effect of a lower light intensity (section 2.3.1.1) together with higher soil nitrate levels may cause variation between grasses and clovers (Hight *et al.* 1968) in their capacity to utilize nitrogen. At reduced radiation, grass growth was depressed at low or high levels of N, but at low N plant stands compensated for the low levels of irradiance by increasing the leaf area index to a value similar to that of the stand under full sun (Cruz 1996).

Legume performance under agroforestry declines in the long term largely due to the effects of reduced radiation (Balocchi and Phillips 1997). Moreover, evidence also suggests that differences in the response to fertilizer by plant species under shade is also likely to be driven by the differences in mineralization rates (Wilson and Wild 1994).

2.3.3 Defoliation

2.3.3.1 Defoliation responses of pasture species

Defoliation of pasture species may be by either cutting or grazing (Crawley 1983; Richards 1993). Defoliation influences the productivity and quality as well as the persistence of forages. Responses of plants to defoliation can be considered at two levels: physiological responses defined as occurring over a short period of time (Richards 1993), and morphological responses which are taken as being long term (Chapman and Lemaire 1993). When photosynthetic capacity is reduced due to defoliation, photosynthetic rate and nutrient uptake ability of the plant are reduced.

2.3.3.2 Defoliation and its effects on production

Production responses to defoliation vary due to differences in the environment and with pasture species (Kang *et al.* 1995; Donaghy *et al.* 1997), cutting height and cutting interval (Fulkerson and Slack 1995; Rutkowska and Lewicka 1995; Harris *et al.* 1997), season (Lawson *et al.* 1997), tree species (Ella *et al.* 1991), and defoliation management (Turner *et al.* 1998). For example, frequent defoliation of cocksfoot-white clover pasture during autumn in the United States resulted in greater nutritive value than mature stockpiled herbage (Turner *et al.* 1998). In general, severe defoliation in white clover alters the partitioning of assimilates more in favour of the stolon apex and less to the stolon itself irrespective of cultivar and harvesting occasions (Frankow-Lindberg 1997), and causes the loss of viability of axillary buds (Hay and Newton 1996).

2.3.3.3 Physiological changes in plants due to defoliation

After defoliation the allocation of photosynthate to roots reduces, but increases to shoot meristems and leaf growth regions (Bassmann and Dickmann 1985). This compensatory process of increased export from source to growing shoot sinks contributes to a rapid re-establishment of the photosynthetic canopy after defoliation (Richards 1993). But under shade, carbohydrate reserves are reduced with reduced light so defoliation of shaded swards could reduce its capacity for regrowth (Wong and Wilson 1980) due to continual decline in photosynthetic area and light interception, low total nonstructural carbohydrate yield in residual biomass after defoliation, as well as low tiller density (Wong and Stür 1996).

2.3.3.4 Defoliation and regrowth

The contribution of carbohydrate reserves to shoot regrowth of grasses after defoliation has been widely researched (Richards 1993; Wong and Stür 1996; Sanderson *et al.* 1997). High concentration of fructans in live enclosed leaves appear to be associated with survival after defoliation (Volaire and Gandoin 1996). Wong and Stür (1996) concluded that the concentration of total non-structural carbohydrate was a critical factor in the regrowth and survival of grasses in shaded environments. Sanderson *et al.* (1997) also extensively reviewed the remobilization of carbohydrates and noted that in many temperate grasses, fructan is the storage carbohydrate which is remobilised for regrowth of plants after defoliation. However, cocksfoot cultivars for drought surviving abilities in the Mediterranean dry lands, reported that there was no consistent relationship between water soluble carbohydrate reserves in the plant bases and recovery growth (Volaire and Gandoin 1996).

Level of nitrogen in the stubble could also be related to the growth of tissue after defoliation (Matsunaka *et al.* 1997; Sanderson *et al.* 1997). High tissue nitrogen concentration could be more important than level of reserve carbohydrate for alfalfa plants (Volaire and Gandoin 1996; Sanderson *et al.* 1997). But under shade, more frequent defoliation accentuates the detrimental effects to the plant. It could be due to progressive weakening of plants recovering from a low stubble leaf area (Wong and Wilson 1980) even though plants under shade adapt by reducing dark respiration (Ludlow *et al.* 1974), and through other adaptive changes like increased shoot/root ratio, larger leaves (Ludlow 1978), and higher leaf area index (Wong and Wilson 1980; Paez *et al.* 1997).

2.4 Brief introduction to pasture species used in the thesis

2.4.1 Grasses

2.4.1.1 *Dactylis glomerata* L. (Cocksfoot)

Cocksfoot , or orchardgrass is a tufted perennial with flattened tillers, the leaves of which are bluish green and without auricles (Langer 1990). The ligule is white and conspicuous, and leaf and sheath are both hairless. The inflorescence is a panicle bearing spikelets crowded together in clumps, each spikelet possesses 3-4 florets (Langer 1990).

Cocksfoot is grown in New Zealand (Lolicato and Rumball 1994; Rumball *et al.* 1997b) and other temperate regions of the world (Reed and Sutherland 1996). Cocksfoot is commonly mixed with compatible temperate pasture species (Grzegorczyk *et al.* 1996) like white clover, lotus (Annicchiarico *et al.* 1995; Aleksandrova 1995), and perennial ryegrass. It tends to dominate in heavily grazed pastures (Barker *et al.* 1985).

Cocksfoot is regarded as a medium soil fertility grass in New Zealand pasture (Daly 1990). 'Grassland Wana' is a persistent, prostrate cultivar regarded as having potential in agroforestry (Hocking 1990).

2.4.1.2 *Lolium perenne* L. (Perennial ryegrass)

Perennial ryegrass is the most important grass species in New Zealand, and is adapted to medium to high fertility soils, except in those areas with very dry summers (Hunt and Easton 1989). It is also an important species for pasture renewal (Charlton and Belgrave 1992).

Perennial ryegrass is a hairless plant with flattened tillers bearing dark leaves, which are very shiny on the lower surface. The auricles are very small and often absent, while the ligule is short and not conspicuous. The leaf sheath is bright red in colour at the base. The inflorescence of ryegrass is a spike, having spikelets each subtended by a single glume and containing 3-10 fertile florets (Langer 1990).

As a species perennial ryegrass is quite variable, as crosses within the species and with other ryegrass species readily occur. Since it has been a component of pastures for a long time, many strains have developed and some have been firmly established in the seed trade as well (Langer, 1990). 'Grasslands Nui', once the most widely sown cultivar in New Zealand, is a slightly more open plant with wider leaves. It is very acceptable to stock, persistent, and shows tolerance to rust infection (Langer 1990).

Perennial ryegrass and cocksfoot exhibit similar patterns of clonal growth and population structure, but not under tree canopies (Brock *et al.* 1996). Perennial ryegrass establishes faster than *Festuca rubra* under shade (Barker and Hunt 1997). Perennial ryegrass also tillers faster than cocksfoot under a wide range of condition, but not under heavy shading.

2.4.1.3 *Poa trivialis* L. (Poa trivialis)

Poa trivialis is more shade tolerant than perennial ryegrass and *Poa pratensis* (Bar and Schulz 1995). 'Laser' rough bluegrass, a cultivar of *Poa trivialis*, was released in 1988. It originates from plants selected from old turf in New Jersey, Pennsylvania, New York and California. Laser is leafy and moderately low growing. It has good tolerance of cool shade and wet soils (Hurley *et al.* 1990). *Poa trivialis* is a potential species for agroforestry (Hocking 1990). However, *Poa trivialis* is a low producing grass and is usually regarded as a weed of laxly grazed pastures on wet soils.

2.4.1.4 *Holcus lanatus* L. (Yorkshire fog)

Yorkshire fog is a perennial grass from Europe which is widely distributed in New Zealand (Madden and Harris 1961). The plant is often considered as a weed. However, it can be useful to grow under less fertile and relatively shaded conditions. Yorkshire fog is covered with dense hairs, the leaves are greyish green in colour and the leaf sheaths have distinct purple veins. The plant has no auricle, and the ligule is comparatively short and toothed (Madden and Harris 1961). The cultivar 'Massey Basyn' is widely used, it is productive and can be used in a range of soils and climates. However, its palatability is often questioned (Jacques 1974), particularly when it reaches the flowering stage, but the re-growth is usually well grazed. (Watt 1978). The main cause of unpalatability is probably lignification of the culm (Watt 1978). Yorkshire fog was one of the more persistent pasture species under *Pinus radiata* in the Tikitere agroforestry experiment (Knowles *et al.* 1995).

2.4.1.5 *Agrostis capillaris,* syn. *A. tenuis* Sibth. (Browntop)

Browntop is a perennial grass which originated from Europe, and has now become wide spread in New Zealand (Madden and Harris 1961). It is a loosely tufted grass with a dense bottom growth of leafy shoots. Plants in general spread laterally by short rhizomes. The leaf blades are erect and flat. The blade and sheath of browntop are hairless. Browntop is also found in pastures on fertile soils. 'Grasslands Muster' is the only cultivar of browntop bred for grazing (Madden and Harris 1961). Browntop is relatively intolerant of heavy shade (Brauen *et al.* 1993).

2.4.1.6 *Festuca arundinacea* Schreb. (Tall fescue)

Tall fescue is a perennial grass which was introduced to New Zealand from Europe one hundred years ago (Langer 1990). Its leaves are dark green in colour and are distinctly ribbed on the upper surface. The auricle is quite prominent, but the ligule is not. At flowering, tall fescue forms a large open panicle in which each spiklet contains 3-10 florets which separate at maturity (Langer 1990). Tall fescue is relatively slow to establish, however, it is considered more drought tolerant than perennial ryegrass. Tall fescue is adapted to wet and dry soils, but requires medium to high fertility (Anderson 1982).

2.4.2 Herbs

2.4.2.1 *Plantago lanceolata* L. (Plantain)

Plantain is a herb with a reputation as a plant with animal health benefits. 'Grasslands Lancelot' plantain is the first cultivar bred for pasture use in New Zealand and was given Plant Breeders Rights in 1993 (Rumball *et al.* 1997a). Naturalised plantain is a component of most hill pasture.

Grasslands Lancelot is a glabrous to pubescent perennial with a rosette growth form. Compared to the broadly based genepool, it is more uniform in growth and is more erect, with a higher number of vegetative shoots. The leaves are lanceolate to ovate lanceolate, entire to weakly toothed, 3-7 nerved, and with tips usually acuminate and inflexed (Rumball *et al.* 1997a).

When feeding on pure swards of plantain growth rates of animals are low. However, animal performances from plantain/legume mixtures have matched those of other species in legume mixtures (Rumball *et al.* 1997a). Plantain would be best used as a component of mixed swards, particularly for dry regions (Rumball *et al.* 1997a).

2.4.3 Legumes

2.4.3.1 *Trifolium repens* L. (White clover)

White clover is the most commonly grown pasture legume species in New Zealand. It has creeping stolons that root from internodes and have vertical leaf petioles bearing trifoliate leaves (Forde *et al.* 1989). White clover is a glabrous legume with leaflets that have a distinctly serrated margin and a light coloured centric leaf mark. The inflorescence is borne on a separate stem (peduncle) and consists of a varied number of individual flowers, usually 20-40, each having white to pink petals (Langer 1990). Clover plants form rosettes with a network of branched stolons which have the ability to develop roots as well as branches from each node, this imparts defoliation tolerance (Chapman 1983).

White clover is relatively intolerant of heavy shade, but has the potential for agroforestry under light shade.

2.4.3.2 *Trifolium subterraneum* L. (Subterranean clover)

Subterranean clover is an annual, which can bury its seeds below the soil surface. It is a highly prostrate plant but adventitious roots are absent (Langer 1990). The plant is densely hairy with a conspicuous stipule which often bears colourful marks. The inflorescence consists of 3-6 fertile, and a number of sterile flowers (Langer 1990). Subterranean clovers are adapted to growing during mild winters, and require medium fertility soils. It has higher shade tolerance than white clover.

2.4.3.3 *Lotus pedunculatus* Cav. (Lotus)

Lotus is a perennial legume of Europe, and, or North African origin, and has a long history of use in New Zealand (Levy 1970), particularly where soils are wet and infertile. It forms a crown and a tap root which are eventually supplemented by a network of rhizomes and fibrous roots (Lambert *et al.* 1974). The leaves are trifoliate but stipules are like leaflets resulting in a compound leaf with 5 leaflets. The inflorescence bears 4-6 flowers.

'Grasslands Maku' is the most widely grown cultivar. It is valued for its growth on acid, infertile soils, and also for erosion control. Maku tolerates low levels of phosphate which are common in hill based silvo-pastoral systems. It is widely used as ground cover under *Pinus radiata* (West *et al.* 1991; Balocchi and Phillips 1997).

2.5 Conclusions

Agroforestry is the land use science which deals with the interactions between trees, crops, and of both with animals in the same unit of land. It involves the coexistence of trees with agriculture, both in time and space. Agroforestry in New Zealand is dominated by silvo-pastoralism. Very few studies have looked at overall pasture production under trees and in New Zealand, most of those studies are confined to radiata pine. Deciduous trees have also been used in New Zealand, but information based on decidious silvo-pastoral systems in terms of their impact on pasture production, soil fertility, and many other critical issues is limited.

Strong interactions exist between trees, pastures, and animals which are largely dependent on tree density, and animal as well as pasture species. Generally, herbaceous yield under trees decreases as tree basal area increases. As well as low pasture production, herbage quality can be decreased resulting in reduced feed intake and performance of livestock. The effects of shade will, however, vary according to the nature of the tree species and species of animal involved.

Trees may provide environmental and nutritional advantages for animals through the provision of shelter and pasture in the same locality. Shade, windbreaks, shelterbelts, and trees in pasture all have potential for alleviating climatic stress on animals and increasing pasture production, but more work is needed to quantify these benefits.

Plants respond to shade by showing morphological responses such as an increase in specific leaf area, shoot to root ratio, and stem length, and a decrease in dry matter allocation to roots. Shade can have both positive and negative effects on understorey crops. Positive effects are, however, mostly seen in tropical environments, and could be largely due to the conservation of soil moisture and better mineralization processes. Negative effects are mostly associated with the reduction in transmitted light under the canopy. Response of plants to shading varies according to the morphology of the species, heterogeneity of soils, composition of pastures, genetic variation of plants as well as differences in photosynthetic pathways. Pasture species are also sensitive to the fertility status of soils, particularly to that of nitrogenous fertilizer. Responses to fertilizer by plant species under shade are commonly different from under full sun.

Light is the critical factor for growth and persistence of forage. Very few pasture species persist well under shading. It is assumed that under low light, successful plants will have high photosynthetic efficiency and allocation of resources to larger leaf areas.

Light intensity and quality are the two major aspects to consider in understanding the effects of light on pasture under a tree canopy. Quantity (intensity) of light, which is estimated by measuring intercepted photosynthetically active radiation (PAR), can affect growth as well as anatomy of a plant. In general, all components of growth are depressed by a low energy input, but root growth and tillering are particularly affected. The response to low-light stress generally results in changes in physiological processes. Effects on nutritive value and chemical composition also occur. Therefore, low intensity of light has a marked effect on the productive performance of pasture species.

Likewise, the quality of light also effects the herbage performance. It is known that red and far-red light controls photoconversion of phytochrome, and the red:far-red (R:FR) ratio, is considered a relevant parameter for plant physiology. Changes in light quality can affect tiller production, and also change the plant form, common effects of which could be reduced branching and thinner leaf production with a more horizontal orientation. It is also believed that reduction in the R:FR ratio under the canopy may affect the understorey independently of the effects of reduced PAR. However, many of these conclusions should be considered with caution in relation to the management of tree-pasture systems due to most of the evidence being drawn from experiments conducted with artificial shading.

Tree pasture interactions are a complex phenomenon to understand. The level of interaction is affected by tree density, canopy cover, seasonal variation, as well as the tree species. Under competitive conditions, only species that can capture more resources will persist. This indicates that the success of silvo-pastoral systems depends on the identification of suitable shade-tolerant species and management practices which are productive and ensure the persistence of the introduced pasture species.

Pasture productivity varies with species as well as the understorey environment (e.g. light, moisture, nutrients). Tree species with appropriate density and management are therefore essential to maintain pasture production under shade. Pruning of trees allows penetration of more light and reduces competition with pastures for resources. Aspects of defoliation management like defoliation height, interval, and effects of season also influence pasture productivity and persistence. Severe defoliation under shade is harmful in terms of growth and production. Defoliation stress depends on intensity and timing. Plants subjected to defoliation under shade exhibit a decline in photosynthetic area, low carbohydrate yield in residual biomass and decreased tiller density.

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3. Screening pasture species for shade tolerance

This chapter is based on a paper published in the Proceedings Agronomy Society of New Zealand 27:119-128 (Devkota *et al.* 1997)

3.1 Summary

The effects of shade on tillering ability as well as biomass production of hill pasture species which differed in morphology and for shade tolerance were determined. A split-plot design with four replicate blocks was employed for the experiment, in which five levels of shade were applied with in 1.25 × 0.84 × 0.45 m metal frames covered by Sarlon cloth to shade light from all directions. The main plot treatments were 14, 18, 27, 43, and 73% of the ambient photosynthetically active radiation (PAR). Ten different pasture species: *Dactylis glomerata* L. cv. Grasslands Wana; *Lolium perenne* L. cv. Grasslands Nui, high endophyte; *Holcus lanatus* L. cv. Massey Basyn; *Plantago lanceolata* L. cv. Grasslands Lancelot; *Festuca arundinacea* Schreb. cv. Grasslands Advance; *Agrostis capillaris* cv. Grasslands Muster; *Poa trivialis* cv. Sabre; *Trifolium repens* L. cv. Grasslands Tahora, *Trifolium subterraneum*, L. cv. Karridale; and *Lotus uliginosus* cv. Grasslands Maku were grown in pots as subplots. Twelve to fourteen plants were maintained per pot, and plants were watered daily. Water and fertilizer were non-limiting. The experiment ran from 5 June to 6 September 1996. Shoot dry weight, tillers/runners/stolons/number of branches per plant, and specific leaf area were determined at 15-day intervals for 5 harvests. At each harvest, plants were clipped to 50 mm height. Shade had a marked effect on tillering ability of all grass plants. However, mean tiller numbers per plant at the final harvest in the lowest PAR (14% ambient) were significantly higher ($P<0.0001$) for *Holcus lanatus* (4) and *Dactylis glomerata* (4) than for the other grass species. Similarly, *Lotus uliginosus* produced a higher ($P<0.0001$) number of branches (4) in 14% ambient PAR than other legumes. This trend was also observed for relative tiller numbers per plant (to that of 73% ambient PAR), where *Dactylis glomerata* had about 20% of its tiller production in the highest level of shade (14% ambient PAR) compared with *Lolium perenne* which had 5%. The results are discussed in terms of the desired attributes of shade tolerant pasture species.

3.2 Introduction

Large areas of land used for agriculture in New Zealand are susceptible to soil erosion (Clough and Hicks 1993). One technology to cope with this situation has been the planting of conservation trees, particularly poplars and willows (Anonymous 1995; Miller *et al.* 1996). The impact of shading by these trees on the productivity and persistence of hill pastures has received little research attention (Hawke 1991; Knowles 1991; Pollock *et al.*1994). However, research with widely spaced *Pinus radiata* has suggested that *Holcus lanatus* L., *Dactylis glomerata* L. and *Lotus uliginosus* are more shade tolerant than other hill pasture species (Seo *et al.* 1989; West *et al.* 1991).

Shading is the most significant factor determining the output from pastures grown in plantations (Shelton *et al.* 1987). Decreasing irradiance reduces the growth of pasture species and influences the outcome of competitive relations between plant species (Shelton *et al.* 1987). Low irradiance also affects morphological attributes of pasture species, through altered partitioning of photosynthate which may impact on productive performance (Kephart and Buxton 1993). The abilities of plants to regenerate leaf area to maximise interception of available radiation, and to generate tillers and stolons from main stems, are the critical factors that determine production and persistence of pasture species under low irradiance (Chen 1993).

Tree shade also affects the quality of transmitted light, decreasing the ratio of red to far red wavelengths (R:FR). Effects of R:FR on the productive performance of pasture plants have been widely reported (Thomson 1993; Murphy and Briske 1994; Teuber and Laidlaw 1996). In general, low R:FR stimulates morphological changes, such as increased plant height and reduced tillering.

Despite research on the impact of shade on the performance of pasture species (Eriksen and Whitney 1981; Samarakoon *et al.* 1990; Kephart and Buxton 1993) there is little information available on effects of a range of light intensities, particularly at low levels of transmitted light (high levels of shade) found under mature stands of conservation trees on the growth and morphology of hill pasture species. This study aimed to screen hill pasture species for their biomass and morphological responses to a range of levels of transmitted photosynthetically active radiation (PAR) in glasshouse conditions. This was part of a programme to determine suitable pasture species for silvo-pastoral systems based on deciduous trees. Accordingly, three legume species, six grass species, and one herb species were chosen for their different morphological characteristics and observed responses to shade.

3.3 Materials and methods

The experiment was conducted from 5 June to 6 September 1996 (95 days) at the Plant Growth Unit (PGU), Massey University. A split-plot design was used with four replicate blocks: the main plots were shade treatments and subplots were pasture species. Plants were grown under control conditions (without shade) or under a range of shade levels. Shade levels were imposed by differing densities of neutral shade cloth (Sarlon) supported on hollow metal frames (1.25×0.84×0.45 m) arranged on benches that were 0.9 m above the ground. The shade frames were aligned in a north-south direction and completely enclosed the pots. Five levels of transmitted photosynthetically active radiation (PAR: μmoles photons m^{-2} s^{-1}, 400-700 nm) were created. The transmitted PAR for the five treatments was 73, 43, 27, 18, and 14% of the ambient PAR under full sun light as determined on a daily basis from 1200 to 1300 h throughout the experiment using a LI-COR (Model LI-185) quantum sensor. The treatment with 73% ambient PAR, or 27% shade, was not covered by shade cloth, as this was the percentage of ambient PAR transmitted through the glasshouse. PAR was measured inside and outside the glasshouse simultaneously. Red:Far Red (R:FR) ratio during clear sky days was measured three times a day (morning, afternoon, and evening) with a Skye sensor, inside and outside the glasshouse, and under the shade cloth treatments.

Details of the pasture species and cultivars used are given in Table 3.1. Seeds of pasture species were sown on 4 June 1996 in PB 5 (3 litre capacity) black polypots filled with potting mix (80% tree bark + 20% pumice), and always kept under their allocated shade treatments. Dolomite 300 g, agricultural lime 300 g, iron sulphate 50 g, and Osmocote plus (16 N-3.5 P-10.8 K) 400 g per 100 litre were blended with the potting mix, which was rated for medium to long term (<9 months) greenhouse crops. Twelve to fourteen-

Table 3.1 Pasture species and cultivars used in the experiment.

Pasture species
1. White clover (*Trifolium repens* L.) cv. Grasslands Tahora 2. Lotus (*Lotus uliginosus*) cv. Grasslands Maku 3. Subterranean clover (*Trifolium subterraneum* L.) cv. Karridale 4. Browntop (*Agrostis capillaris*) cv. Grasslands Muster 5. Cocksfoot (*Dactylis glomerata* L.) cv. Grasslands Wana 6. Yorkshire fog (*Holcus lanatus* L.) cv. Massey Basyn 7. Tall fescue (*Festuca arundinacea* Schreb) cv. Grasslands Advance 8. Perennial ryegrass (*Lolium perenne* L.) cv. Grasslands Nui 9. Poa trivialis (*Poa trivialis*) cv. Sabre 10. Plantain (*Plantago lanceolata* L.) cv. Grasslands Lancelot

plants were maintained per pot, and plants were watered daily. The pots within cages were re-randomized weekly. Seeds of legumes were inoculated with the appropriate strain of Rhizobium.

The glasshouse temperature was maintained at 25^0C until seeds of all plants were fully germinated. Thereafter, day temperature was 15-17^0C and night temperature 8-10^0C.

The first harvest was on 10 July, 35 days after sowing. Subsequent harvests were on 25 July, 9 August, 23 August, and 6 September. At each harvest, all the plants were clipped to 50 mm above the media surface. Shoot material above 50 mm was dried at 70^0 C for 24 hours and weighed, and added to the above ground shoot mass at the final harvest. From the 25 July harvest onwards, five fully expanded leaves were randomly taken from each pot to measure leaf area, and leaf dry weight for estimation of specific leaf area. At each harvest, the number of tillers per pot for grasses and branches per pot for legumes were counted. Plant height and leaf/petiole length were also measured at each harvesting date. Specific leaf area was analysed by considering harvests as repeated measures. Statistical analysis was by analysis of variance using the GLM model of a SAS package (SAS Institute Inc. 1989), and the linear regression of shoot weight and of relative shoot weight with the percent of transmitted PAR using SAS. Treatment means were compared with Fisher's protected LSD test at $\alpha = 0.05$ (Steel and Torrie 1980). Data transformations were not required.

3.4 Results

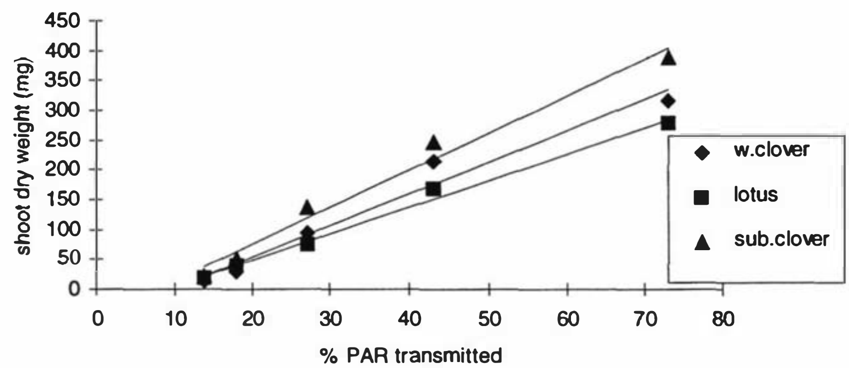
3.4.1 Growth environment

Mean PAR at noon in the shade treatments was 318, 188, 117, 81, and 60 μmoles photons m^{-2} s^{-1} resulting in 73, 43, 27, 18, and 14% PAR transmitted, respectively. The mean ambient PAR outside the glasshouse was 432 μmoles photons m^{-2} s^{-1}. R:FR ratio at noon inside the glasshouse was 1.3 to 1.4, while outside it was 1.4. There was no effect of shade cloth on R:FR.

3.4.2 Plant growth

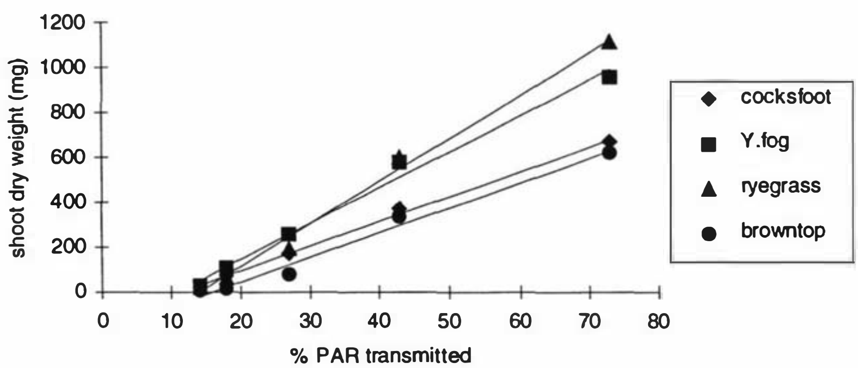
The shoot dry weight per plant of all legumes and grasses showed a significant ($P<0.0001$) linear increase with % PAR transmitted, producing their highest yield at 73% PAR and lowest at 14% PAR (Fig. 3.1). At 73% PAR, perennial ryegrass had the highest shoot dry weight per plant (1113.8 mg), and lotus the least (277.4 mg). However, at the lower level of PAR (14%), subterranean clover shoot dry weight (22.1 mg/plant) was higher ($P<0.0001$) than white clover (13.5 mg/plant), and comparatively better than that of lotus (17.4 mg/plant). Yorkshire fog (29.7 mg/plant) produced the highest shoot dry weight at low PAR (14%) followed by perennial ryegrass (24.7 mg/plant), and cocksfoot (22.3 mg/plant), whereas browntop (6.3 mg/plant) and Poa (10.8 mg/plant) had the lowest shoot dry weight of the grasses (Fig. 3.1).

The response of relative shoot dry weight of the species to shading differed from that for absolute shoot dry weight. The three legume species produced relatively more shoot dry weight at all levels of shade than the grass species and plantain (Fig. 3.2a, b, c). Within the legumes, the relative shoot dry weight of lotus increased in comparison to subterranean clover and white clover as the intensity of shade increased (Fig. 3.2a). Within the grass species, the relative shoot dry weight of cocksfoot and Yorkshire fog was greater than that of the other grass species at 14, 18 and 27% PAR transmitted (Fig. 3.2b, c).



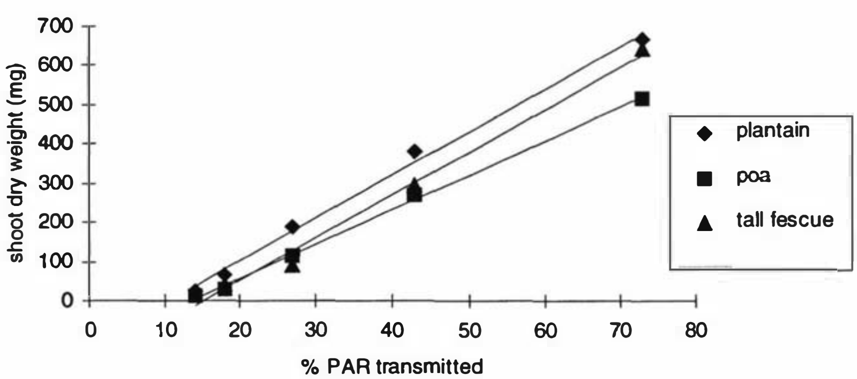
(a)

W .clover Y = 5.282X-51.69, R^2 = 0.96, p<0.01; Sub. Clover Y = 6.321X-49.412, R^2 = 0.98, p<0.001
Lotus Y = 4.449X-39.911, R^2 = 0.99, p<0.0001



(b)

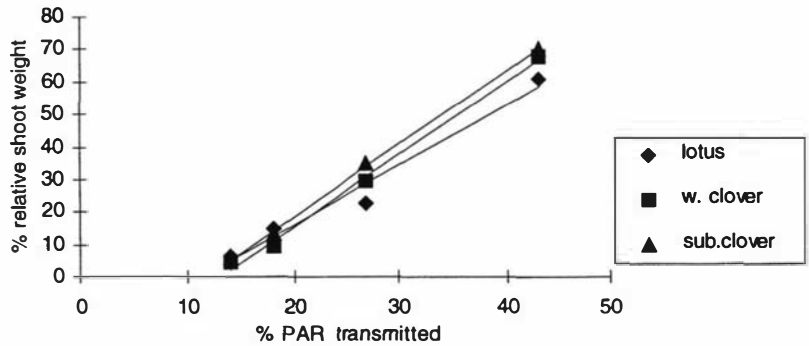
C.foot Y = 11.096X-127.96, R^2 = 0.99, p<0.0001; Rye Y = 19.097X-269.9, R^2 = 0.99, p<0.0001
Y.fog Y = 15.892X-169.15, R^2 = 0.99, p<0.0001; B.top Y = 11.033X-174.82, R^2 = 0.98, p<0.001



(c)

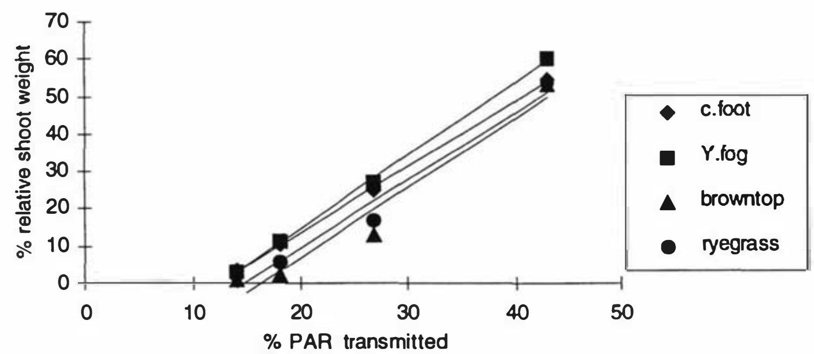
Plantain Y = 10.931X-117.45, R^2 = 0.99, p<0.0001; Poa Y =8.761X-118.25, R^2 = 0.99, p<0.0001
Tall fescue Y = 10.824X-162.2, R^2 = 0.99, p<0.01

Figure 3.1 Effects of different levels of % PAR transmitted on shoot dry weight of (a) legumes, (b) hill grass species, and (c) other species. Standard error of the mean (SEM) for species = 2.06.



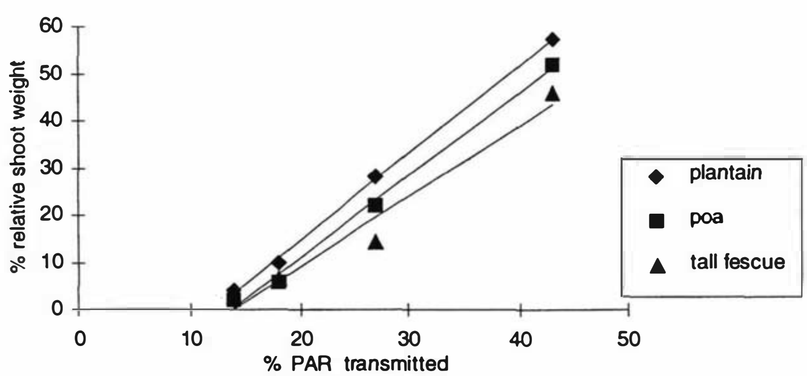
(a)

W .clover Y = 2.237X-29.264, $R^2 = 0.097$, $p<0.001$; Sub.clover Y = 2.241X-26.295, $R^2 = 0.99$, $p<0.001$
Lotus Y = 1.849X-20.987, $R^2 = 0.96$, $p<0.01$



(b)

C.foot Y = 1.768X-21.805, $R^2 = 0.99$, $p<0.001$; Rye Y = 1.804X-26.34, $R^2 = 0.97$, $p<0.01$
Y.fog Y = 1.964X-24.709, $R^2 = 0.99$, $p<0.001$; B.top Y = 1.859X-30.12, $R^2 = 0.94$, $p<0.05$



(c)

Plantain Y = 1.880X-22.659, $R^2 = 0.99$, $p<0.001$; Poa Y = 1.758X-24.366, $R^2 = 0.99$, $p<0.001$
Tall fescue Y = 1.499X-20.968, $R^2 = 0.96$, $p<0.01$

Figure 3.2 Effects of different levels of %PAR transmitted on relative (to that of 73% PAR transmitted) shoot dry weight of (a) legumes, (b) hill grass species, and (c) other species. Standard error of the mean (SEM) for species = 0.3.

3.4.3 Specific Leaf Area (SLA)

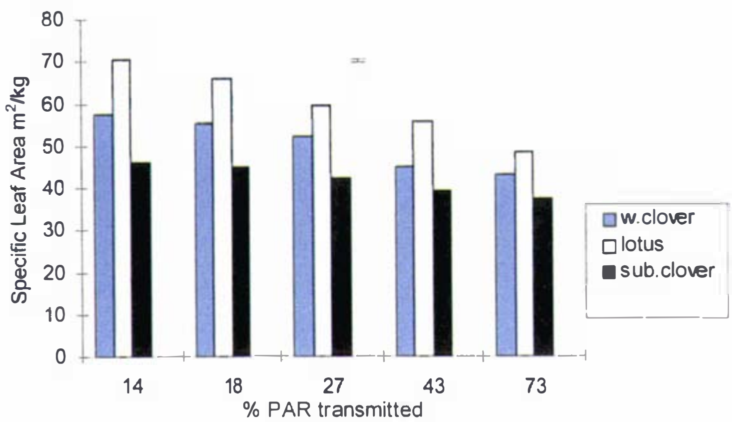
Specific leaf area over all harvests increased (P<0.0001) with decreasing % PAR transmitted for all species. There was a significant interaction between shade level and species. The SLA of subterranean clover and cocksfoot were comparatively unresponsive to the % PAR transmitted, whereas the SLA of Yorkshire fog increased at only 14% PAR transmitted (Fig 3.3a, b). On the other hand, the SLA of Poa, and browntop increased as % PAR decreased, but at 14% PAR their SLA was less than at 27% PAR (Fig 3.3c). The SLA of white clover, lotus, perennial ryegrass, tall fescue and plantain all increased with decreasing % PAR (Fig 3.3a, b, c).

3.4.4 Leaf area

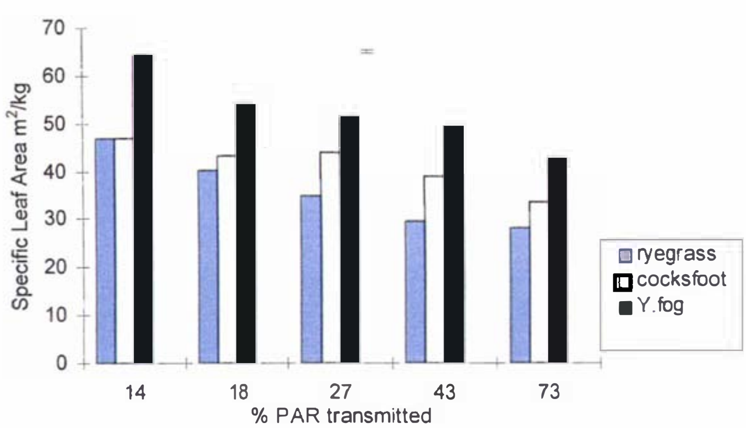
Per plant leaf area over all harvests also increased significantly (P<0.0001) with increasing PAR in all pasture species (Table 3.2). In 73% PAR, Yorkshire fog had the highest leaf area ($118.7\times10^{-4}m^2$) followed by perennial ryegrass (96.0×10^{-4} m^2) and cocksfoot ($94.7\times10^{-4}m^2$) while lotus had the lowest ($41.5\times10^{-4}m^2$). However, under dense shade (14% PAR), the highest leaf area was produced by Yokshire fog ($8.0\times10^{-4}m^2$) which was followed by lotus ($6.3\times10^{-4}m^2$), plantain ($5.0\times10^{-4}m^2$) and cocksfoot ($3.8\times10^{-4}m^2$). Browntop, Poa and tall fescue produced lowest leaf area (Table 3.2).

3.4.5 Tiller and branch numbers per plant

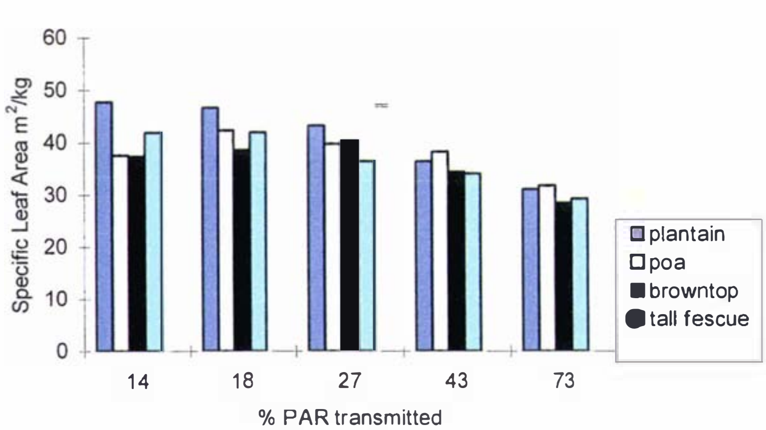
The main effects and the interaction between shade and species for tiller and branch numbers per plant were significantly different (P<0.0001) in absolute as well as in relative terms (Table 3.2). At final harvest, the highest number of tillers in 73% ambient PAR was produced by Yorkshire fog (39) followed by Poa (35) and browntop (30). Under the highest shade (14% ambient PAR transmitted), cocksfoot and Yorkshire fog and lotus produced the greatest number of tillers/branches (4), while subterranean clover, white clover, plantain and tall fescue did not produce any branches/tillers.



(a)



(b)



(c)

Figure 3.3 Specific leaf area (m^2/kg) of (a) legumes, (b) hill grass species, and (c) other species by repeated analysis. Vertical bar represents standard error of the mean for species (0.29).

Grasses like Poa, browntop and Yorkshire fog produced more number of tillers than the number of branches produced by legumes in 73 and 43% ambient PAR. This trend continued, for cocksfoot, Yorkshire fog, and Poa, as PAR decreased to 27 and 18% ambient PAR (increased shade). However, at the lowest PAR level (14% transmission), lotus, Yorkshire fog, and cocksfoot all produced a similar number of branches or tillers, whereas the number of tillers produced by Poa was lower. Among the grasses, ryegrass produced one tiller per plant, and tall fescue none in 14% ambient PAR (Table 3.2).

Among legumes, lotus always produced a higher number of branches per plant than white clover and subterranean clover in 73% (27% shade) to 18% (86% shade) ambient PAR. However, at 14% ambient PAR, only lotus produced branches (Table 3.2).

The response of relative tiller or branch numbers to PAR was different from absolute tiller or branch numbers. Relative to 73% PAR, browntop (99%) followed by lotus (85%), subterranean clover (78%) cocksfoot (76%), and white clover (76%) produced more tillers or branches at 43% ambient PAR. All other species produced about 60-70% of the tillers or branches at 43% ambient PAR relative to 73% ambient PAR. At 27, 18 and 14% ambient PAR, cocksfoot produced relatively more tillers than the other species (Table 3.2). The relative tillering of Yorkshire fog and Poa was similar at the three lower levels of PAR, intermediate between that of cocksfoot and tall fescue and ryegrass (Table 3.2). Among the legumes, relative branching was decreased by low PAR in a similar fashion to the better performed grasses, the exception being at 14% PAR where lotus was the least affected species after cocksfoot, but white and subterranean clovers produced no branches (Table 3.2).

3.4.6 Ranking pasture species for shade tolerance

Ranking of pasture species for shade tolerance on the basis of relative tillers or branches per plant and leaf area per plant in light shade (43 % ambient PAR) and in dense shade (14% ambient PAR) indicated that Yorkshire fog and cocksfoot among the grasses and lotus of the legumes were the most shade tolerant. Browntop was shade tolerant in light shade, but tall fescue was the least shade tolerant species at 14% ambient PAR (Table 3.3). Plantain was intermediate in its ranking for shade tolerance.

Table 3.2 Effects of shade on pasture species tiller or branch numbers per plant, their relative values (to that of 73% PAR), and leaf area at final harvest under glasshouse conditions, 1996.

% PAR / species	Tillers or branches per plant	Relative tillers or branches per plant	Leaf area ($m^2 \times 10^{-4}$) per plant
73% PAR			
White clover	14	-	42.7
Lotus	27	-	41.5
Subterranean clover	9	-	52.4
Browntop	30	-	72.7
Cocksfoot	18	-	94.7
Yorkshire fog	39	-	118.7
Tall fescue	15	-	66.8
Plantain	4	-	82.6
Perennial ryegrass	24	-	96.0
Poa trivialis	35	-	81.3
43% PAR			
White clover	11	76	33.5
Lotus	23	85	35.4
Subterranean clover	7	78	35.7
Browntop	30	99	56.4
Cocksfoot	14	76	71.1
Yorkshire fog	28	71	130.4
Tall fescue	11	73	38.8
Plantain	2	58	71.3
Perennial ryegrass	16	65	70.5
Poa trivialis	24	69	40.0
27% PAR			
White clover	7	50	20.1
Lotus	13	46	22.9
Subterranean clover	4	47	16.5
Browntop	9	31	13.0
Cocksfoot	12	65	34.3
Yorkshire fog	18	45	55.2
Tall fescue	4	25	10.4
Plantain	2	55	39.0
Perennial ryegrass	5	20	23.1
Poa trivialis	15	43	20.9
18% PAR			
White clover	3	23	5.2
Lotus	6	23	13.6
Subterranean clover	3	29	6.8
Browntop	3	11	1.8
Cocksfoot	7	36	17.1
Yorkshire fog	10	24	23.8
Tall fescue	3	22	3.8
Plantain	0	0	13.4
Perennial ryegrass	3	13	16.6
Poa trivialis	6	17	5.0
14% PAR			
White clover	0	0	2.4
Lotus	4	16	6.3
Subterranean clover	0	0	3.2
Browntop	2	8	0.4
Cocksfoot	4	19	3.8
Yorkshire fog	4	9	8.0
Tall fescue	0	0	0.9
Plantain	0	0	5.0
Perennial ryegrass	1	4	1.9
Poa trivialis	3	9	0.7
Analysis of variance			
Shade P (A)	<0.0001	<0.0001	<0.0001
Species P (B)	<0.0001	<0.0001	<0.0001
Interactions P (A *B)	<0.0001	<0.0001	<0.0001
LSD (P <0.05) for shade	0.81	4.15	2.90
LSD (P <0.05) for species	0.68	3.31	1.94
SEM for shade (d.f. = 4)	0.26	1.29 (d.f.=3)	0.94
SEM for species (d.f. = 9)	0.24	1.18 (d.f.=9)	0.69
SEM for A*B (d.f.= 36)	0.54	2.36 (d.f.=27)	1.55

LSD= Least significant difference, SEM= standard error of the mean, d.f.= degrees of freedom

Table 3.3 Rank of pasture species for their shade tolerance on the basis of relative tillers/branches per plant (to that of 73% PAR), and leaf area at 43% and 14% PAR at final harvest under glasshouse conditions, 1996.

Pasture species	43 % PAR		14 % PAR	
	Relative tillers or branches	Leaf area ($m^2 \times 10^{-4}$) per plant	Relative tillers or branches	Leaf area ($m^2 \times 10^{-4}$) per plant
Browntop	1	5	5	10
Lotus	2	9	2	2
Subterranean clover	3	8	7	5
Cocksfoot	4	3	1	4
White clover	4	10	7	6
Tall fescue	6	7	7	8
Yorkshire fog	7	1	3	1
Poa trivialis	8	6	3	9
Perennial ryegrass	9	4	6	7
Plantain	10	2	7	3

3.5 Discussion

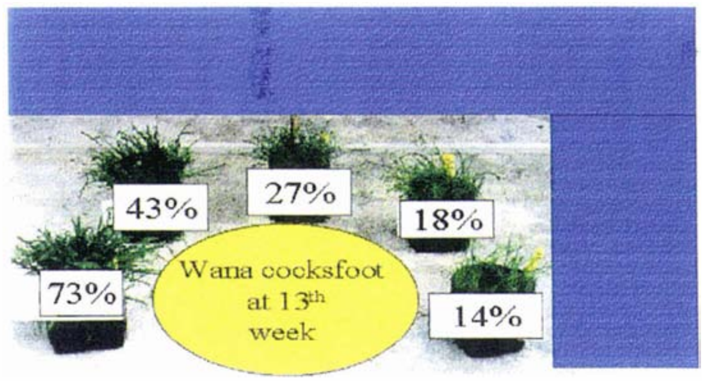
A shade tolerant pasture species needs to have good annual and seasonal dry matter production under defoliation, and to be able to regenerate. In this screening experiment the most shade tolerant species were those that maintained a comparatively high absolute and relative shoot yield in low PAR, due to maintaining a higher leaf area and higher relative numbers of tillers or branches. On these criteria Yorkshire fog and cocksfoot were the most shade tolerant grasses, and lotus the most shade tolerant legume. Among the grasses tall fescue, perennial ryegrass and Poa trivialis exhibited poor shade tolerance. Browntop was one of the lowest ranked grass species in heavy shade, but was more tolerant of light shade, in terms of tillering, but not in terms of shoot yield. Lotus was the most shade tolerant legume at higher shade levels, but its shoot yield was less than that of white clover and subterranean clover possibly because lotus takes longer to establish than other legumes, so the shoot yield of lotus in long term may not differ. Plantain ranked in the middle of the species screened for shade tolerance.

Seo *et al.* (1989) found that under pine trees, cocksfoot was the most shade tolerant species and that it persisted well. West *et al.* (1991) found that initial stands of pure

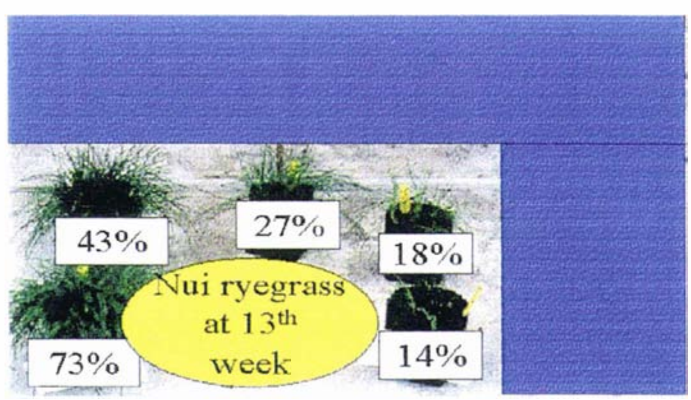
Maku lotus changed to progressively to a mixture of Yorkshire fog, and reported Yorkshire fog as a shade tolerant grass. Gadgil *et al.* (1986), West *et al.* (1988), and West *et al.* (1991) all indicated that lotus is one of the most successful legumes under shade, and can be readily established on a range of sites. This experiment also showed that lotus was the best legume to grow under heavy shade.

Perennial ryegrass (Figure 3.4a) and white clover were more affected by shade than cocksfoot (Figure 3.4b), Yorkshire fog and lotus. Percival *et al.* (1984) in their study on pasture yield under radiata pine, also reported that the yields of ryegrass and white clover declined with increasing tree density (higher level of shade) and these species were mainly replaced by annual grasses and Yorkshire fog. Likewise, Brauen *et al.* (1993) reported that browntop grows well only in full sun or moderate shade. Poa trivialis has been reported to have good tolerance of cool shade (Hurley *et al.* 1990; Bar and Schulz 1995), but this was not shown in this experiment. Similarly, subterranean clover has been reported by Lodge (1996) as being shade tolerant at seedling emergence, and as mature plants, and Pardini *et al.* (1995) found that subterranean clover under forest cover in productive and non-productive Mediterranean sites was shade tolerant. However, results from this experiment showed that subterranean clover may only be tolerant of moderate shade. Additionally, it was observed that subterranean clover etiolated faster in the shade in comparison to lotus, which would make it susceptible to having its growing points grazed.

The comparatively greater shoot dry weights of Yorkshire fog and cocksfoot in heavy shade could be associated with their ability to produce more tillers in absolute as well as in relative terms (Table 3.2). Yorkshire fog and cocksfoot also had a greater leaf area in heavy shade conditions than the other grasses. Cocksfoot specific leaf area was less responsive to low light than the other grasses, suggesting it has a different adaptive mechanism to low light. Possibly, the shade tolerance of lotus was related to its upright growing habit, which would facilitate greater interception of PAR in comparison to other legumes. Lotus can form new plants from rhizomes (West *et al.* 1991) which could also be an added advantage for better persistence under shade.



(a)



(b)

Figure 3.4 Performance of (a) cocksfoot and (b) perennial ryegrass at different PAR levels.

The relatively poor shade tolerance of white clover and perennial ryegrass appeared to result from the sensitivity of the stolons and tillers respectively, to low light. The shoot yield of these species was comparatively low at 14% PAR, due to the low number of leaves per plant resulting from the suppression of tillers or stolons. Absolute and relative numbers of tillers or branches per plant could be important characters that determine the shade tolerance of pasture species. In general, all components of growth are depressed by a low energy input, but tillering ability of plants is particularly dependent on carbohydrate supply (Cooper and Tainton 1968). Persistence of pasture species under shade could be evaluated on their ability to produce tillers or branches which will contribute to the accumulation of shoot weight. If a particular species is able to produce more tillers, it may also withstand defoliation better than those plants with less tillers/branches. To be agronomically useful a shade tolerant pasture species needs defoliation tolerance as well as shade tolerance.

The levels of ambient PAR transmitted in this experiment may not exactly represent the situation under conservation trees. Both light quantity and light quality signals could be important in the reactions of plants to shade. R:FR values for deciduous woodlands ranged from 0.36 to 0.97 (Smith 1982) in comparison to about 1.2 in open areas. Smith further pointed out that morphogenetic reactions occur in response to reductions in the total fluence rate. To validate the results of this glasshouse experiment, a field experiment and also the glasshouse experiment were conducted to determine the effects of shade on the selected pasture species. Chapter 4 describes results for the effects of different levels of shade on the cocksfoot selections and perennial ryegrass in glasshouse conditions (experiment 4.1), and also under alder tree shade created by pruning trees to different heights (experiment 4.2).

3.6 Conclusions

The results of this study demonstrated that shade had a marked effect on tillering as well as on shoot dry weight accumulation of hill pasture species under glasshouse conditions. However, mean tillers per plant in the lowest PAR (14%) level were significantly higher for cocksfoot than other species. Similarly, lotus was the best legume under the lowest PAR where it produced a higher ($P<0.0001$) number of branches than the other legumes. Likewise, relative tiller numbers per plant (to that of 73% PAR), also indicated that cocksfoot had about 20% of its tiller production in the highest level of shade (14% PAR) compared with perennial ryegrass which had only 5 %. The greater leaf area per plant of Yorkshire fog, cocksfoot and lotus also suggested that these pasture species are likely to be the most productive under the lowest PAR. The results indicated that pasture species like cocksfoot and lotus can be grown under heavy shade provided that other management practices are optimum.

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4. Performance of perennial ryegrass and cocksfoot cultivars under glasshouse conditions and alder shade

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Part of these results (Experiment 4.2) has been published in the Proceedings Agronomy Society of New Zealand 28:129-135 (Devkota *et al.* 1998)

4.1 Summary

The previous experiment indicated that cocksfoot had a superior performance in shade. In this experiment ten cocksfoot selections and Grasslands Nui perennial ryegrass were compared under three levels of shade in a glasshouse, and seven cocksfoot selections and Grasslands Nui perennial ryegrass were field tested under eleven year old alder trees in February 1997 at the Horticultural Research Centre, Aokautere, near Palmerston North. A split-plot design with four replicate blocks was employed for both experiments. The main plot treatments were three levels of available PAR (73%, 32% and 24% of full sunlight) for the glasshouse study, and three levels (77%, 27%, and 17%) for the field study, created by pruning lower branches of alder trees to different heights. The sub-plot treatments were pasture species, grown entirely under shade cloth for the glasshouse study, and grown at first in a glasshouse and then transferred in pots to the field for the field study. Four and five plants per pot were used in the glasshouse experiment and the field experiment, respectively. Water and fertilizer were non-limiting in both experiments. The first experiment ran from 18 December 1996 to 4 May 1997 (138 days) in the glasshouse, and the second experiment ran from 18 December 1996 to 2 February 1997 (46 days) in the glasshouse then 3 February to 30 April 1997 (87 days) in the field (total of 133 days). Tillers per plant and shoot dry weight were assessed five times at 15 day intervals, and leaf area, leaf dry weight, specific leaf area, for both experiments. Root dry weight per plant was also determined for the field experiment at the final harvest.

Shade affected perennial ryegrass more than all the cocksfoot selections, especially at the lowest PAR level, in both the glasshouse and the field experiment. Tillers per plant under tree shade, and also at the low PAR level in the glasshouse for perennial ryegrass were 18 compared with 28-29 ($P<0.0001$) for Wana cocksfoot and 24-27 for PG 74 at the final harvest. Leaf area per plant for perennial ryegrass was also significantly ($P<0.0001$) lower than for Wana cocksfoot, and similarly for relative specific leaf area (Experiment 4.2), and leaf dry weight at the low PAR level, indicating Wana and PG 74 are particularly shade tolerant cultivars. Specific leaf area, leaf area, and tillers per plant were key indicators of performance of the cocksfoot selections under heavy shade. The

results are discussed in terms of the attributes that relate to the performance of cocksfoot and perennial ryegrass in shaded environments such as silvo-pastoral systems.

4.2 Introduction

The planting of conservation trees (Miller *et al.* 1996) has become a common land use practice in recent years for erosion control, income diversification, or both (Pollock *et al.* 1994). When trees are planted primarily for erosion control rather than timber production then income is affected by the effect of the trees on pasture production: the extent of decreased pasture production under trees depends on the degree of canopy closure and the characteristics of the canopy (Hawke and Knowles 1997). Plantings of deciduous conservation trees such as alders, poplars, and willows provide a less shaded environment than evergreen trees. Nevertheless, shade from deciduous trees in silvo-pastoral systems will still affect the productivity of pasture by decreasing growth rate and persistence (Ditschal *et al.* 1997).

Trees may be planted at both high or low densities to allow grazing of the pasture until tree canopy closure (Pollock *et al.* 1994). Growth and production of pasture are important criteria to understand the performance of pasture species under such shady conditions (Deinum *et al.* 1996; Devkota *et al.* 1997).

Plants exhibit both physiological and morphological responses when growing in the shade. For example, shade intolerant species have a high (20-30 μmoles photons m^{-2} s^{-1}) light compensation point (LCP) for photosynthesis (Boardman 1977; Herrera *et al.* 1991) compared with 0.5-10 (μmoles photons m^{-2} s^{-1}) for shade tolerant species (Boardman 1977). Saturating intensities of 400-600 μmoles photons m^{-2} s^{-1} for shade intolerant plants (Boardman 1977), and 60-300 μmoles photons m^{-2} s^{-1} for shade tolerant C_3 plants (Boardman 1977) have also been reported. The general responses to low-light stress include increases in plant leaf area to maximize light interception and to enhance the efficiency of carbon utilization (Sanderson *et al.* 1997), resulting in higher leaf area ratios and reduced specific leaf weight (Chen 1993). Accordingly some plant species tolerate heavy shade better than others. For example cocksfoot in heavy shade

(14% of full sunlight PAR) was superior to perennial ryegrass in biomass production due to higher leaf area, and tillering, in both absolute and relative terms (Devkota *et al.* 1997; Chapter 3).

Leaf area development, shoot initiation, plant height, growth rate, and production of pastures vary directly with the amount of sunlight available under the canopy (Shelton *et al.* 1987; Kephart and Buxton 1993; Sanderson *et al.* 1997). As well as decreasing the quantity of light, the tree canopy also absorbs red (R) wavelengths (660nm) more than far-red (FR) wavelengths (730nm) such that R:FR ratio of light decreases towards the base of the canopy (Sanderson *et al.* 1997). In general, low R:FR stimulates morphological changes such as increased height and decreased tillering (Thomson 1993; Teuber and Laidlaw 1996; Sanderson *et al.* 1997).

In the first experiment (Chapter 3), pasture species were screened for their biomass and morphological responses to a range of levels of photosynthetically active radiation without considering light quality in the glasshouse with cocksfoot showing heavy shade tolerance. In these experiments (Chapter 4), the emphasis will be to evaluate whether any differences in shade tolerance attributes exist among cocksfoot selections in glasshouse conditions and under alder tree shade. Accordingly, ten cultivars of cocksfoot and one cultivar of perennial ryegrass were evaluated under three levels of light in the glasshouse, and seven cultivars of cocksfoot and one cultivar of perennial ryegrass were field tested under 11 year old alder trees for their morphological characteristics and responses to shade and light quality.

4.3 Materials and methods

4.3.1 Design and treatments

Experiment 4.1 was conducted from 18 December, 1996 to 4 May, 1997 (138 days) at the Plant Growth unit (PGU), Massey University. A split-plot design was used with four blocks: the main plots were shade treatments and subplots were pasture species. Plants were grown under two shade levels. One main plot in each replication was also maintained under full sun light conditions inside the glasshouse (control; without shade cloth). Shade levels were imposed by differing densities of neutral shade cloth (Sarlon) supported on hollow metal frames (1.25 × 0.84 × 0.45 m) arranged on benches that were 0.9 m above the ground. The shade frames were aligned in a north-south direction (across the sun direction) in order to avoid direct radiation during low sun elevation. Three levels of transmitted photosynthetically active radiation (PAR, μmoles photons m^{-2} s^{-1}, 400-700 nm) were created. The transmitted PAR for the three treatments averaged 73, 32 and 24% of the ambient PAR under full sun light determined on clear sunshine days (8 occasions) from 1200 to 1300 h during the experiment using a LI-COR (Model LI-185) portable quantum sensor. The treatment with 73% ambient PAR was not covered by shade cloth, as this was the percentage of ambient PAR transmitted through the glasshouse. PAR was measured inside and outside the glasshouse at the same time. R:FR ratio was not measured during this experiment, but was considered the same as in the previous glasshouse experiment (Chapter 3: Section 4.3.1).

The practical constraints of the glasshouse and field site limited the number of cocksfoot selections that could be used. Cocksfoot cultivars Grasslands Wana, Grasslands Kara, Tekapo and Saborto were chosen, as they are the commonly used cultivars in New Zealand. PG lines were included as they were considered shade tolerant (Allan Stewart, personal communication). Grasslands Wana was also one of the most shade tolerant cocksfoot cultivars in the previous experiment (Chapter 3).

Table 4.1 Pasture species and cultivars used in Experiment 4.1.

	Pasture species
1	Cocksfoot (*Dactylis glomerata* L.) cv. Grasslands Tekapo (tetraploid)
2	Cocksfoot (*Dactylis glomerata* L.) cv. Grasslands Kara (tetraploid)
3	Cocksfoot (*Dactylis glomerata* L.), PG 321, subsp. izcoi (tetraploid)
4	Cocksfoot (*Dactylis glomerata* L.), PG 306, subsp. Marina (tetraploid)
5	Cocksfoot (*Dactylis glomerata* L.), PG 301, subsp. Marina (tetraploid)
6	Cocksfoot (*Dactylis glomerata* L.), PG 74, subsp. izcoi (diploid)
7	Cocksfoot (*Dactylis glomerata* L.) cv. Grasslands Wana (tetraploid)
8	Cocksfoot (*Dactylis glomerata* L.) cv. Grasslands Apanui (tetraploid
9	Cocksfoot (*Dactylis glomerata* L.) cv. Saborto (tetraploid)
10	Cocksfoot (*Dactylis glomerata* L.) cv. Dora (tetraploid)
11	Perennial ryegrass (*Lolium perenne* L.) cv. Grasslands Nui

Details of the pasture species and cultivars used are given in Table 4.1. Seeds were sown on December 18, 1996 in PB $6^1/_2$ (3.9 litre) black polypots filled with potting mix (80% tree bark + 20% pumice). Dolomite 300g, agricultural lime 300g, iron sulphate 50g, and Osmocote plus (16N-3.5P-10.8K) 400 g per 100 litre were blended with the potting mix, which was rated for medium to long term (< 9 months) greenhouse crops. Four plants were maintained per pot. Plants were watered daily.

Experiment 4.2 was conducted from 18 December 1996 to 30 April 1997 (134 days).

Plants were grown in pots in a glasshouse under full sunlight (Plant Growth Unit, Massey University), and then transferred to the field in the pots on 3 February 1997. The field site was at Horticultural Research Centre, Aokautere, near Palmerston North under 11 year old alder trees. Pots in the field were arranged in a split plot design with four replicate blocks. The main plots were shade treatments created by pruning trees to different heights from ground level, and subplots were mixed species swards. Pruning heights were to 2.5 m, 5.0 m and 7.0 m from the ground, which resulted in three levels of transmitted PAR (17, 27, and

Table 4.2 Pasture species and cultivars used in Experiment 4.2.

	Pasture species
1	Cocksfoot (*Dactylis glomerata* L.) cv. Grasslands Tekapo (tetraploid)
2	Cocksfoot (*Dactylis glomerata* L.) cv. Grasslands Kara (tetraploid)
3	Cocksfoot (*Dactylis glomerata* L.), PG 321, subsp. izcoi (tetraploid)
4	Cocksfoot (*Dactylis glomerata* L.), PG 306, subsp. Marina (tetraploid)
5	Cocksfoot (*Dactylis glomerata* L.), PG 301, subsp. Marina (tetraploid)
6	Cocksfoot (*Dactylis glomerata* L.), PG 74, subsp. izcoi (diploid)
7	Cocksfoot (*Dactylis glomerata* L.) cv. Grasslands Wana (tetraploid)
8	Perennial ryegrass (*Lolium perenne* L.) cv. Grasslands Nui

77% of full sunlight, hereafter called heavy, medium, and light shade, respectively) as determined by measuring on three occasions (7 February, 19 March, and 14 April, 1997) on clear sky days between 1200 to 1300h using a LI-COR (Model LI-185) quantum sensor. The R:FR ratio of the light was also measured on the three occasions with a Skye sensor just above the swards under the trees.

Details of the pasture species and cultivars used are given in Table 4.2. Seeds of the pasture species were sown on 28 December 1996 in PB $6^1/_2$ (3.9 litre) black polypots filled with potting mix (80% tree bark + 20% pumice).

Dolomite 300g, agricultural lime 300g, iron sulphate 50g, and Osmocote plus (16N-3.5P-10.8K) 400 g per 100 litre were blended with the potting mix, which was rated for medium to long term (< 9 months) greenhouse crops. Five plants were maintained per pot. Pots in the field were buried in the soil with approximately the top 30 mm above soil level. Plants were watered daily when there was no rain.

4.3.2 Measurements

4.3.2.1 Experiment 4.1

Plants were harvested on 22 February, 1997 (67 days after sowing), 9 March, (81 days after sowing), 23 March (95 days after sowing), 6 April (109 days after sowing), 20 April (123 days after sowing), and 4 May (137 days after sowing) 1997. At each harvest, all the plants were clipped to 50mm above the media surface. Shoots above 50 mm were dried at 70 ^{0} C for 24 hours, weighed, and added to the above ground shoot mass at the final harvest. At each harvest, the number of tillers per pot was counted. At the final harvest, one plant was randomly selected in each pot and all the leaves and stems were separated. Leaf area was measured, then leaves and stems dried at 70 ^{0} C for 24 hours. Plant height per pot at each harvest was measured for any 3 randomly selected plants.

4.3.2.2 Experiment 4.2

Plants were harvested on 5 March 1997 (77 days after sowing), on 19 March (91 days after sowing), 2 April (105 days after sowing), 16 April (119 days after sowing), and 30 April (133 days after sowing) 1997. At each harvest, all the plants were clipped to 50mm above the media surface. Shoots above 50 mm were dried at 70 ^{0} C for 24 hours, weighed, and added to the above ground shoot mass at the final harvest. At each harvest, the number of tillers per pot was counted. At the final harvest, one plant was randomly selected in each pot, leaf area measured and dry weight determined as in the case of experiment 4.1 (section 4.3.2.1). Roots of all the plants in each pot were washed and oven dried at 70 ^{0} C for 24 hours to calculate per plant root dry weight.

4.3.3 Statistical analysis

PROC GLM programme of SAS version 6.12 (SAS 1997) was used for all analyses. Residuals were examined for their normality. There was no need of data transformation. Tillers per plant in Experiment 4.1 were also analyzed separately by the SAS GLM procedure using the model of repeated measures (SAS 1997) over the harvesting times. Treatment means in the case of Experiment 4.1 were compared using orthogonal contrasts when necessary. The α level was set at 0.05. PROC CANDISC of SAS version 6.12 (SAS 1997) was used to carry out canonical variate analysis (CVA) for the treatments in Experiment 4.1.

4.4 Results

4.4.1 Experiment 4.1

4.4.1.1 Light environment

Mean PAR at noon in the shade treatments was 720, 318, and 232 μmoles photons m^{-2} s^{-1} resulting in 73, 32 and 24% ambient PAR respectively. The mean ambient PAR outside the glasshouse was 989 μmoles photons m^{-2} s^{-1}. Results of the previous experiment (Chapter 3) showed that there was no effect of shade cloth on R:FR ratio.

4.4.1.2 Shoot dry weight

The cumulative shoot dry weight (g/plant) of the grasses at different PAR levels are presented in Table 4.3. Table 4.3 shows that all the grasses produced their highest yield at 73% PAR and lowest at 24% PAR, indicating the significant (P<0.05) effects of shade on the grass cultivars and selections. Equally, there were significant differences (P<0.0001) in shoot dry weight among the grass cultivars and selections for different levels of shade (%PAR transmitted).

At 73% PAR, perennial ryegrass had the greatest cumulative shoot dry weight per plant and Kara the lowest. PG 74 had the highest shoot dry weight of the cocksfoot selections followed by PG 321 (Table 4.3). At 32% PAR, PG 74 produced higher shoot dry weight than the other cocksfoot cultivars and the perennial ryegrass. Apanui had least dry weight ($P<0.05$). Shoot weight of perennial ryegrass was similar to all other cocksfoot selections except PG 74, and all other PG lines had similar shoot dry weights. At the heavy shade (24% PAR), PG 74 produced the highest shoot dry weight (2.23 g) per plant followed by Wana, whereas the shoot weight of perennial ryegrass (1.25 g per plant) was least (Table 4.3).

Table 4.3 Effects of level of transmitted PAR on cumulative shoot dry weight (g/plant) of cocksfoot selections and perennial ryegrass in glasshouse conditions, 1997.

Cocksfoot selections and perennial ryegrass	% PAR transmitted		
	73% (720 μmoles photons $m^{-2} s^{-1}$)	32% (318 μmoles photons $m^{-2} s^{-1}$)	24% (232 μmoles photons $m^{-2} s^{-1}$)
Apanui	4.0	2.1	1.5
Tekapo	3.6	2.2	1.5
Kara	3.0	2.5	1.7
Wana	3.9	2.4	1.9
Saborto	3.4	2.5	1.8
Dora	3.7	2.3	1.8
PG 321	4.3	2.4	1.7
PG 306	3.6	2.3	1.8
PG 74	4.5	3.1	2.2
PG 301	3.8	2.2	1.4
P.ryegrass (Nui)	4.9	2.2	1.2
Analysis of variance			
Shade (A)	P <0.05		
SEM for shade (d.f. = 2)	0.28		
Cultivars and selections (B)	P <0.0001		
SEM for cultivars and selections (d.f. = 10)	0.11		
Interaction (A*B)	P <0.001		
SEM for A*B (d.f. = 20)	0.20		

d.f.= degrees of freedom; SEM= standard error of the mean

The linear relationship between biomass yield and specific leaf area (SLA) for different levels of PAR is presented in Figure (4.1). The relationship was strong only at low levels of PAR (24%), whilst under medium and high levels of PAR, the relationship was not linear and was weaker (Figure 4.1). There was a general trend in the ratio of SLA to dry weight, with a higher ratio at lower PAR levels (Figure 4.1).

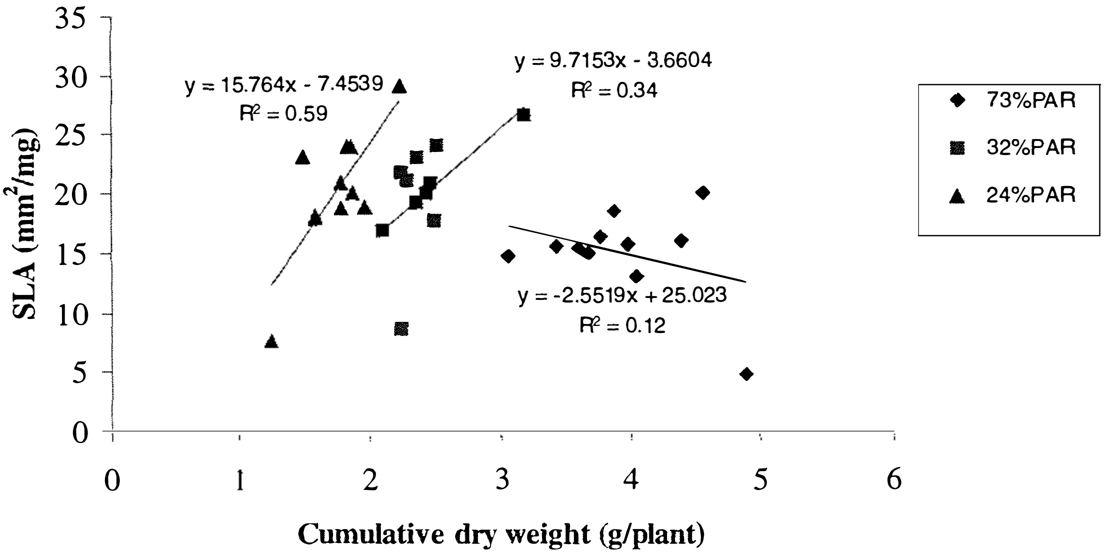


Figure 4.1 Linear regression between dry weight and specific leaf area (SLA) for the cocksfoot selections and perennial ryegrass (Grasslands Nui) under different levels of shade.

4.4.1.3 Tillers per plant

The main effects of shade and cocksfoot cultivars and selections were significant for tillers per plant at the final harvest ($P<0.001$). The highest number of tillers was produced by Tekapo, Wana, and perennial ryegrass in 73% transmitted PAR, while Dora produced the least (Table 4.4). PG lines were similar in tillers per plant which ranged from 30-35. At 32% PAR, PG 306 and Wana produced more tillers than other cultivars of cocksfoot. However, all the selections of cocksfoot other than Dora, and perennial ryegrass were similar and were not significantly different. Under 17% PAR, Wana and PG 306 were the most prolific tillering species (28) followed by PG 74, whereas perennial ryegrass and Dora produced the lowest tillers (18). Analysis by repeated measures over time also revealed that perennial ryegrass had highest tillers per plant at 73% PAR, whereas PG 74 and Wana at 32% PAR, and PG 74, Wana and PG 306 at the lowest PAR (17%), produced more tillers. Dora was the lowest tiller producer at low PAR levels followed by PG 301, Tekapo and perennial ryegrass (Table 4.4).

4.4.1.4 Leaf area, leaf dry weight per plant, and leaf:stem ratio

Table (4.5) shows leaf area per plant of the cocksfoot selections and perennial ryegrass. The main effects of shade and grass cultivars and selections were significant ($P<0.001$) for per plant leaf area. Over all shade levels, PG 74 had the greatest leaf area of the cocksfoot selections, and Apanui the lowest. Leaf area of perennial ryegrass was lower than all the cocksfoot selections (Table 4.5).

Similarly to leaf area, the main effects of shade and grass cultivars and selections were significant ($P< 0.001$) for leaf dry weight per plant (Table 4.5). Among the cocksfoot selections, the highest leaf dry weight per plant was for PG 74 and Tekapo, while Apanui had the lowest per plant dry weight in over all shade levels. Perennial ryegrass produced a lower leaf dry weight compared with all the cocksfoot selections (Table 4.5).

The main effects of shade ($P<0.01$) and grass cultivars and selections ($P<0.05$) were significant for leaf:stem ratio (Table 4.5). Tekapo had the greatest leaf:stem ratio, and PG 74 had the lowest over all shade levels. Leaf:stem ratio of perennial ryegrass was greater than PG 74, but smaller than all the other cocksfoot selections over all shade levels (Table 4.5).

Table 4.4 Effects of shade (different levels of PAR) on tillers per plant of cocksfoot selections and perennial ryegrass under glasshouse conditions, 1997.

% PAR transmitted / Cocksfoot selections and perennial ryegrass	Final harvest (May 4)	Repeated measures over time [1]
73% (720 μmoles photons m^{-2} s^{-1})		
Apanui	33	25
Tekapo	38	27
Kara	30	22
Wana	37	27
Saborto	28	20
Dora	25	18
PG 321	34	24
PG 306	35	26
PG 74	33	26
PG 301	30	22
P.ryegrass (Nui)	37	30
32% (318 μmoles photons m^{-2} s^{-1})		
Apanui	28	20
Tekapo	28	21
Kara	26	21
Wana	32	23
Saborto	26	19
Dora	20	14
PG 321	30	21
PG 306	31	22
PG 74	29	25
PG 301	26	18
P.ryegrass (Nui)	24	22
24% (232 μmoles photons m^{-2} s^{-1})		
Apanui	25	17
Tekapo	22	15
Kara	23	18
Wana	28	21
Saborto	21	17
Dora	18	13
PG 321	25	18
PG 306	28	21
PG 74	27	21
PG 301	21	14
P.ryegrass (Nui)	18	17
Analysis of variance		
Shade (A)	P<0.0001	P<0.01
SEM for shade (d.f.=2)	0.59	0.78
Cultivars and selections (B)	P<0.0001	P<0.0001
SEM for cultivars and selections (d.f.=10)	0.84	0.66
Interactions (A*B)	P<0.01	P<0.01
SEM for A*B (d.f.=20)	1.46	1.15
Time (C)		P<0.0001
Interactions (A*B*C)		NS

SEM= standard error of the mean; NS= non significant at 5% significance level; d.f.= degrees of freedom
[1] considering all harvests

Table 4.5 Effects of shade (different levels of PAR) on per plant leaf area ($mm^2 \times 100$), leaf dry weight (mg), specific leaf area (mm^2/mg), and leaf stem ratio of cocksfoot selections and perennial ryegrass under glasshouse conditions at final harvest, 1997.

% PAR transmitted / Cocksfoot selections and ryegrass	Leaf area	Leaf dry weight	Specific leaf area	Leaf stem ratio
73% (720 µmoles photons m^{-2} s^{-1})				
Apanui	94.1	727.5	12.9	0.6
Tekapo	125.2	815.0	15.2	0.9
Kara	93.0	627.5	14.6	0.6
Wana	119.7	767.5	15.6	0.8
Saborto	118.4	755.0	15.5	0.7
Dora	113.0	690.0	16.3	0.8
PG 321	116.3	730.0	15.9	0.6
PG 306	118.9	787.5	15.0	0.7
PG 74	173.3	860.0	20.0	0.6
PG 301	119.6	655.0	18.5	0.7
P.ryegrass (nui)	33.4	760.0	4.7	1.0
32% (318 µmoles photons m^{-2} s^{-1})				
Apanui	70.0	420.0	16.7	1.2
Tekapo	108.5	502.5	20.9	1.5
Kara	64.6	362.5	17.5	1.1
Wana	92.1	467.5	20.0	1.0
Saborto	114.9	477.5	24.0	1.0
Dora	95.4	412.5	23.0	1.1
PG 321	81.2	385.0	20.9	0.7
PG 306	85.6	445.0	19.2	1.2
PG 74	141.4	537.5	26.5	0.8
PG 301	88.1	402.5	21.7	1.3
P.ryegrass (nui)	24.3	275.0	8.6	0.9
24% (232 µmoles photons m^{-2} s^{-1})				
Apanui	49.2	277.5	17.8	1.1
Tekapo	73.6	410.0	18.0	1.2
Kara	63.8	307.5	20.8	1.1
Wana	64.4	340.0	18.8	1.4
Saborto	75.8	320.0	23.8	1.1
Dora	72.3	305.0	23.9	1.4
PG 321	55.8	302.5	18.6	1.3
PG 306	54.8	282.5	19.8	0.9
PG 74	91.9	332.5	28.9	0.8
PG 301	61.9	270.0	23.0	1.5
P.ryegrass (nui)	21.8	195.0	7.6	0.7
Analysis of variance				
Shade (A)	P<0.001	P<0.0001	P<0.05	P<0.01
SEM for shade (d.f.=2)	5.06	17.18	0.82	0.07
Cultivars and selections (B)	P<0.0001	P<0.0001	P<0.0001	P<0.05
SEM for cultivars and selections (d.f.=10)	6.15	24.10	1.00	0.09
Interactions (A*B)	NS	NS	NS	NS
SEM for A*B (d.f.=20)	10.66	41.75	1.74	0.17
Contrast				
Nui vs all PG lines	P<0.0001	P<0.001	P<0.0001	NS
All PG lines vs rest of the cocksfoot	P<0.01	NS	P<0.01	NS
PG 74 vs rest of the PG lines	P<0.0001	P<0.001	P<0.0001	P<0.05

SEM=standard error of the means; NS= non significant at 5% significance level; d.f.= degrees of freedom

4.4.1.5 Specific leaf area (SLA)

The main effects of shade ($P<0.005$) and grass cultivars and selections ($P<0.0001$) were significant for specific leaf area (SLA) (Table 4.5). PG 74 had the highest SLA over all shade levels. Mean SLA over all the shade levels for cocksfoot selections was 19.4 compared with 6.9 for perennial ryegrass (Table 4.5).

There was a linear relationship between SLA values of grass cultivars and selections (Figure 4.2) at high and low PAR, with substantially higher values of SLA in cocksfoot selections than in perennial ryegrass. Perennial ryegrass had a similar level of plasticity as the cocksfoot selections, but absolute SLA value was significantly higher in the case of cocksfoot selections than that of perennial ryegrass (Figure 4.2).

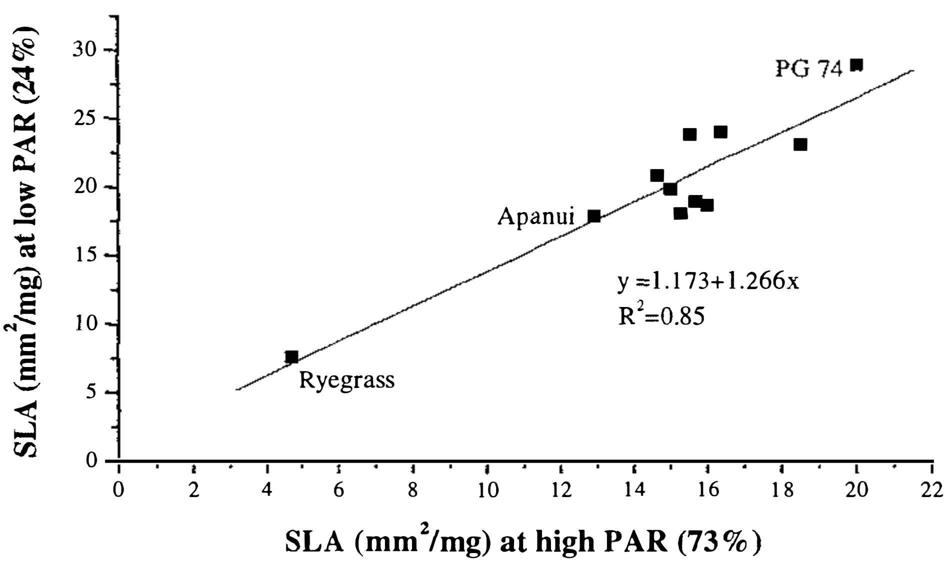


Figure 4.2 Linear relationship between SLA at low and high PAR for ten cocksfoot selections and perennial ryegrass.

4.4.1.6 Multivariate approach

Results from the canonical variate analysis (CVA) considering all PAR levels, and also by considering each PAR level separately are summarized in Tables 4.6 and 4.7.

Table 4.6 Eigenvalues and the proportion of variation accounted for by the canonical variate analysis under different PAR levels.

Eigenvalues		Difference	Proportion	Cumulative
(a) Considering all PAR levels				
1	1.71	0.89	0.63	0.63
2	0.82	0.69	0.30	0.93
3	0.13	0.09	0.04	0.97
4	0.03	0.02	0.01	0.98
5	0.007	.	0.002	1.00
(b) Considering 73% PAR only				
1	3.71	2.39	0.66	0.66
2	1.32	1.03	0.24	0.90
3	0.29	0.16	0.07	0.97
4	0.12	0.03	0.02	0.99
5	0.09	.	0.01	1.00
(c) Considering 32% PAR only				
1	2.55	0.22	0.38	0.38
2	2.33	1.27	0.36	0.74
3	1.06	0.51	0.16	0.90
4	0.54	0.47	0.08	0.98
5	0.07	.	0.01	1.00
(d) Considering 24% PAR only				
1	3.81	0.95	0.49	0.49
2	2.85	2.31	0.37	0.86
3	0.53	0.10	0.06	0.93
4	0.43	0.35	0.05	0.99
5	0.07	.	0.01	1.00

Table 4.7 Information about pooled within canonical structure, and pooled within class standardized coefficients as influenced by different PAR levels.

Variables	Pooled within canonical structure		Pooled within class standardized canonical coefficients	
	CAN1	CAN2	CAN1	CAN2
(a) Considering all PAR only				
Leaf area/plant	0.63	0.27	0.37	0.79
Leaf dry weight	0.11	0.13	0.58	-1.71
Specific leaf area	0.73	0.13	0.88	-0.24
Leaf: stem ratio	-0.01	-0.08	-0.11	0.21
Final tillers/plant	-0.07	0.68	-0.45	1.56
(b) Considering 73% PAR only				
Leaf area/plant	-0.57	0.67	0.19	1.01
Leaf dry weight	0.05	0.45	-0.14	-0.27
Specific leaf area	-0.83	0.48	-1.02	-0.27
Leaf: stem ratio	0.12	0.01	0.19	0.44
Final tillers/plant	0.40	0.71	0.59	0.78
(b) Considering 32% PAR only				
Leaf area/plant	0.57	-0.43	-2.27	1.37
Leaf dry weight	0.47	-0.19	1.52	-1.35
Specific leaf area	0.53	-0.51	2.12	-1.44
Leaf: stem ratio	0.09	-0.07	0.18	0.11
Final tillers/plant	0.68	0.66	0.61	0.90
(b) Considering 24% PAR only				
Leaf area/plant	0.60	-0.49	-0.15	0.32
Leaf dry weight	0.33	-0.32	0.53	-1.42
Specific leaf area	0.45	-0.28	0.96	-0.77
Leaf: stem ratio	-0.06	-0.08	-0.27	0.46
Final tillers/plant	0.67	0.51	0.67	0.99

Consideration of all PAR levels indicated that about 63% separation among the species could be accounted for by the first canonical variate (CV) and the second canonical variate explained a further 30% of the separation (Table 4.6). Similarly, when 73, 32 and 24% PAR were considered separately they all showed that only the first and second variates were necessary to explain most of the variation in the data set (Table 4.6).

PAR levels had a strong influence on SLA and final number of tillers per plant which were highly correlated with CAN1 and CAN2, respectively, as indicated by the information of pooled within canonical structure and pooled within class standardized canonical coefficients. Leaf area per plant was also a major factor explaining differences among the cocksfoot selections. This effect was reflected at each PAR level, where final number of tillers was the most influential parameter affecting differences among the cocksfoot selections, and showed a strong correlation with CAN1 and CAN2 at 73 and 32% PAR. SLA was just as influential as tiller number per plant, but its affect was stronger at 32 and 24% PAR than at 73% (Table 4.7).

4.4.1.7 Grouping species in terms of their similar performance

Plotting CAN1 and CAN2 of the class means on canonical variables showed groupings of cultivars and selections in terms of their coefficients (Figure 4.3, 4.4).

It is clear from Figure 4.3 that at 73% PAR, PG 74, Dora, and Nui were clearly separated from the rest of the selections. Wana, Tekapo and PG 306 appeared in a cluster. The rest of the selections were scattered without forming any close group (Figure 4.3a). At 32% PAR, Nui and Dora cocksfoot were still separated from the other selections of cocksfoot (Figure 4.3b). At 24% PAR, separation was more distinct for PG 74, Nui and Dora as in the case of 73% PAR, while Wana, Apanui, PG 306, and PG 321 were all within the same cluster (Figure 4.4c). Considering all PAR levels, grouping was similar to that in 73% PAR where perennial ryegrass, PG 74, and Dora were isolated from the rest of the selection, and Wana was grouped with PG 306 and Tekapo and Apanui (Figure 4.4d).

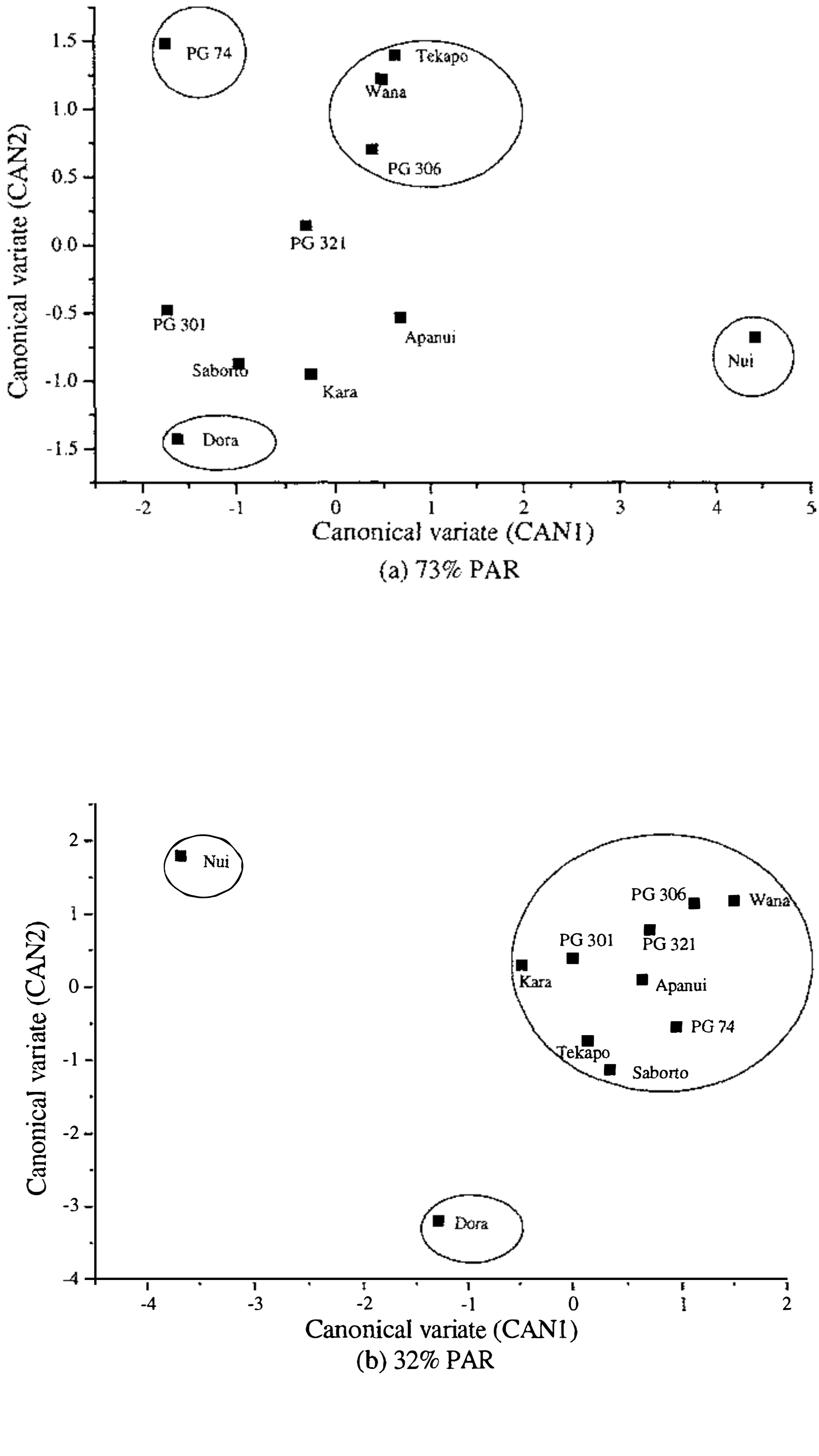
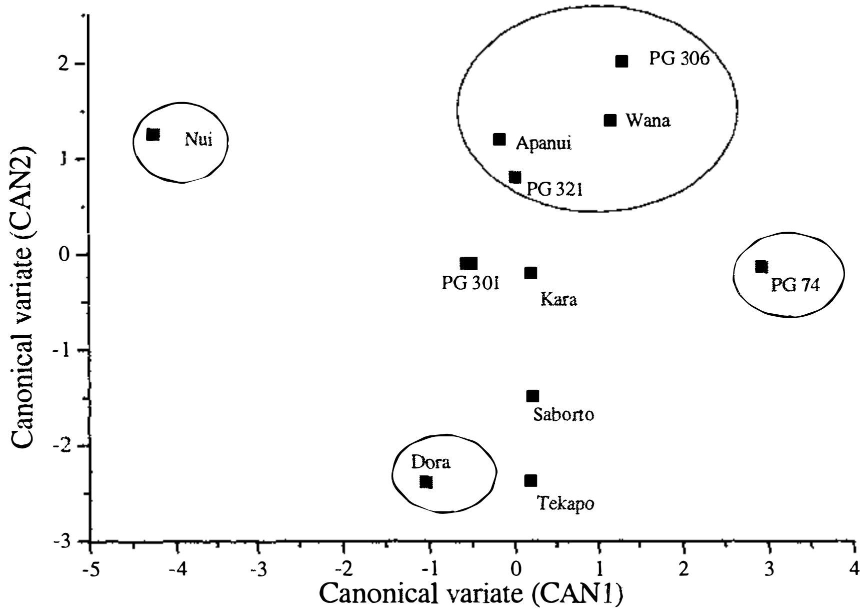
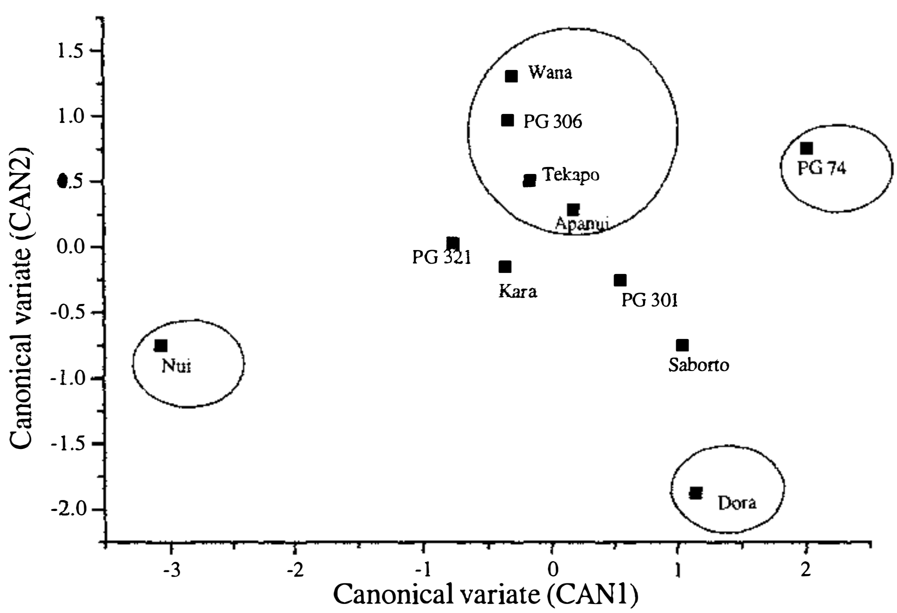


Figure 4.3 Plot of mean canonical variate scores (CAN1 * CAN2) using leaf area, leaf dry weight, SLA, leaf : stem, and final tillers as variables; (a) 73% PAR, and (b) 32% PAR.



(c) 24% PAR



(d) considering all shade

Figure 4.4 Plot of mean canonical variate scores (CAN1 * CAN2) using leaf area, leaf dry weight, SLA, leaf :stem, and final tillers as variables; (c) 24% PAR , and (d) all PAR levels.

4.4.2 Experiment 4.2

4.4.2.1 Light environment

Mean noon PAR and R:FR ratio are given in Table 4.8.

Table 4.8 Light environment and shade levels of Experiment 4.2.

Main plots (shade levels)	Pruning height above ground (m)	Mean PAR (μ moles photons $m^{-2}s^{-1}$)	% full sun light	R:FR ratio
Heavy	2.50	166	17	0.96
Medium	5.00	262	27	1.17
Light	7.00	759	77	1.24

4.4.2.2 Shoot dry weight

The cumulative shoot dry weights (g/plant) of the grass cultivars and selections at different shade levels are presented in Table 4.9. All of the grasses produced their highest yield under light shade and lowest under heavy shade, indicating the significant ($P<0.001$) effects of shade. There were also significant differences among the cocksfoot cultivars and selections and perennial ryegrass shade level (Table 4.9).

Under light shade, perennial ryegrass had the greatest shoot dry weight. The shoot dry weight of Wana was significantly greater than all the other cocksfoot selections except for PG 306. Under medium shade perennial ryegrass still had a significantly greater shoot dry weight than any ofl the cocksfoot selections. Within the cocksfoot selections Wana, which had the highest shoot dry weight, was significantly greater than only Kara. There were no significant differences between perennial ryegrass and any of the cocksfoot selections under heavy shade. Perennial ryegrass shoot dry weight under heavy shade was 33% of that at light shade, whereas shoot dry weight of Wana cocksfoot was 47% of that under light shade (Table 4.9).

Table 4.9 Effects of level of transmitted PAR on cumulative shoot dry weight (g/plant) of cocksfoot selections and perennial ryegrass under alder trees, 1997.

Cocksfoot selections and perennial ryegrass	Shade levels		
	Light (759 µmoles photons $m^2 s^{-1}$)	Medium (262 µmoles photons $m^2 s^{-1}$)	Heavy (166 µmoles photons $m^2 s^{-1}$)
Tekapo	3.5	3.1	1.8
Kara	4.0	2.7	2.2
Wana	5.0	3.5	2.3
PG 321	3.7	2.9	1.7
PG 306	4.3	2.8	1.6
PG 74	3.7	2.9	2.2
PG 301	3.7	3.0	1.9
Perennial ryegrass	5.9	3.9	1.9
Analysis of variance			
Shade (A)	P <0.0001		
SEM for shade (d.f. = 2)	0.10		
Cultivars and selections (B)	P <0.0001		
SEM for (B) (d.f. = 7)	0.15		
Interaction (A*B)	P <0.01		
SEM for A*B (d.f. = 14)	0.27		

SEM= standard error of the mean; d.f.= degrees of freedom

4.4.2.3 Tillers per plant

The main effects of shade and cocksfoot selections and the perennial ryegrass were significant for tillers per plant at the final harvest in absolute (P<0.001), and in relative (P<0.01) terms (Table 4.10). The highest number of tillers was produced by Wana cocksfoot (34) followed by PG 306 and PG 321 (31 each) considering the mean tiller number per plant over all shade levels. The lowest tiller number per plant over all shade levels was for Kara and PG 74 (26), while tiller number per plant of perennial ryegrass was 28 (Table 4.10).

Table 4.10 Effects of level of transmitted PAR on tillers per plant of cocksfoot selections and perennial ryegrass at final harvest, under alder trees, 1997.

Shade levels /cocksfoot selections and perennial ryegrass	Tillers per plant	Relative tillers per plant
Light shade (pruned up to 7m height)		
Tekapo	32	100
Kara	29	100
Wana	41	100
PG 321	38	100
PG 306	36	100
PG 74	31	100
PG 301	32	100
Perennial ryegrass	37	100
Medium shade (pruned up to 5.0m height)		
Tekapo	30	94
Kara	28	97
Wana	33	80
PG 321	30	81
PG 306	34	94
PG 74	25	81
PG 301	28	89
Perennial ryegrass	29	78
Heavy shade (pruned up to 2.5m height)		
Tekapo	25	79
Kara	22	77
Wana	29	71
PG 321	24	65
PG 306	23	64
PG 74	24	77
PG 301	23	73
Perennial ryegrass	18	47
Analysis of variance		
Shade (A)	P <0.0001	P <0.01
SEM for shade (d.f.=2)	0.68	2.48
Cultivars and selections (B)	P <0.001	P <0.005
SEM for (B) (d.f.=7)	1.25	4.15
Interactions (A*B)	NS	NS
SEM for A*B (d.f.=14)	2.17	5.87

SEM= standard error of the mean; NS= non significant at 5% significance level; d.f.= degrees of freedom

4.4.2.4 Specific Leaf Area (SLA)

The effect of shade, and the interaction between shade and cocksfoot selections and perennial ryegrass for specific leaf area (SLA) were not significant. However, the SLAs among the cocksfoot selections and perennial ryegrass were significantly different (Table 4.11). Perennial ryegrass had the lowest SLA and was significantly different to the cocksfoot selections. SLA of the perennial ryegrass over all PAR levels was approximately half that of the cocksfoot selections (Table 4.11).

4.4.2.5 Leaf area per plant

Shade and grass cultivars (cocksfoot selections and perennial ryegrass) significantly affected ($P<0.01$) leaf area per plant (Table 4.11). Perennial ryegrass always had the lowest leaf area per plant and was significantly different from all cocksfoot selections except Kara. Leaf areas of the cocksfoot selections did not differ but all were, however, significantly greater than perennial ryegrass (Table 4.11).

Table 4.11 Effects of shade on leaf area per plant (mm^2), leaf dry weight (mg), specific leaf area (SLA) (mm^2/mg), and root dry weight (mg) per plant of cocksfoot selections and perennial ryegrass under alder trees, 1997.

Shade levels/c. selections and ryegrass	Leaf area	Leaf dry wt.	SLA	Root dry wt.
Light shade (pruned up to 7.0m height)				
Tekapo	12660	660	19.7	540
Kara	14300	550	26.0	480
Wana	17030	740	22.7	560
PG 321	17820	750	23.4	470
PG 306	15790	720	21.9	530
PG 74	12420	560	22.2	410
PG 301	15420	760	19.7	530
Perennial ryegrass	10710	810	12.8	780
Medium shade (pruned up to 5.0m height)				
Tekapo	10010	530	19.0	380
Kara	7320	330	22.0	300
Wana	11340	490	23.1	440
PG 321	12230	540	22.5	360
PG 306	10210	480	20.9	380
PG 74	9400	380	24.6	320
PG 301	12870	580	21.8	290
Perennial ryegrass	5480	500	11.1	470
Heavy shade (pruned up to 2.5m height)				
Tekapo	5670	270	19.5	170
Kara	6430	250	25.2	230
Wana	8160	360	22.4	210
PG 321	8050	330	24.0	130
PG 306	6030	250	23.8	160
PG 74	5840	230	25.0	220
PG 301	8150	330	24.5	180
Perennial ryegrass	1560	140	11.1	210
Analysis of variance				
Shade (A)	P <0.01	P <0.001	NS	P <0.0001
SEM for shade (d.f.=2)	980	40	7	7
Cultivars and selections (B)	P <0.0001	P <0.01	P <0.0001	P <0.001
SEM for (B) (d.f.=7)	830	30	7	20
Interactions (A*B)	NS	NS	NS	P <0.05
SEM for A*B (d.f.=14)	1440	60	12	40

SEM=standard error of the mean; NS= non significant at 5% significance level; d.f.= degrees of freedom

4.4.2.6 Leaf dry weight per plant

Similarly to leaf area, shade ($P<0.001$) and of cocksfoot selections and perennial ryegrass were significantly ($P<0.01$) affected the leaf dry weight per plant (Table 4.11). Considering the mean leaf dry weight over all shade levels greatest leaf dry weight per plant was for PG 301 (556 mg) followed by PG 321 (540 mg), and Wana (530 mg). The lowest leaf dry weight per plant was for PG 74 (390 mg). Perennial ryegrass had a leaf dry weight per plant of 483 mg over all shade levels (Table 4.11).

4.4.2.7 Root dry weight per plant

In general, root dry weight per plant decreased in all species from light to heavy shade. Highest root weight per plant was for perennial ryegrass (780 mg) under light shade followed by Wana. Root weight of PG 74 was the lowest and significantly different to some of the other cocksfoot selections (Table 4.11). Under medium shade, perennial ryegrass had still a larger root weight (470mg) than the cocksfoot selections, but was significantly different only from Kara, PG 74 and PG 301. Among the cocksfoot selections Wana had the highest root weight and PG 301 the lowest. Under heavy shade, however, root dry weight per plant of all the cocksfoot selections/perennial ryegrass was similar (Table 4.11).

4.5 Discussion

The ability of species to maintain production under shade indicates shade *tolerance*, and a sharp decrease in production indicates shade *intolerance* (Toledo *et al.* 1989). A shade tolerant pasture species needs to have good annual and seasonal dry matter production under defoliation, and to be able to regenerate (Devkota *et al.* 1997). Leaf area development, growth rate and yield of forage varies directly with the amount of sunlight available to the canopy (Sanderson *et al.* 1997). However, tillering ability and biomass production of the herbage are the cumulative expression of processes of the plant affected by shade.

Cocksfoot selections maintained a higher relative shoot mass than perennial ryegrass especially at low PAR, due to higher leaf area, higher absolute (both in glasshouse and tree shade) and relative (under tree shade) tiller numbers, as well as a higher specific leaf area. The shoot dry weight of Wana and PG 74 cocksfoot at low PAR (heavy shade) was about half that in high PAR. For Nui perennial ryegrass shoot dry weight under low PAR was only about one third of that under high PAR in both the glasshouse and under alder. At a medium level of shade, however, the performance of perennial ryegrass relative to that of light shade was near to the mean shoot yield of cocksfoot selections, especially under tree shade (75% for the cocksfoot selections versus 67% for perennial ryegrass). Tiller production in cocksfoot selections was more shade tolerant than in perennial ryegrass in shade under trees, and also under low PAR in glasshouse conditions. These results are in line with an earlier screening experiment with grasses and legumes in pots in glasshouse conditions (Devkota *et al.* 1997).

In these studies (Experiment 4.1-4.2), perennial ryegrass was affected more by shade than cocksfoot selections. Percival et al. (1984) and Hunt and Easton (1989) have also indicated low levels of perennial ryegrass production under heavy shade. Pollock *et al.* (1997) reported that cocksfoot production under *Pinus radiatas* at Lincoln was higher than perennial ryegrass/clover and perennial ryegrass only pasture.

Shoot yield of perennial ryegrass was comparatively low under heavy shade due to the low absolute (Tables 4.4, 4.10) as well as relative tillering (Table 4.10), low leaf area (Tables 4.5, 4.11), and low SLA (Table 4.5). One possible reason for fewer tiller numbers in perennial ryegrass, especially under tree shade, could be a high level of sensitivity towards the changes in light quality (lower R:FR ratio) in the lower levels of the canopy (Deregibus *et al.* 1983). Average R:FR ratio in the heavy shade under alder was 0.96. The exact effects of a lower R:FR ratio on the tillering of plants is an issue of debate, however, R:FR ratio could serve as a signal to indicate canopy cover which is thought to interact with other stimuli related to the availability of resources like water, assimilates, and nutrients to determine the rate of tiller formation (Everson *et al.* 1988). Such an effect may be greater for species like perennial ryegrass. On the other hand, the lower numbers of tillers maintained by perennial ryegrass in the glasshouse study, where natural R:FR ratio was maintained, suggests that there could be some other factors involved. Nonetheless, an important result was that the performance of perennial ryegrass in shade (27% PAR) under trees was similar to the cocksfoot selections, and also in the glasshouse (32% PAR) study. However, perennial ryegrass did not tolerate the heavy shade in either experiment.

The comparatively greater shoot dry weight of Wana cocksfoot in shade could be associated with its ability to continue to produce tillers, especially in terms of absolute tillers (Table 4.10). Wana was more shade tolerant than some of the other cocksfoot selections used in the experiments.

The ability of Wana cocksfoot to grow in heavy shade of trees could be associated with its high SLA (Table 4.11). SLA of all the cocksfoot selections in shade was greater in comparison to perennial ryegrass (about 5 %) (Table 4.11). Relative leaf area for perennial ryegrass in shade was also very low in comparison to cocksfoot, which was about 50% for all selections (Table 4.10).

PG 74, a diploid cocksfoot selection, was similar to Wana in terms of shoot dry weight production (Table 4.9) in heavy shade (17% PAR), but not in terms of absolute tiller numbers per plant. One reason for the comparatively fewer tillers in PG 74 compared with Wana under tree shade could be that diploid cocksfoot is mainly confined to forest floors (Bretagnolle and Thompson 1996), and perhaps adapt to the heavy shade by allocating more resources to leaves rather than to develop new tillers. This remains to be determined. In the glasshouse study, however, PG 74 was best in terms of dry weight production, tillering and leaf area production, followed by Wana. Therefore, the results of these experiments showed that Wana and PG 74 were both shade tolerant selections compared to the other cocksfoot selections, and Nui perennial ryegrass.

Grasslands Tekapo is a relatively new Grasslands Wana-type cultivar (Lolicato and Rumball 1994), but the shoot dry weight producing ability of Tekapo in heavy shade in the field experiment as well as in the glasshouse study at low PAR was not as good as that of Wana. However, at medium shade, shoot dry weight production of Grasslands Tekapo was similar to Wana, which was equally reflected by the higher % of relative tillering under medium shade.

Canonical variate analysis (Table 4.12) based on the glasshouse experiment (excluding cumulative shoot dry weight), particularly helped to identify cocksfoot selections and perennial ryegrass with similar performances.

Table 4.12 Summary table of canonical variate analysis (CVA) on glasshouse experiment.

PAR level	Proportion of variation explained	Pooled within canonical structure (individual influence of the variable)	Pooled within-class standardized canonical coefficients (relative influence)	Distinct groupings by CAN1 × CAN2
<u>73% PAR</u>				
CAN1	0.66	-0.83 (SLA)	-1.02 (SLA)	(a) PG 74
		-0.57 (Leaf area)	0.59 (Tillers)	(b) Dora
CAN2	0.23	0.71 (Tillers)	1.01(Leaf area)	(c) Nui
		0.67 (Leaf area)	0.78 (Tillers)	(d) Wana, Tekapo, PG 306
<u>32% PAR</u>				
CAN1	0.38	0.68 (Tillers)	2.12 (SLA)	(a) Nui
		0.57 (Leaf area)	-2.27 (Leaf area)	(b) Dora
CAN2	0.35	0.66 (Tillers)	1.37 (Leaf area)	(c) Wana, PG 74,
		-0.51 (SLA)	0.90 (Tillers)	PG 306 PG 321, Apanui
<u>24% PAR</u>				
CAN1	0.49	0.67 (Tillers)	0.96 (SLA)	(a) Nui
		0.60 (Leaf area)	0.67 (Tillers)	(b) Dora
CAN2	0.37	0.51 (Tillers)	0.99 (Tillers)	(c) PG 74
		-0.49 (Leaf area)	-1.40 (Leaf weight)	(d) Wana, PG 321, PG 306, Apanui
<u>Overall</u>				
CAN1	0.63	0.73 (SLA)	0.88 (SLA)	(a) Nui
		0.63 (Leaf area)	0.58 (Leaf weight)	(b) Dora
CAN2	0.30	0.68 (Tillers)	1.56 (tillers)	(c) PG 74
		0.27 (Leaf area)	0.79 (Leaf area)	(d) Wana, PG 306, Tekapo

Individual (pooled within canonical structure) as well as relative influence of the attributes (pooled within-class standardized canonical coefficients) were both important in determining the variation among the cocksfoot selections and perennial ryegrass at different levels of shade. That is some attributes had a strong role in determining the production of pasture, but not all the attributes were important for pasture growth under shade. Tiller numbers and leaf area per plant were the most important attributes to influence the canonical coefficients, while SLA was the main attribute that determined the variations among pasture species in relative terms. The combined effects of these attributes largely determined the production of pastures under shade. Higher tiller numbers, leaf area per plant, and SLA meant better production under shade and vice versa. Accordingly, Nui perennial ryegrass and cocksfoot selection, Dora, were the least shade tolerant selections, while PG 74 was more shade tolerant at low PAR. Likewise, Wana, PG 306, and Tekapo of the cocksfoot selections were also equally shade tolerant at low PAR.

Canonical variate analysis (CVA) showed the variation in the selections of cocksfoot and Nui perennial ryegrass in terms of shade tolerance ability. This was consistent with the shoot dry matter production of the selections under different shade, demonstrating that Wana and PG 74 of the cocksfoot selections were superior at low PAR, while perennial ryegrass was shade intolerant. CVA, however, also indicated that PG 306 was always grouped with Wana. The performance of PG 306 is probably related to tiller numbers per plant other than the other attributes (Table 4.4, 4.5). Tekapo had a similar number of tillers at each PAR level to Wana and PG 306, but did not have similar SLA (Tables 4.4, 4.5, Figure 4.3, 4.4).

Change in SLA could be seen as an allocation issue. Other allocation changes of plants under shade, such as reduction in root mass, high shoot/root ratio, and increased leaf: stem ratio, although perhaps of value ecologically (Wilson 1997), may not be directly relevant attributes for the production of pasture under shade. Absolute and relative tillers per plant and shoot dry weight along with leaf area and SLA are important attributes that determine productivity of pastures under shade (Devkota *et al.* 1997). The cocksfoot selections, particularly Wana and PG 74 were often superior to perennial ryegrass in heavy shade for these attributes, which are also important for defoliation tolerance.

4.6 Conclusions

Results of these experiments indicated that shade affected perennials ryegrass more than any of the cocksfoot selections, especially at the low PAR level in both the glasshouse and field studies. Perennial ryegrass had a similar performance in both the field and glasshouse studies, where in shade per plant tillers were quite low compared with Wana and PG 74. Per plant leaf area of perennial ryegrass was also significantly ($P<0.0001$) lower than for Wana, as was leaf dry weight at the low PAR level. PG lines, other than PG 74, were similar in performance, but were not promising under shade. Dora was the cultivar with the lowest production under low PAR in the glasshouse, and Kara was the lowest in the field. Specific leaf area, leaf area, and tillers per plant were associated with better performance of cultivars under shade. The results of the study also demonstrated that there was a difference in terms of production for the cocksfoot selections, but selections from both tetraploids and diploids could be equally suited to heavy shade. The consistent result from the field and glasshouse studies was that perennial ryegrass was less productive and potentially less persistent under shade than the cocksfoot cultivars.

4.7 References

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5. Effects of light intensity and quality on pasture species

5.1 Summary

The effects of varied PAR and R:FR ratio on tillering and shoot dry weight production of hill pasture species, which differed in morphology and shade tolerance, were evaluated. A split plot design was used with low (16 and 17%) and medium (38 and 39%) % transmitted PAR (μmoles photons m^{-2} s^{-1}, 400-700 nm), and two natural (1.33 and 1.34) and two reduced (0.57 each) red (655-665 nm) to far-red (725-735nm) ratios (R:FR) of light as main plots. The treatment combination was such that each low and medium PAR level had a natural and a reduced R:FR ratio. PAR levels with natural R: FR ratio were imposed by differing densities of neutral shade cloth (Sarlon) with a layer of clear filter, while low R:FR ratio was created with the use of a blue filter. Shade cloth and filters were supported together on hollow metal frames (1.25 × 0.84 × 0.45 m) arranged on benches that were 0.9 m above the ground. PAR level was determined each day measurement from 1200 to 1300 h during the experiment using a LI-COR (Model LI-185) quantum sensor, while R:FR ratios were the mean of 3 measurements.

Nine pasture cultivars of seven pasture species: *Dactylis glomerata* L., Grasslands Wana (cocksfoot); *Dactylis glomerata* L., PG 74 (cocksfoot); *Dactylis glomerata* L., PG 321 (cocksfoot); *Lolium perenne* L. (perennial ryegrass); *Holcus lanatus* L. (Yorkshire fog); *Agrostis capillaris* (browntop); *Poa trivialis*; *Trifolium repens* L. (white clover), and *Lotus uliginosus* (lotus) were grown in pots as subplots with four replicate blocks. Six plants were maintained per pot, and plants were watered daily. Water and fertiliser were non-limiting. Plants were at first grown in a glasshouse under full available sunlight, and were then transferred to the shade frames after 60 days. All the fully expanded laminae of each plant were removed before imposing shade treatments. In the shade, plants were not clipped and grew without harvesting.

The experiment ran from 10 June to 9 October, 1997 (121 days). Plants were harvested on 9 October, 61 days after imposing shade. One plant was randomly selected in each pot to determine leaf area, leaf dry weight, stem dry weight, SLA,

and number of leaves and tillers. The remaining five plants were clipped to the media surface and shoot dry weight per plant determined. Root dry weight of all the plants in the pots was also determined. Chlorophyll concentration was measured once during September.

Results showed that there was no effect of R:FR ratio (P>0.05) on the shoot dry weight per plant. Similarly, the interaction for PAR×R:FR was not significant (P>0.05) nor were species×R:FR and species×PAR×R:FR. There were, however, significant differences (P<0.05) for PAR, species, and interaction of PAR×species for shoot dry weight. At low PAR, *Lolium perenne*, *Dactylis glomerata* (Wana) and *Holcus lanatus* had the highest and similar yields, whereas the yield of white clover and lotus were similar and less than for all the grass species. Effects of PAR as well as R:FR were significant (P<0.001) for total tillers per plant and net tillers/plant developed in the shade. *Poa trivialis*, *Agrostis capillaris* and *Lolium perenne* had the highest number of tillers/plant at the low PAR and low R:FR, however, the high number of tillers for Poa and browntop did not result in higher shoot dry weight for these species at the low PAR, mainly due to their low weight per tiller. Likewise, SLA was significantly (P<0.01) increased by low PAR but not by low R:FR. However, there was an interaction between species and R:FR for SLA. Among the legumes, lotus produced a higher (P<0.001) number of branches at the low PAR than white clover. Similarly, greater shoot dry weight per plant, number of branches/plant, and total leaves per plant of lotus than of white clover was also found at low PAR with reduced R:FR. The results are discussed in terms of the effects of PAR and R:FR on the yield and yield components with respect to the attributes of shade tolerant pasture species.

5.2 Introduction

The growth, development and productivity of plants are dependent on both the quantity and quality of light (Loomis *et al.* 1963; Kasperbauer and Hunt 1998). Reduction in the quantity as well as quality of light may cause morphological changes in plants, as well as reducing overall growth, and can influence the outcome of competitive relations between plant species (Shelton *et al.* 1987).

Effects of R:FR on the productive performance of pasture plants have been widely studied (Dergibus *et al.* 1983; 1985; Thomson 1993; Murphy and Briske 1994; Smith 1994; Teuber and Laidlaw 1996; Wan and Sosebee 1998; Kasperbauer and Hunt 1998). In general, low R:FR stimulates apical dominance causing morphological changes, such as increased plant height, stem elongation and reduced tillering (Dergibus *et al.* 1983; 1985; Smith 1994; Wan and Sosebee 1998).

Light regulates plant growth and development via informational signals detected by phytochrome (Smith 1994; Sanderson *et al.* 1997; Wan and Sosebee 1998). That is, the colour of light received by a growing plant influences where and how the photosynthate is used, known as the photomorphogenic function of light (Kasperbauer and Hunt 1998). For example, red (R) and far-red (FR) are absorbed by and act through a photoreversible regulatory phytochrome pigment system (Kasperbauer and Hunt 1998). The ratio of the red and far-red (R:FR) quanta influences plant development (Lee *et al.* 1994; Smith 1994). Generally, not only the amount of light received by a plant decreases, but the R:FR ratio also decreases under a dense canopy because of selective absorption of red light relative to far-red and diffusion of different wavelengths by green tissue (Smith 1994; Wan and Sosebee 1998). Branching is affected more by shade with both low photosynthetically-active radiation (PAR) and low R:FR than by neutral shade (low PAR and high R:FR) (Wan and Sosebee 1998).

The first glasshouse experiment screening pasture species for shade tolerance (Chapter 3) focused on levels of PAR (400-700nm), independent of changes in R:FR under a canopy. However, with the reduction in the total amount of light, R:FR is also reduced in the natural environment (Smith 1994). It is difficult to determine the role of R:FR independently of light intensity on the plant's performance in a field study. The only way to examine the role of R:FR is to investigate the growth of plants under controlled conditions, in which R:FR ratio is varied whilst the amount of PAR is held constant (Smith 1994).

Chapter 4 examined effects of shade on different cocksfoot selections and perennial ryegrass in a glasshouse and under trees. In this experiment, pasture species were screened for their biomass and morphological responses to a fixed low and medium levels of PAR (% transmitted photosynthetically active radiation), each combined with natural as well as reduced R:FR ratios in glasshouse conditions so that effects of R:FR could be determined independently of light intensity. It is hypothesised that the morphological responses of pastoral plants are less affected by low R:RF under a low level of PAR than a high level of PAR, since survival could be more important for a plant at a low level of PAR, and hence the efficiency of utilization of light energy is more important (Corré 1983a) than the quality of light.

5.3 Materials and methods

5.3.1 Design and treatments

The experiment was conducted for 121 days for legumes (10 June to 9 October, 1997), and 112 days (20 June-9 October, 1997) for grasses at the Plant Growth Unit (PGU), Massey University. Different sowing times for legumes and grass were intended to adjust for differences in germination period. A split-plot design was used with four blocks. The main plots were % transmitted PAR (μmoles photons m^{-2} s^{-1}, 400-700 nm) and R:FR ratios (ratio of photon irradiance between 655 and 665 nm, and 725 and 735nm) (Smith 1994) with 2 × 2 factors of PAR and R:FR, i.e. medium PAR: 38% (181 μmoles photons m^{-2} s^{-1}) with natural R:FR (1.33-1.34), and 39% PAR (189 μmoles photons m^{-2} s^{-1}) with low R:RF (0.57), and low PAR: 16% PAR (78 μmoles photons m^{-2} s^{-1}) with natural R:FR (1.32-1.37), and 17% PAR (84 μmoles photons m^{-2} s^{-1}) with low R:RF (0.57). Thus, the transmitted PAR was 39, 38, 17, and 16% of the ambient PAR under full sunlight as determined on each day from 1200 to 1300 h during the experiment using a LI-COR (Model LI-185) portable quantum sensor, while R:FR ratios were the mean of 3 measurements by using Skye sensor. Subplots were pasture species.

PAR levels with natural R:FR ratio were imposed by differing densities of neutral shade cloth (Sarlon) with a layer of clear filter (Effects filters, 30 clear, Chris James and Co. LTD; Lighting Filters, 43 Colville Road, Acton, London W38BL) while low R:FR ratio was created with the use of steel blue filters (Effects filter, 117 steel blue). Shade cloths and filters were supported together on hollow metal frames (0.25 × 0.84 × 0.45 m) arranged on benches that were 0.9 m above the ground. The shade frames were aligned in a north-south direction (across the sun direction) in order to avoid direct radiation during low sun elevation, but the pots were not fully enclosed to facilitate aeration and to reduce temperature increase due to the use of filters. In the east-west direction the frames completely enclosed the pots. Thus, in each cage as main plot, pots of 9 cultivars were accommodated where each pot had only one cultivar with 6 plants per pot. 6 plants per pot for the 3.9 litre pot size was optimum in terms of spacing, and also for ease of handling as determined on the basis of knowledge of previous experiments.

Details of the pasture species and cultivars used are given in Table 5.1. Seeds of the pasture species were sown on 9 June for legumes, and 20 June, 1997 for grasses in PB $6^1/_2$ (3.9 litre) black polypots filled with potting mix (80% tree bark + 20% pumice). Dolomite 300g, agricultural lime 300g, iron sulphate 50g, and Osmocote plus (16N-3.5P-10.8K) 400 g per 100 litre were blended with the potting mix, which was rated for medium to long-term (< 9 months) greenhouse crops. Six plants were retained per pot. Plants were watered daily.

Table 5.1 Pasture species and cultivars used in the Experiment.

Pasture species
1. White clover (*Trifolium repens* L.) cv. Grasslands Tahora
2. Lotus (*Lotus uliginosus*) cv. Grasslands Maku
3. Cocksfoot (*Dactylis glomerata* L.) cv. Grasslands Wana, (tetraloid)
4. Cocksfoot (*Dactylis glomerata* L.), PG 74, subsp. Izcoi (diploid)
5 Cocksfoot (*Dactylis glomerata* L.), PG 321 subsp. Izcoi (tetraploid)
6 Perennial ryegrass (*Lolium perenne* L.) cv. Grasslands Nui
7 Yorkshire fog (*Holcus lanatus* L.) cv. Massey Basyn
8 Browntop (*Agrostis capillaris*) cv. Grasslands Muster
9. Poa trivialis (*Poa trivialis*) cv. Sabre

The pots within cages were re-randomized weekly. Seeds of legumes were inoculated with the appropriate rhizobia. The glasshouse temperature was maintained at 25^{0}C until seeds of all plants were fully germinated. Thereafter, day temperature was 15-17^{0}C and night temperature 8-10^{0}C.

Plants were at first grown in a glasshouse under full available sunlight, and were then transferred to the shade frames on 10 August 1997. All the fully expanded lamina were clipped at ligule before imposing shade treatments to avoid confounding effects of full sunlight. Clipped laminae were later oven dried at 70^0 C for 24 hours and weighed and added to the cumulative biomass. Leaves were not clipped once plants were under the shade, and plants were harvested only at the end of experiment.

5.3.2 Measurements

Plants were harvested on 9 October 1997 (61 days after imposing shade). One plant was randomly selected in each pot and all the leaves, stems, mature and immature leaves were separated. Leaf area was measured, then leaves and stems dried at 70 ^{0} C for 24 hours to calculate cumulative biomass per plant. Number of tillers was also determined for the same plant. The remaining five plants were clipped to the media surface. Shoots were dried at 70 ^{0} C for 24 hours, weighed, and added to the above ground shoot mass at the final harvest. The roots of all the six plants were removed, washed, and dried at 70 ^{0} C for 24 hours to calculate per plant root dry weight. During September, one plant in each pot of the each treatment was randomly selected and marked. The number of tillers, and leaves of the marked plants were counted each week for four weeks, and chlorophyll concentration was measured once. To determine the chlorophyll concentration, a fresh sample of about 2 g of leaf was ground in acetone (30-40ml), kept in the cool room (-1^{0}C) over-night and then centrifuged for 10 minutes at 4000 rpm, diluted to a known volume (50ml) by adding acetone, and the absorbance read at 664 and 647 nm in a spectrophotometer (U-2000 double beam, Hitachi, Ltd. Tokyo Japan) (Holden 1965; Harborne 1973).

5.3.3 Statistical analysis

PROC GLM programme of SAS version 6.12 (SAS 1997) was used for all analyses. Residuals were examined for their normality, and transformation was carried out when needed. Type of data transformation has been indicated on the appropriate result table. Treatment means were compared using orthogonal contrasts. The α level was set at 0.05.

For all the tables SEM denotes standard error of the mean; NS, nonsignificant at P<0.05; d.f., degrees of freedom; Wc, white clover; rye, perennial ryegrass; and Y.fog., Yorkshire fog.

5.4 Results: experiment 5

5.4.1 Growth environment

Mean PAR at noon in the shade treatments was 189, 181, 84, and 78 µmoles photons m^{-2} s^{-1} resulting in 39, 38, 17, and 16% PAR transmitted respectively to that of available PAR inside the glasshouse. The mean ambient PAR outside and inside the glasshouse was 675, and 482 µmoles photons m^{-2} s^{-1} respectively. Mean R:FR ratio in each PAR level was 0.57, 1.33, 0.57, and 1.34, respectively, as determined by the three measurements during the experiment periods, while R:FR inside as well as outside the glasshouse was 1.4.

5.4.2 Shoot dry weight

There was no effect of R:FR ratio (P>0.05) on the shoot dry weight per plant of the pasture species studied. Similarly the interaction of PAR × R:FR, species × R:FR, and species × PAR × R:FR were not significant (P>0.05). However, there were significant (P<0.05) effects of PAR, species, and PAR × species on the shoot dry weight (Table 5.2). Higher shoot dry weight was produced by all the species at medium PAR than at-

Table 5.2 Effect of level of PAR and R:FR on shoot dry weight (g /plant) of grass and legume species at final harvest in glasshouse conditions, 1997.

Species/cultivars	% transmitted PAR and R:FR ratio			
	Medium PAR		Low PAR	
	38% PAR, Natural R:FR (1.33-1.34)	39% PAR, Low R:FR (0.57)	16% PAR, Natural R:FR (1.32-1.37)	17% PAR, Low R:FR (0.57)
White clover	1.4	1.0	0.4	0.3
Lotus	1.0	1.1	0.4	0.4
Cocksfoot (Wana)	1.9	1.8	1.2	1.0
Cocksfoot (PG 74)	1.6	1.2	0.8	0.5
Cocksfoot (PG 321)	1.8	1.7	0.7	0.7
Perennial ryegrass (Nui)	2.8	2.7	1.2	1.1
Yorkshire fog	2.7	2.8	1.3	0.9
Browntop	1.9	1.8	0.6	0.8
Poa trivialis	1.9	1.7	0.9	1.0
Analysis of variance	**probability**	**SEM**		
PAR (A) (d.f. = 1)	P<0.001	0.03		
R:FR (B) (d.f.=1)	NS	0.03		
(A*B) (d.f.=1)	NS	0.04		
Species (C) (d.f.=8)	P<0.001	0.06		
C*A (d.f.=8)	P<0.001	0.09		
(C*A*B) (d.f.=8)	NS	0.12		
Contrasts				
Legumes vs rest	P <0.001			
Wc vs lotus	NS			
Rye vs PG 74, PG 321, Wana, Y.fog, Poa, browntop	P <0.001			

low PAR. At medium PAR, Yorkshire fog and perennial ryegrass had produced most shoot dry weight followed by Wana cocksfoot and browntop. Shoot dry weights of white clover and lotus were similar and lower than all the grass species (Table 5.2). At low PAR, perennial ryegrass, Wana cocksfoot and Yorkshire fog were similar and had the highest shoot dry weight, whereas shoot dry weight of white clover and lotus was similar and less than all the grass species. Perennial ryegrass and Yorkshire fog had 45 and 39% shoot dry weight, respectively, of their medium PAR shoot dry weight at low PAR, compared with 59% for Wana cocksfoot (Table 5.2).

5.4.3 Yield components

Only the effects of PAR and species significantly affected ($P<0.05$) the yield components leaf area, leaf dry weight, and stem dry weight. There was no effect ($P>0.05$) of R:FR or any interactions on shoot, leaf dry weight, and leaf area (Table 5.2, 5.3, and 5.4), but there was an effect on stem dry weight (Table 5.5).

Leaf area per plant increased with increased PAR in all pasture species (Table 5.3). Yorkshire fog had the highest leaf area in medium as well as in low PAR. Leaf areas of the Wana cocksfoot was higher than that of perennial ryegrass and legumes. Leaf area of legume was the lowest among all the species studied. Similar results were also observed for leaf dry weight per plant, which was higher in medium PAR than in low. Perennial ryegrass leaf dry weight was significantly higher ($P<0.0001$) than the rest of the species. Leaf dry weight of legumes was the lowest. Lotus had more leaf dry weight than white clover (Table 5.4).

Stem dry weight per plant had also similar response to that of leaf area and leaf dry weight, but there was a significant effect of R:FR on the stem dry weight along with PAR (Table 5.5). Stem dry weight was higher in 38% PAR, natural R:FR compared to 39% PAR and low R:FR in all species, except for lotus. Browntop was least affected by low R:FR followed by Yorkshire fog. Similarly, reduction in R:FR reduced the stem dry weight of species under low PAR, except for PG 321, Nui, browntop, and Poa, which increased under low PAR, and low R:FR treatments (Table 5.5).

Table 5.3 Effect of level PAR and R:FR on leaf area (mm^2/plant) of grass and legume species at final harvest in glasshouse conditions, 1997.

Species	% transmitted PAR and R:FR ratio			
	Medium PAR		Low PAR	
	38% PAR, Natural R:FR (1.33)	39% PAR, Low R:FR (0.57)	16% PAR, Natural R:FR (1.34)	17% PAR, Low R:FR (0.57)
White clover	24656	25729	10033	13496
Lotus	25085	31384	12197	8953
Cocksfoot (Wana)	40279	34445	28152	27759
Cocksfoot (PG 74)	35948	27139	19450	11428
Cocksfoot (PG 321)	41193	33015	24203	23905
Perennial ryegrass (Nui)	33237	28614	23634	26921
Yorkshire fog	75664	66468	51596	47853
Browntop	29882	21729	15229	15335
Poa trivialis	27671	15199	15840	14023
Analysis of variance	**probability**	**SEM**		
PAR (A) (d.f. = 1)	P<0.001	1231		
R:FR (B) (d.f.=1)	NS	1231		
(A*B) (d.f.=1)	NS	1619		
Species (C) (d.f.=8)	P<0.0001	2428		
(C*A*B) (d.f.=8)	NS	4856		
Contrasts				
Legumes vs rest	P <0.0001			
Wc vs lotus	NS			
Rye vs PG 74, PG 321, Wana, Y.fog, Poa, browntop	NS			

Table 5.4 Effect of level of PAR and R:FR on leaf dry weight (mg/plant) of grass species and Legume species at final harvest in glasshouse conditions, 1997.

Species	% transmitted PAR and R:FR ratio			
	Medium PAR		Low PAR	
	38% PAR, Natural R:FR (1.33)	39% PAR, Low R:FR (0.57)	16% PAR, Natural R:FR (1.34)	17% PAR, Low R:FR (0.57)
White clover	570	543	247	223
Lotus	573	627	203	170
Cocksfoot (Wana)	1530	1347	860	767
Cocksfoot (PG 74)	1073	850	523	287
Cocksfoot (PG 321)	1410	1297	893	747
Perennial ryegrass (Nui)	2003	1803	997	1230
Yorkshire fog	1857	1663	1093	993
Browntop	1293	920	563	620
Poa trivialis	1233	813	710	697
Analysis of variance	**probability**	**SEM**		
PAR (A) (d.f. = 1)	P<0.0001	34		
R:FR (B) (d.f.=1)	NS	34		
(A*B) (d.f.=1)	NS	50		
Species (C) (d.f.=8)	P<0.0001	75		
(C*A*B) (d.f.=8)	NS	149		
Contrasts				
Legumes vs rest	P <0.0001			
Wc vs lotus	NS			
Rye vs PG 74, PG 321, Wana, Y.fog, Poa, browntop	P<0.0001			

Table 5.5 Effect of Level of PAR and R:FR on stem dry weight (g/plant) of grass and legume species at final harvest in glasshouse conditions, 1997.

Species	% transmitted PAR and R:FR ratio			
	Medium PAR		Low PAR	
	38% PAR, Natural R:FR (1.33)	39% PAR, Low R:FR (0.57)	16% PAR, Natural R:FR (1.34)	17% PAR, Low R:FR (0.57)
White clover	1.3	0.7	0.3	0.1
Lotus	0.7	0.8	0.3	0.2
Cocksfoot (Wana)	1.1	0.7	0.7	0.2
Cocksfoot (PG 74)	0.6	0.4	0.2	0.2
Cocksfoot (PG 321)	0.9	0.8	0.3	0.4
Perennial ryegrass (Nui)	1.1	0.9	0.3	0.4
Yorkshire fog	1.0	0.9	0.4	0.4
Browntop	1.1	1.0	0.3	0.3
Poa trivialis	1.0	0.8	0.3	0.4
Analysis of variance	**probability**	**SEM**		
PAR (A) (d.f. = 1)	P<0.0001	0.03		
R:FR (B) (d.f.=1)	P<0.05	0.03		
(A*B) (d.f.=1)	NS	0.04		
Species (C) (d.f.=8)	P<0.01	0.06		
(C*A*B) (d.f.=8)	NS	0.13		
Contrasts				
Legumes vs rest	NS			
Wc vs lotus	NS			
Rye vs PG 74, PG 321, Wana, Y.fog, Poa, browntop	NS			

Effect of PAR was significant (P<0.001) for all the parameters related to tillering; total tillers/plant, net tillers/plant developed in the shade, and tiller weight per plant. However, R:FR only significantly affected the total and net tillers per plant (P<0.001), and not tiller weight. In contrast, species were significantly different (P<0.001) for all the tiller related parameters. There were, however, no significant (P>0.05) interactive effects of PAR, R:FR, and species for all these tillers parameters, except the pasture species with PAR (P<0.001) for the net tillers (Tables 5.6, 5.7, 5.8).

Table 5.6 Effect of level of PAR and R:FR on $\log_e$ total tillers or stolons/branches per plant of grass and legume species at final harvest in glasshouse conditions, 1997. Values in parentheses are back transformed.

Species	% transmitted PAR and R:FR ratio			
	Medium PAR		Low PAR	
	38% PAR, Natural R:FR (1.33)	39% PAR, Low R:FR (0.57)	16% PAR, Natural R:FR (1.34)	17% PAR, Low R:FR (0.57)
White clover	2.97 (19.4)	2.65 (14.1)	2.21 (9.1)	1.73 (5.6)
Lotus	3.79 (44.2)	3.61 (36.9)	3.39 (29.6)	3.19 (24.2)
Cocksfoot (Wana)	3.00 (20.0)	2.95 (19.1)	2.62 (13.7)	2.22 (9.2)
Cocksfoot (PG 74)	2.82 (16.7)	2.56 (12.9)	1.97 (7.1)	1.73 (5.6)
Cocksfoot (PG 321)	2.78 (16.1)	2.62 (13.7)	2.18 (8.8)	2.31 (10.0)
Perennial ryegrass (Nui)	3.28 (26.5)	3.29 (26.8)	2.97 (19.4)	2.67 (14.4)
Yorkshire fog	3.27 (26.3)	3.09 (21.9)	2.86 (17.4)	2.76 (15.7)
Browntop	3.52 (33.7)	3.67 (39.2)	3.13 (22.8)	3.24 (25.5)
Poa trivialis	4.03 (56.2)	3.78 (43.8)	3.55 (34.8)	3.47 (32.1)
Analysis of variance	**probability**	**SEM**		
PAR (A) (d.f. = 1)	P<0.0001	0.01		
R:FR (B) (d.f.=1)	P<0.001	0.01		
(A*B) (d.f.=1)	NS	0.04		
Species (C) (d.f.=8)	P<0.0001	0.06		
(C*A*B) (d.f.=8)	NS	0.13		
Contrasts				
Legumes vs rest	NS			
Wc vs lotus	P<0.0001			
Rye vs PG 74, PG 321, Wana, Y.fog, Poa, browntop	NS			

Table 5.7 Effect of level of PAR and R:FR on $\log_e$ net tillers or stolons/ branches per plant of grass and legume species developed in the shade at final harvest in glasshouse conditions, 1997. Values in parentheses are back transformed.

Species	% transmitted PAR and R:FR ratio			
	Medium PAR		Low PAR	
	38% PAR, Natural R:FR (1.33-1.34)	39% PAR, Low R:FR (0.57)	16% PAR, Natural R:FR (1.32-1.37)	17% PAR, Low R:FR (0.57)
White clover	2.80 (16.4)	2.16 (8.67	1.32 (3.7)	0.59 (1.8)
Lotus	3.62 (37.3)	3.45 (31.5)	3.15 (23.3)	2.82 (16.7)
Cocksfoot (Wana)	2.82 (16.7)	2.77 (15.9)	2.30 (9.9)	1.83 (6.2)
Cocksfoot (PG 74)	2.64 (14.0)	2.36 (10.5)	1.52 (4.5)	1.29 (3.6)
Cocksfoot (PG 321)	2.64 (14.0)	2.40 (11.0)	1.87 (6.4)	2.08 (8.0)
Perennial ryegrass (Nui)	3.04 (20.9)	3.07 (21.5)	2.57 (13.0)	2.42 (11.2)
Yorkshire fog	2.97 (19.4)	2.46 (11.7)	2.32 (10.1)	2.07 (7.9)
Browntop	3.25 (25.7)	3.43 (30.8)	2.74 (15.4)	2.85 (17.2)
Poa trivialis	3.88 (48.4)	3.61 (36.9)	3.28 (26.5)	3.24 (25.5)
Analysis of variance	**probability**	**SEM**		
PAR (A) (d.f. = 1)	P<0.001	0.02		
R:FR (B) (d.f.=1)	P<0.001	0.02		
(A*B) (d.f.=1)	NS	0.05		
Species (C) (d.f.=8)	P<0.0001	0.08		
(C*A) (d.f.=8)	P<0.001	0.12		
(C*A*B) (d.f.=8)	NS	0.17		
Contrasts				
Legumes vs rest	P<0.05			
Wc vs lotus	P<0.0001			
Rye vs PG 74, PG 321, Wana, Y.fog, Poa, browntop	NS			

Higher numbers of total tillers or branches per plant were produced by all the species at the medium PAR than at the low PAR. The highest number of tillers was on Poa and on browntop among the grasses, and lotus had more branches per plant than white clover in the case of legumes. This trend was similar under low PAR (Table 5.6). Tiller numbers of Wana cocksfoot, PG 74 cocksfoot and PG 321 cocksfoot were smaller than for perennial ryegrass, but were not significantly different (P>0.05). In general, a lower number of tillers were produced by all species under low R:FR compared with natural R:FR, except in the case of browntop (Table 5.6).

Table 5.8 Effect of level of PAR and R:FR on tiller weight per plant (mg) of grass species at final harvest in glasshouse conditions, 1997.

Species	% transmitted PAR and R:FR ratio			
	Medium PAR		Low PAR	
	38% PAR, Natural R:FR (1.33-1.34)	39% PAR, Low R:FR (0.57)	16% PAR, Natural R:FR (1.32-1.37)	17% PAR, Low R:FR (0.57)
Cocksfoot (Wana)	138	115	108	108
Cocksfoot (PG 74)	101	98	112	99
Cocksfoot (PG 321)	150	149	113	115
Perennial ryegrass (Nui)	119	101	73	109
Yorkshire fog	111	118	89	93
Browntop	80	50	41	38
Poa trivialis	41	40	31	35
Analysis of variance	**probability**	**SEM**		
PAR (A) (d.f. = 1)	P<0.05	4.6		
R:FR (B) (d.f.=1)	NS	4.6		
(A*B) (d.f.=1)	NS	4.4		
Species (C) (d.f.=8)	P<0.0001	5.8		
(C*A*B) (d.f.=8)	NS	11.5		
Contrasts				
Rye vs PG 74, PG 321, Wana	P<0.01			
Rye vs PG 74, PG 321, Wana, Y.fog, Poa, browntop	NS			

Similarly to total tillers, higher numbers of net tillers or branches per plant were produced by all the species at the medium PAR, than at the low PAR. Accordingly, highest net tillers per plant were measured in Poa and browntop among the grasses, and lotus had more net branches per plant than white clover (Table 5.7). This trend was similar under low PAR. R:FR ratio also affected the net tillers/branches per plant: more tillers or branches per plant were produced by all species at natural R:FR than at reduced R:FR except browntop in both medium and low PAR (Table 5.7).

Except PG 74 cocksfoot, which had a higher tiller weight at low PAR than at medium PAR mainly due to having fewer tillers, all other species had higher tiller weight at the medium PAR than at low PAR. Under medium PAR, PG 321 and Wana cocksfoot had the highest tiller weight/plant followed by Yorkshire fog, and perennial ryegrass. This trend was similar under low PAR as well (Table 5.8).

Table 5.9 Effect of level of PAR and R:FR on total number of leaves per plant of grass and legume species at final harvest in glasshouse conditions, 1997.

Species	% transmitted PAR and R:FR ratio			
	Medium PAR		Low PAR	
	38% PAR, Natural R:FR (1.33)	39% PAR, Low R:FR (0.57)	16% PAR, Natural R:FR (1.34)	17% PAR, Low R:FR (0.57)
White clover	100	81	32	24
Lotus	145	155	89	71
Cocksfoot (Wana)	78	76	65	43
Cocksfoot (PG 74)	73	56	27	22
Cocksfoot (PG 321)	63	68	36	44
Perennial ryegrass (Nui)	100	96	77	71
Yorkshire fog	98	86	80	73
Browntop	158	154	89	107
Poa trivialis	241	193	153	128
Analysis of variance	**probability**	**SEM**		
PAR (A) (d.f. = 1)	P<0.0001	2.12		
R:FR (B) (d.f.=1)	P<0.05	2.12		
(A*B) (d.f.=1)	NS	3.61		
Species (C) (d.f.=8)	P<0.0001	5.42		
(C*A*B) (d.f.=8)	NS	10.85		
Contrasts				
Legumes vs rest	NS			
Wc vs lotus	P<0.0001			
Rye vs PG 74, PG 321, Wana, Y.fog, Poa, browntop	NS			

There was a significant effect of PAR (P<0.001) and R:FR (P<0.05) on the total number of leaves per plant. However, none of the interactive effects of PAR, R:FR, and species were found to affect total number of leaves per plant except the interaction of species with PAR (P<0.001) (Table 5.9). In Yorkshire fog, perennial ryegrass and Wana cocksfoot, total number of leaves per plant was 17-30% under low PAR relative to medium PAR compared with 39% on PG 321 cocksfoot. Total number of leaves per plant was reduced by 69% in white clover under low PAR relative to medium PAR, whereas the reduction was only 47% in lotus. Poa and browntop had more total leaves per plant than the rest of the grass species at medium PAR. Lotus had more total number of leaves per plant than white clover at both PAR levels, and reduction in number of leaves at low PAR was much greater in white clover than in lotus. Total number of leaves per plant was higher on perennial ryegrass than on cocksfoot, but the-

Table 5.10 Effect of PAR and R:FR on specific leaf area (mm^2/mg) of grass and legume species at final harvest in glasshouse conditions, 1997.

Species	% transmitted PAR and R:FR ratio			
	Medium PAR		Low PAR	
	38% PAR, Natural R:FR (1.33)	39% PAR, Low R:FR (0.57)	16% PAR, Natural R:FR (1.34)	17% PAR, Low R:FR (0.57)
White clover	43.2	46. 8	38.4	60.0
Lotus	43.6	49.5	59.7	53.6
Cocksfoot (Wana)	26.3	25.7	32.6	36.8
Cocksfoot (PG 74)	33.7	31.6	37.2	39.0
Cocksfoot (PG 321)	29.4	24.9	29.0	32.0
Perennial ryegrass (Nui)	16.0	16.1	23.7	22.1
Yorkshire fog	41.0	39.6	47.2	48.1
Browntop	23.3	23.4	27.4	24.4
Poa trivialis	22.8	18.7	22.1	20.3
<u>Analysis of variance</u>	<u>probability</u>	<u>SEM</u>		
PAR (A) (d.f. = 1)	P<0.01	0.85		
R:FR (B) (d.f.=1)	NS	0.85		
(A*B) (d.f.=1)	NS	0.95		
Species (C) (d.f.=8)	P<0.001	1.43		
(C*A*B) (d.f.=8)	P<0.05	2.87		
<u>Contrasts</u>				
Legumes vs rest	P <0.001			
Wc vs lotus	P<0.05			
Rye vs PG 74, PG 321, Wana, Y.fog, Poa, browntop	P<0.001			

relative decrease in the total number of leaves per plant on Wana cocksfoot and perennial ryegrass at the low PAR was similar (Table 5.9)

5.4.4 Specific leaf area (SLA)

PAR significantly affected SLA (P<0.01), but there was no effect of R:FR on SLA, and also the interaction between PAR and R:FR was not significant (P>0.05). There was a significant effect (P<0.0001) of species on SLA, and also a significant interaction of species × R: FR (P<0.01), and PAR × species × R:FR (P<0.05) (Table 5.10).

All the species had a higher SLA under low PAR than under medium PAR, but species such as browntop, Poa and Yorkshire fog had similar SLA at both PAR levels. At low PAR, lotus had the highest SLA, whereas the Poa had the lowest. SLA of Wana cocksfoot was higher than perennial ryegrass at both PAR levels. SLA of PG 321 cocksfoot and PG 74 cocksfoot were similar to that of Wana cocksfoot (Table 5.10).

R:FR had no effect on SLA. Yorkshire fog had the highest SLA followed by PG 74 cocksfoot and Wana cocksfoot among the grass species, while lotus had a higher SLA than white clover. SLA of perennial ryegrass and Poa were lowest among the species under both natural and low R:FR (Table 5.10).

5.4.5 Leaf:stem ratio

Species and PAR significantly affected (P<0.01) the leaf:stem ratio. There were no interactive effects of PAR, R:FR, and species, except the interaction of species with PAR (Table 5.11). Higher leaf: stem ratio was found at low PAR for all species except lotus, which had similar ratio at low and medium PAR (Table 5.11). At medium PAR, leaf: stem ratio was highest for perennial ryegrass, and lowest for white clover. At low PAR, the highest leaf: stem ratio was for perennial ryegrass, followed by Wana cocksfoot and Yorkshire fog (Table 5.11).

Table 5.11 Effect of level of PAR and R:FR on leaf:stem ratio of grass and legume species at final harvest in glasshouse conditions, 1997.

Species	% transmitted PAR and R:FR ratio			
	Medium PAR		Low PAR	
	38% PAR, Natural R:FR (1.33)	39% PAR, Low R:FR (0.57)	16% PAR, Natural R:FR (1.34)	17% PAR, Low R:FR (0.57)
White clover	0.5	0.7	0.7	1.8
Lotus	0.8	0.7	0.7	0.7
Cocksfoot (Wana)	1.3	1.8	1.6	3.1
Cocksfoot (PG 74)	1.8	1.7	2.2	1.5
Cocksfoot (PG 321)	1.5	1.5	2.9	1.8
Perennial ryegrass (Nui)	1.8	2.0	2.6	2.6
Yorkshire fog	1.8	1.8	2.3	2.3
Browntop	1.3	0.9	1.7	1.7
Poa trivialis	1.2	1.0	2.0	1.7
Analysis of variance	**probability**	**SEM**		
PAR (A) (d.f. = 1)	P<0.01	0.07		
R:FR (B) (d.f.=1)	NS	0.07		
(A*B) (d.f.=1)	NS	0.08		
Species (C) (d.f.=8)	P<0.0001	0.12		
(C*A) (d.f.=8)	P<0.01	0.17		
(C*A*B) (d.f.=8)	NS	0.25		
Contrasts				
Legumes vs rest	P<0.0001			
Wc vs lotus	NS			
Rye vs PG 74, PG 321, Wana, Y.fog, Poa, browntop	P<0.001			

5.4.6 Root dry weight

Effects of PAR and R:FR on root dry weight were similar to the effects on leaf:stem ratio, where only the effects of PAR (P<0.001), species, and interactive effect of PAR × species were significant (P<0.0001). There was no effect of R:FR on root dry weight (Table 5.12).

Table 5.12 Effect of level of PAR and R:FR on root dry weight (g/plant) of grass and legume species at final harvest in glasshouse conditions, 1997.

Species	% transmitted PAR and R:FR ratio			
	Medium PAR		Low PAR	
	38% PAR, Natural R:FR (1.33)	39% PAR, Low R:FR (0.57)	16% PAR, Natural R:FR (1.34)	17% PAR, Low R:FR (0.57)
White clover	0.13	0.12	0.06	0.04
Lotus	0.21	0.16	0.04	0.03
Cocksfoot (Wana)	0.93	0.80	0.23	0.19
Cocksfoot (PG 74)	0.61	0.41	0.16	0.10
Cocksfoot (PG 321)	0.64	0.58	0.19	0.15
Perennial ryegrass (Nui)	0.89	0.82	0.20	0.17
Yorkshire fog	0.85	0.81	0.16	0.15
Browntop	0.30	0.32	0.08	0.06
Poa trivialis	0.50	0.35	0.14	0.11
Analysis of variance	**probability**	**SEM**		
PAR (A) (d.f. = 1)	P<0.001	0.02		
R:FR (B) (d.f.=1)	NS	0.02		
(A*B) (d.f.=1)	NS	0.01		
Species (C) (d.f.=8)	P<0.001	0.02		
(C*A) (d.f.=8)	P<0.001	0.35		
(C*A*B) (d.f.=8)	NS	0.04		
Contrasts				
Legumes vs rest	P<0.001			
Wc vs lotus	NS			
Rye vs PG 74, PG 321, Wana, Y.fog, Poa, browntop	P<0.001			

All the species had higher root dry weight at medium PAR than at low PAR, where Wana cocksfoot, followed by perennial ryegrass and Yorkshire fog had the highest root dry weight and white clover had the lowest (Table 5.12). At low PAR, root dry weight of Wana cocksfoot was the highest, whereas lotus, white clover and browntop had their lowest root dry weight (Table 5.12).

Table 5.13 Effect of level of PAR and R:FR on chlorophyll 'a' concentration (mg/g) of grass and legume species in glasshouse conditions, 1997.

Species	% transmitted PAR and R:FR ratio			
	Medium PAR		Low PAR	
	38% PAR, Natural R:FR (1.33)	39% PAR, Low R:FR (0.57)	16% PAR, Natural R:FR (1.34)	17% PAR, Low R:FR (0.57)
White clover	2.5	2.9	2.6	2.6
Lotus	2.5	2.3	2.5	3.0
Cocksfoot (Wana)	2.6	2.5	2.3	2.5
Cocksfoot (PG 74)	2.3	2.1	2.4	2.3
Cocksfoot (PG 321)	2.2	1.9	2.3	2.3
Perennial ryegrass (Nui)	1.8	2.1	1.5	1.7
Yorkshire fog	2.1	2.0	1.9	2.2
Browntop	3.1	3.3	3.3	3.2
Poa trivialis	2.4	3.0	2.5	3.0
Analysis of variance	**probability**	**SEM**		
PAR (A) (d.f. = 1)	NS	0.10		
R:FR (B) (d.f.=1)	NS	0.10		
(A*B) (d.f.=1)	NS	0.08		
Species (C) (d.f.=8)	P<0.001	0.12		
(C*A*B) (d.f.=8)	NS	0.25		
Contrasts				
Legumes vs rest	P<0.05			
Wc vs lotus	NS			
Rye vs PG 74, PG 321, Wana, Y.fog, Poa, browntop	P<0.01			

5.4.7 Chlorophyll concentration

Chlorophyll 'a' and 'b' concentration were not affected by PAR, R:FR ratio, and any interactions between them. There were only species differences in terms of chlorophyll concentration (Table 5.13, 5.14).

Browntop, Poa, white clover, and Wana cocksfoot had significantly higher concentrations of chlorophyll 'a' than other species. Perennial ryegrass had the lowest chlorophyll 'a', concentration. Except for lotus, PG 74 cocksfoot, and PG 321 cocksfoot, all species had higher chlorophyll concentrations at medium PAR than at the low PAR (Table 5.13). Concentration for chlorophyll 'b' were similar to those for

Table 5.14 Effect of level of PAR and R:FR on chlorophyll 'b' concentration (mg/g) of grass and legume species in glasshouse conditions, 1997.

Species	% transmitted PAR and R:FR ratio			
	Medium PAR		Low PAR	
	38% PAR, Natural R:FR (1.33)	39% PAR, Low R:FR (0.57)	16% PAR, Natural R:FR (1.34)	17% PAR, Low R:FR (0.57)
White clover	1.0	0.7	1.2	0.9
Lotus	1.1	0.8	1.0	1.3
Cocksfoot (Wana)	1.1	0.8	1.1	0.9
Cocksfoot (PG 74)	10.	0.7	1.0	0.8
Cocksfoot (PG 321)	0.9	0.8	1.1	0.8
Perennial ryegrass (Nui)	0.8	0.9	0.8	0.6
Yorkshire fog	0.8	0.7	0.8	0.8
Browntop	1.2	1.4	1.3	1.2
Poa trivialis	0.9	1.1	1.0	1.2
Analysis of variance	**probability**	**SEM**		
PAR (A) (d.f. = 1)	NS	0.05		
R:FR (B) (d.f.=1)	NS	0.05		
(A*B) (d.f.=1)	NS	0.05		
Species (C) (d.f.=8)	P<0.001	0.07		
(C*A*B) (d.f.=8)	NS	0.15		
Contrasts				
Legumes vs rest	NS			
Wc vs lotus	NS			
Rye vs PG 74, PG 321, Wana, Y.fog, Poa, browntop	P<0.01			

chlorophyll 'a', but all the species had lower concentrations of chlorophyll 'b' at medium PAR than at low PAR, except perennial ryegrass and browntop (Table 5.14).

There was a significant effect of PAR (P<0.05) and R: FR (P<0.01) on the ratio of chlorophyll 'a'/'b' (Table 5.15). However, no interactive effects of PAR, R:FR, and species were found (Table 5.15).

All the species had higher ratio of chlorophyll 'a'/'b' at medium PAR than at low PAR (Table 5.15). White clover, Yorkshire fog, and Wana cocksfoot followed by lotus had the highest ratio of chlorophyll 'a'/'b', whereas the ratio in perennial ryegrass was the lowest at medium PAR. At low PAR, however, the highest ratio was for Yorkshire fog followed by PG 74 cocksfoot and browntop. Lotus and Nui had the lowest ratio at the low PAR.

Table 5.15 Effect of level of PAR and R:FR on chlorophyll a:b ratio of grass and legume species in glasshouse conditions, 1997.

Species	% transmitted PAR and R:FR ratio			
	Medium PAR		Low PAR	
	38% PAR, Natural R:FR (1.33)	39% PAR, Low R:FR (0.57)	16% PAR, Natural R:FR (1.34)	17% PAR, Low R:FR (0.57)
White clover	2.4	4.5	2.3	2.8
Lotus	2.3	2.8	2.4	2.3
Cocksfoot (Wana)	2.5	3.0	2.2	2.7
Cocksfoot (PG 74)	2.4	3.0	2.4	2.7
Cocksfoot (PG 321)	2.5	2.6	2.2	2.8
Perennial ryegrass (Nui)	2.3	2.5	2.1	2.7
Yorkshire fog	2.7	2.9	2.6	2.8
Browntop	2.5	2.8	2.5	2.7
Poa trivialis	2.8	2.7	2.6	2.5
Analysis of variance	**probability**	**SEM**		
PAR (A) (d.f. = 1)	P<0.05	0.05		
R:FR (B) (d.f.=1)	P<0.01	0.05		
(A*B) (d.f.=1)	NS	0.09		
Species (C) (d.f.=8)	NS	0.14		
(C*A*B) (d.f.=8)	NS	0.28		
Contrasts				
Legumes vs rest	NS			
Wc vs lotus	P<0.01			
Rye vs PG 74, PG 321, Wana, Y.fog, Poa, browntop	NS			

The ratio of chlorophyll 'a'/ 'b' was higher at reduced R:FR than at to natural R:FR for all species except Poa, which had a similar ratio at both PAR levels (Table 5.15). White clover had the highest ratio at low R:FR followed by Wana cocksfoot, Yorkshire fog, and PG 74 cocksfoot, whereas the ratio of chlorophyll 'a'/ 'b' for perennial ryegrass at the natural R:FR was the lowest compared to the rest of the species (Table 5.15).

5.5 Discussion

The results showed that there was no interaction between PAR and R:FR for all of the parameters measured. On the other hand, a significant interaction of PAR × species was measured for shoot dry weight, leaf:stem ratio, root dry weight, log net tillers, and total number of leaves per plant, but not for leaf area, leaf dry weight, stem dry weight, SLA, tiller weight and chlorophyll concentration. There were no interactive effects of R:FR × species, and PAR × R:FR × species for any parameters except SLA. The effect of R:FR was not significant for most of the parameters studied, except stem dry weight, log total tillers, log net tillers, total leaf number per plant, and the chlorophyll 'a'/ 'b' ratio.

Effects of R:FR on plant species have been widely studied, particularly to investigate the evolution of plant function (Schmitt and Wulff 1993) and the structure of natural vegetation (Smith 1982; Deregibus *et al.* 1983; 1994). Studies on the effects of R:FR have often focussed either at the seedling stage to determine the sensitivity to light competition (Jefferson and Muri 1997), or to understand the effects of increased or decreased ratio of R:FR light on a particular plant part such as the growing point of white clover, and the shoot base of grasses (Casal *et al.* 1985, 1986, 1987a, b; Solangaarachchi and Harper 1987; Thompson 1993; Hay *et al.* 1997), which are important from physiological points of view (Keating and Carberry 1993), instead of the morphology and production potential of the plants. The results of this study clearly indicated that PAR is more important to the pasture species than R:FR ratio from the production point of view. Results showed that apart from some interactive effects of R:FR as in the case of stem dry weight, tillers, and total leaves per plant, other parameters related to the yield and yield components were not affected by R:FR ratios. This evidence combined with significant effects of PAR for all the parameters except chlorophyll concentration, clearly indicated the relative importance of PAR over R:FR.

The ability of plant species to tolerate low light (shading) has its basis in photosynthesis, viz. in the efficiency of utilization of light energy (Corré 1983a, b). The role of photomorphogenic light is mainly to work as a regulator of photosynthate allocation in growing plants (Kasperbauer and Hunt 1998).

Table 5.16 Summary table of the parameters measured: mean values of the PAR and R:FR and the differences.

Parameters	PAR			R :FR		
	Mean of medium PAR (38, 39%) (a)	Mean of low PAR (17, 16%) (b)	Ratio of relativity index % [1]	Mean of natural R:FR (38, 16%PAR) (a)	Mean of low R:FR (39, 17% PAR) (b)	Ratio of relativity index % [1]
Dry weight (g/plant)	1.86	0.78	41	1.40	1.29	92
Leaf area (mm^2/plant)	34296	21666	63	29663	15206	51
Leaf dry weight (mg/plant)	1189	656	55	979	866	88
Specific leaf area (mm^2/mg)	30	36	117	33	34	102
Stem dry weight (g/plant)	0.92	0.36	39	0.70	0.58	82
Leaf :stem ratio	1.33	1.88	141	1.58	1.62	102
Root dry weight (g/plant)	0.52	0.12	23	0.35	0.29	82
Log total tillers /plant	3.20	2.67	83	3.01	2.86	95
Log net tillers per plant developed inside the shade	2.96	2.23	75	2.70	2.49	96
Tiller weight (mg/plant)	100	82	82	93	90	99
Total number of leaves/plant	112	68	60	94	86	90
Chlorophyll 'a' (mg/g)	2.40	2.43	101	2.36	2.46	104
Chlorophyll 'b' (mg/g)	0.91	0.98	107	0.98	0.91	92
Ratio of chlorophyll 'a' / 'b'	2.73	2.50	91	2.42	2.80	115

[1] value of low (b)/value of medium (a) ×100

Generally, the values for all the parameters were greater at medium PAR than at low PAR, and at natural R:FR than at reduced R:FR (Table 5.16). However, reduction at the low PAR, in comparison to medium PAR was much greater than at the low R:RF compared with natural R:FR. This further strengthened the findings of previous studies (Chapters 3, 4), based on alteration of PAR only. However, these conclusions are limited as they relate to only two levels of PAR and R:FR ratios. A lower R:FR ratio than measured in this experiment could have had a greater effect on the parameters measured.

In this experiment, mean PAR at medium and low shade were maintained 181-189 μmoles photons m^{-2} s^{-1} and 78-84 μmoles photons m^{-2} s^{-1}, respectively, where reduced

R:FR ratio was 0.57 compared with 1.33 for natural R:FR. The lower R:FR ratio was similar to the R:FR ratio of 0.4-0.6 under dense tree canopies as reported by Wilson (1997), and that for deciduous wood lots of 0.36-0.97 (Smith 1982).

Of the parameters measured, root weight was most affected followed by shoot dry weight and leaf dry weight (Table 5.9). Considering the PAR effects only, it was noted root dry weight at low PAR was only about 23% of the medium PAR, whereas in terms of R:FR ratios, root dry weight at the reduced R:FR was more than 80% of that of natural R:FR. Similarly, mean shoot dry weight of the pasture species at low PAR was only about 41% of the medium PAR compared to 92% at reduced R:FR to that of natural R:FR. Likewise, mean leaf dry weight of the pasture species was only about 55% at low PAR of that at medium PAR, whereas at low R:FR, it was nearly 90% of that of natural R:FR.

Comparatively, tiller related attributes were least affected at low PAR and also at low R:FR. At low PAR, >75% of the total tillers and net tillers/plant was produced by the pasture species compared to that of medium PAR, while it was >95% in the case of low R:FR relative to that of natural R:FR. This also indicated that tillering was least affected under low R:FR in this study relative to the reduction from medium PAR to the low PAR. However, there was a significant effect of R:FR on the tillering ability of pasture species studied (Table 5.9, 5.10). But, this could be largely also due to the influence of R:FR only on some species like white clover, while on average, effects of R:FR seem negligible relative to those of natural R:FR. Significant effects of R:FR on the pasture species also suggested that there could be a different response of light quality as per differences in species. Casal *et al.* (1986), however, reported that tillering was reduced in perennial ryegrass at low R:FR. But, mean net tillers of all the species in this study indicated that there were no marked effects of reduced R:FR on tillering. Low or no effect of R:FR on tillering in this study, however, partly could be due to the general application of reduced R:FR inside the shade frame rather than specifically treating the individual plant parts. Hay *et al.* (1997) reported the localised response of R:FR to the apical bud of white clover in order to get the effects of reduced R:FR treatment.

Yorkshire fog, Wana cocksfoot, browntop, and Poa had higher shoot dry weight than the rest at medium PAR, but at low PAR, perennial ryegrass, Wana cocksfoot and Yorkshire fog had similar and higher shoot dry weight than the other species. One of the important parameters, SLA which had the interaction for PAR as well as species and R:FR indicates the different response of SLA to the species. This also indicated that there could be an important relationship between SLA and shoot dry weight per plant which could be varied by changes in both PAR and R:FR. Higher SLA of Wana cocksfoot, lotus, PG 74 cocksfoot and Yorkshire fog than of perennial ryegrass indicated the importance of SLA in terms of higher shoot dry weight.

In general, responses to low-light stress include an increase in plant leaf area (Sanderson *et al.* 1997) which is usually at the expense of leaf thickness (Kephart *et al.* 1992; Kephart and Buxton 1993) resulting in increased SLA. European tall-shrub species increased SLA in shade (Grubb *et al.* 1996), and pasture species like white clover grown at the reduced light of 30 J m^{-2} s^{-1} also had greater SLA and longer petioles than unshaded plants (Dennis and Woledge 1983). Dennis and Woledge (1983) demonstrated that white clover grown in dim light or shade had a higher SLA, which is interpreted as an adaptation to shade in that for each unit weight of leaf dry matter a greater area is exposed to the available light. Higher SLA therefore means greater ability of pastures to adapt and produce more in shade. Devkota *et al.* (1997) reported that lotus, Yorkshire fog, and Wana cocksfoot all produced relatively higher SLA and shoot dry weight than other species in heavy shade (14% transmitted PAR).

Wana cocksfoot was one of the most shade tolerant cultivars in terms of shoot dry weight per plant, mainly due to the larger leaf area per plant, higher number of tillers and SLA per plant. This is consistent with the results of the previous studies (Chapters 3, 4) and also with the findings of other researchers (Seo *et al.* 1989) that Wana is a shade tolerant cultivar and that it persists well under shade. However, total leaf number seems less important for Wana cocksfoot than to perennial ryegrass and Yorkshire fog, as Wana cocksfoot had lower number of leaves per plant compared to those species, but had a greater shoot dry weight in the shade.

Perennial ryegrass also had a greater shoot dry weight per plant like Wana cocksfoot, which was in contrast to the results of the previous studies (Chapters 3,4). As in the case of Wana cocksfoot, greater shoot dry weight of perennial ryegrass was mainly supported by the higher leaf area per plant, higher leaf dry weight, and higher number of tillers per plant, but not by changed SLA. Perennial ryegrass had a lower SLA compared with Wana cocksfoot and Yorkshire fog (Table 5.10).

One important reason for the greater shoot dry weight per plant of perennial ryegrass could be the establishment of pasture species under full sunlight at the beginning of the experiment (section 5.2.1). Similarly, pasture species were not defoliated for the entire experimental period unlike the previous experiments. Perennial ryegrass establishes faster than other species even under shade (Barker and Hunt 1997), and thus could have the advantage of capturing higher resources due to the maintenance of higher tiller numbers and leaf area per plant compared with other species. Nevertheless, this suggests that, provided the optimum leaf area and tiller density are maintained by optimum grazing/defoliation management, perennial ryegrass could be a useful improved grass species to grow under shade despite being a shade intolerant species.

Shoot dry weight per plant of Yorkshire fog was lower than Wana cocksfoot and perennial ryegrass at low PAR in this study. West *et al.* (1991) also reported that Yorkshire fog was more vigorous than lotus as a forest understorey during the early establishment phase from May to September. However, Yorkshire fog in this experiment did not produce the highest shoot dry weight per plant despite having the highest leaf area per plant. Higher SLA, total tiller numbers and net tiller numbers per plant as well as higher chlorophyll ‘a’/ ‘b’ ratio were the main contributing factors for the higher shoot dry weight per plant of Yorkshire fog in low shade.

Shoot dry weight per plant of the cocksfoot cultivars such as PG 74 and PG 321 was between the legumes and the high producing grasses such as Wana cocksfoot and perennial ryegrass. However, PG 74 cocksfoot had the higher SLA at the low PAR compared with Wana cocksfoot and perennial ryegrass, while PG 321 had higher leaf:stem ratio compared with both Wana and perennial ryegrass, especially under low PAR with natural R:FR, and both the cultivars had the highest tiller weight per plant, specially under low PAR with natural R:FR. Lower shoot dry weight per plant of these species compared with Wana cocksfoot could be due to lack of defoliation management. Results of the previous studies (Chapters 3, 4) indicated that these species also produced similar shoot dry weight per plant with Wana cocksfoot under heavy shade and regular defoliation management.

Browntop and Poa produced high shoot dry weight per plant at medium PAR, but not at low PAR. Higher shoot dry weight per plant of these species at medium PAR was due to the higher number of tillers/plant, and chlorophyll concentration rather than leaf area (Table 5.7), leaf dry weight (Table 5.8), and specific leaf area (Table 5.18). In the previous experiments (Chapter 3), shoot dry weight production of both browntop, and Poa was worse under heavy shade and periodic defoliation.

Production was poorer for the legumes than the grass species at both shade levels. However, lotus was less affected than white clover under low PAR in terms of shoot dry weight per plant. The leaf area of lotus was higher than the white clover at medium PAR, but was lower than white clover at low PAR. Still, white clover had the lowest shoot dry weight per plant at low PAR which could be mainly due to the lower number of leaves (Table 5.16), and fewer stolons/plant, possibly resulting from the suppression of stolons (Tables 5.9, 5.10, 5.12 and 5.13). White clover also had the highest SLA at low PAR and low R:FR. Leaf dry weight per plant of white clover at low R:FR was reduced compared to its comparatively higher leaf area (Table 5.4). The relatively poor performance of white clover thus appeared to result from the sensitivity of its stolons to low light.

Similar shoot dry weight, higher SLA, number of branches/plant, and total leaves per plant for lotus than white clover, indicated the suitability of lotus compared to white clover for growth under shade, as found in Chapter 3. Gadgil *et al.* (1986), West *et al.* (1988), and West *et al.* (1991) also indicated that lotus is one of the most successful legumes under shade, and can be readily established on a range of sites.

5.6 Conclusions

The effect of R:FR ratio was not significant for most of the parameters measured except stem dry weight, tiller numbers and total number of leaves per plant. PAR was a more important factor than light quality in influencing pasture growth under shade, and grass species were more productive than legumes at low PAR. Perennial ryegrass, Wana cocksfoot and Yorkshire fog had the highest and similar shoot dry weight per plant under low shade without defoliation. Poa and browntop had the highest tillers/plant at low PAR, as well as low R:FR. However, the higher number of tillers for these two species did not support a high shoot dry weight at the low PAR, mainly due to the low tiller weight. Shoot dry weight was more affected in white clover than lotus at low PAR, and they were both more severely affected than the grass species. However, lotus had a higher SLA, and a higher number of branches per plant than white clover, especially under low PAR with natural R:FR. White clover was more affected by light quality than lotus and the grass species. Yorkshire fog and Wana cocksfoot had a greater leaf area production under the low PAR, and were less affected by the changes in light quality than the other species. The effects of R:FR on the tillering of Yorkshire fog and Wana cocksfoot were not as severe as for other species under low PAR.

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6. Effect of defoliation frequency on the performance of Nui perennial ryegrass and Wana cocksfoot under glasshouse conditions

Page

6.1 Summary

Two experiments were conducted to determine the relative growth rate (RGR) of two grass species at the seedling stage, and also to obtain more information on their tillering and biomass producing ability at different PAR/RF ratios and defoliation frequencies.

Experiment 6.1 was conducted from 15 April to 19 June 1998 at the Plant Growth Unit (PGU), Massey University. A split-plot design was employed with three replicate blocks. The main plots were three levels of % transmitted PAR, μmoles photons m^{-2} s^{-1}, 400-700 nm, and R: FR ratio (photon irradiance between 655 and 665 nm, and between 725 and 735nm). *Dactylis glomerata* L. cv. Grasslands Wana, and *Lolium perenne* L. cv. Grasslands Nui were compared as sub-plots. Among three PAR levels, one was natural PAR under the glasshouse. For the other two PAR levels filters were used, one was covered with neutral shade cloth (Sarlon) plus a layer of clear filter (Effects filters, 130 clear) while the other was covered with neutral shade cloth plus the steel blue filter (Effects filter, 117) so that PAR levels of the two treatments were similar, but the blue filter provided a low R:FR while the clear filter had a natural R:FR ratio. Two plants were grown per pot. Water and fertiliser were non- limiting. Seven pots of each treatment were maintained to conduct destructive harvests in each successive week in order to carry out growth analysis.

Experiment 6.2 was conducted from 15 April, 1998 to 10 August, 1998 under similar conditions to experiment 6.1. Six plants were maintained per pot. Plants were watered daily. 3 PAR/RF levels were used as main plots. Nui perennial ryegrass and Wana cocksfoot were grown in pots as sub-plots, and were defoliated at weekly (W1) and three weekly (W3) intervals as sub-sub plots. At each defoliation, clipped biomass was oven dried to calculate per plant cumulative herbage dry weight, and plants were fully harvested on 10 August, 1998. Total tillers in each treatment were counted weekly. Likewise tiller site usage value was also calculated.

Results showed that the total (above and underground) RGR of Wana was always higher than Nui at all PAR/RF, in contrast to the consistently higher absolute mass per plant of

Nui over Wana at each PAR level. RGR of Wana was also less affected by reduced PAR compared with Nui. However, RGR of both species was not affected by low R:FR.

Results of the defoliation experiment showed that effect of PAR/RF was significant for cumulative shoot dry weight ($P<0.001$), leaf area development ($P<0.01$), leaf dry weight ($P<0.001$), SLA ($P<0.01$), tillers per plant ($P<0.001$), and root dry weight per plant at the final harvest ($P<0.0001$). Species differences were also significant for all these measurements. At low PAR, Wana produced more shoot dry weight than Nui under both defoliation frequencies. Wana outperformed Nui, especially at low PAR, mainly due to the ability to produce higher leaf area and higher leaf dry weight. SLA of Wana was significantly higher ($P<0.001$) than that of Nui for W1 as well as W3 defoliation. Wana had significantly more tillers per plant than Nui at both low PAR plus natural and reduced R:FR. Site usage value was also higher for Wana at low PAR plus natural R:FR. Leaf appearance interval was shorter for Wana than Nui at all light levels. In this experiment Nui was more affected by defoliation than Wana. Its low level of site usage value reflected that under heavy shade and defoliation condition Nui would have less chance of producing tillers than Wana. Wana could continue to produce leaf in spite of high defoliation intensity.

6.2 Introduction

Many plant species have a constant relative growth rate (RGR) (Hunt 1982) over a wide range of irradiance. Plants grown in a low light intensity in the seedling development phase, before the morphological adaptations to low light are accomplished, can have decreased RGR because the relative increase in leaf area cannot compensate for the lower light (Corré 1983). However, studies on the differing reactions of RGR in different light environments in pasture species are scarce.

Perennial forages are defoliated once or more during the growing season. Removing the aboveground phytomass causes a large stress on the stubble, roots, and rhizomes by depriving them partially or totally of assimilates (Richards 1993; Sanderson *et al.* 1997). The growth of perennial forages after defoliation is an important aspect of grazing system management (Li *et al.* 1997). The removal of biomass by defoliation, generally results in a reduction in absolute growth rate (AGR) depending on the RGR and the amount of defoliated biomass (Hilbert *et al.* 1981; Li *et al.* 1997; Thornton and Millard 1997).

The extent to which physiological and morphological responses influence pasture production depends on the defoliation regime and the balance obtained between the supply and demand of growth resources by plants (Chapman and Lemaire 1993). In general, defoliation reduces the supply of photosynthate to roots, but increases it to shoot meristems and leaf growth regions (Bassmann and Dickmann 1985). This kind of compensatory process of increased export from source to growing shoot sinks contributes to a rapid re-establishment of the photosynthetic canopy to restore homeostatic growth after defoliation (Richards 1993; Chapman and Lemaire 1993). If, however, the limitation is more significant due to frequent or severe defoliation, plants are unable to restore their original resource supply rates. Moreover, a very low level of leaf area index (LAI) left after defoliation markedly reduces photosynthesis because of insufficient green leaf tissue (Chapman and Lemaire 1993).

The effects of defoliation could differ between plant species in the shade due to different plant architecture (Gautier *et al.* 1999), differences in ability to regenerate leaf area after defoliation (Wilson and Ludlow 1991), and also differences in the capacity to maintain leaf area in response to defoliation frequency (Nassiri and Elgersma 1998). The growing region of the leaf is a strong sink that can deprive other sinks, such as tiller buds. Hence, defoliation of pasture plants under low light intensity will have a greater effect than under high light intensity due to the decline in photosynthetic leaf area and therefore light interception leading to a lower tiller density (Wong and Stür 1996).

The previous experiments of pasture species showed the importance of PAR over R:FR ratio with a marked effect of shade on tillering as well as on shoot dry weight accumulation. Also, there were differences in species in terms of shade tolerance (Chapters 3,4,5). Two further experiments were conducted to determine the RGR of selected species at the seedling stage, and also to obtain more information on the tillering and biomass producing ability at different PAR/RF ratios and defoliation frequencies.

The objective of this research was to determine the morphological and growth responses of perennial ryegrass and cocksfoot to defoliation at high light intensities with natural R:FR ratio, and low light intensities with natural as well as reduced R:FR ratio. The species were chosen to represent heavy shade tolerance (cocksfoot, cv. Grasslands Wana) and relative shade intolerance (perennial ryegrass, cv. Grasslands Nui) as determined by the previous studies (Chapters 3,4,5).

6.3 Materials and methods

6.3.1 Design and treatments

Experiment 6.1 was conducted from 15 April, 1997 to 9 June, 1997 (56 days) at the Plant Growth unit (PGU), Massey University. A split- plot design was used with three replicate blocks: the main plots were three levels of light intensity and subplots were two pasture species. Shade levels were imposed with different densities of neutral shade cloth (Sarlon) supported on hollow metal frames (1.25 × 0.84 × 0.45m) arranged on benches that were 0.9 m above the ground. The shade frames were aligned in a north-south direction (across the sun direction) in order to avoid direct radiation during low sun elevation thus completely enclosed the pots. Three levels of transmitted photosynthetically active radiation (PAR; μmoles photons $m^{-2}s^{-1}$,400-700nm) were created. The transmitted PAR for the three treatments was 69, 25 and 24% of the ambient PAR determined on a daily basis from 1200 to 1300 h throughout the experiment using a LI-COR (Model LI-185) portable quantum sensor. The treatment with 69% ambient PAR, or 31% shade, was not covered by shade cloth, as this was the percentage of ambient PAR transmitted through the glasshouse. For the other two PAR levels, one was covered with neutral shade cloth (Sarlon) plus a layer of clear filter (Effects filters, 130 clear, Chris James and Co. LTD; Lighting Filters, 43 Colville Road, Acton, London) while the other was covered with neutral shade cloth plus the steel blue filter (Effects filter, 117) so that PAR levels of the two treatments were similar, but the blue filter provided a low R:FR while the clear filter had a natural R:FR ratio. PAR was measured inside and outside the glasshouse at the same time. Red:Far Red (R:FR) ratio during clear sky days was measured two times during 1200 to 1300h with a Skye sensor under the filters as well as in the open inside the glasshouse.

Details of the pasture species and cultivars used are given in Table 6.1. Seeds of the pasture species were sown on 15 April, 1998 in PB $6^1/_2$ (3.9 litres) black polypots filled with potting mix (80% tree bark + 20% pumice). Dolomite 300g, agricultural lime 300g, iron sulphate 50g, and Osmocote plus (16N-3.5P-10.8K) 400 g per 100 litre were blended with the potting mix, which was rated for medium to long-term (<9 months) greenhouse crops. There were seven pots for each treatment so that weekly destructive harvests for growth analysis could be made. Two plants were grown per pot, and plants were watered daily.

Experiment 6.2 was conducted from 15 April, 1998 to 10 August, 1998 (118 days) using the same method as Experiment 1, but with different design and treatments. The transmitted PAR for the three treatments was 71, 25 and 24% of the ambient PAR determined on a daily basis from 1200 to 1300 h throughout the experiment using a LI-COR (Model LI-185) portable quantum sensor. The treatment with 71% ambient PAR, or 29% shade, was not covered by shade cloth, as this was the percentage of ambient PAR transmitted through the glasshouse. The other two levels of PAR were obtained with the same arrangement of filters and shade cloth as in Experiment 6.1. The slight difference in the levels of PAR in Experiment 6.2 compared to that of Experiment 6.1 was probably due to the longer period over which the experiment was conducted. Red:Far Red (R:FR) ratio during clear sky days for this experiment was measured three times during 1200 to 1300h with a Skye sensor under the shade of the blue and clear filters, which also included the first two times of measurement for Experiment 6.1.

Pasture species used in experiment 6.2 were the same as those in Table 6.1. Seeds of the pasture species were sown on 15 April, 1998 in PB $6^1/_2$ (3.9 litres) black polypots filled with potting mix (80% tree bark + 20% pumice). Dolomite 300g, agricultural lime 300g, iron sulphate 50g, and Osmocote plus (16N-3.5P-10.8K) 400 g per 100 litre were blended with the potting mix, which was rated for medium to long-term (< 9 months) greenhouse crops. Six plants were maintained per pot. Plants were watered daily.

A split-split plot design was used with three replicate blocks: the main plots were shade treatments; two species, Nui ryegrass, and Wana cocksfoot were maintained in pots as the subplots, and sub-sub plots were Nui and Wana plants in subplots defoliated either weekly (W1) or three weekly (W3) (Figure 6.1).

Table 6.1 Pasture species and cultivars used in the Experiment.

Pasture species
1. Cocksfoot (*Dactylis glomerata* L.) cv. Grasslands Wana
2. Perennial ryegrass (*Lolium perenne* L.) cv. Grasslands Nui

6.3.2 Measurements

6.3.2.1 Experiment 6.1

Plants were first harvested on 28 April, 1998 (two weeks after sowing). Subsequent harvests were at 7day intervals; 5 May, 12 May, 19 May, 26 May, 2 June and 9 June 1998. At each harvest, one pot from each treatment was randomly selected. All the leaves and stems of both plants were separated, then were dried at 70 ^{0} C for 24 hours. Roots of both plants per pot were washed and then oven dried at 70 ^{0} C for 24 hours. Total dry weights of stem, leaf, and root per pot were converted to per plant values.

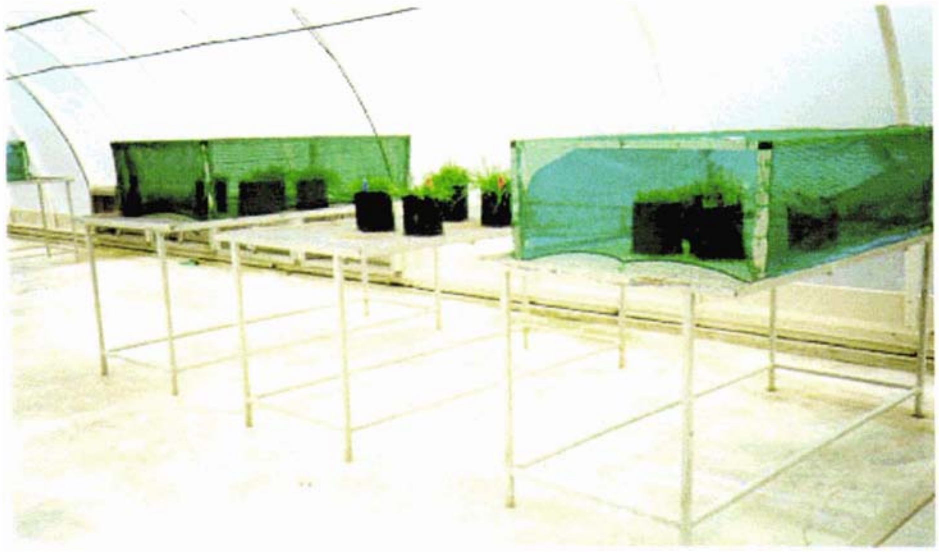


Figure 6.1 Experimental set-up showing one replication: 24% PAR plus reduced R:FR with the use of filters, and 25% PAR plus natural R:FR ,without filters.

6.3.2.2 Experiment 6.2

Defoliation was first imposed on 8 June, 55 days after sowing, at 50 mm above the media surface. Three cycles of three-weekly defoliation were completed by 10 August, 1998. At each defoliation, clipped biomass was oven dried at 70 ^{0} C for 24 hours and added to the cumulative herbage mass per plant. On 10 August 1998, one plant from each treatment was randomly selected, all the leaves and stems separated and the leaf area measured. Leaves and stems were then dried at 70 ^{0} C for 24 hours and added to the cumulative mass per plant. The remaining 5 plants were harvested at the base, and oven dried at 70 ^{0} C for 24 hours and added to the cumulative mass. Roots of all six plants were washed and oven dried at 70 ^{0} C for 24 hours to calculate root mass per plant.

Total tillers in each pot were counted weekly. Site Usage was calculated as:

$$SU = \{\ln(tn_b) - \ln(tn_a)\}/LI$$

Where, SU= site usage, tillers/leaf; tn_b= tiller numbers per plant at time 'b'; tn_a= tiller numbers per plant at time 'a', and LI = leaf appearance interval in days (Skinner and Nelson 1992). Leaf Appearance Interval (LI) for each treatment was determined by counting the days for each new leaf to appear. Since the defoliation treatment was imposed at weekly (W1) or three-week (W3) intervals, it was practically impossible to mark a single tiller and count the days to leaf appearance for the weekly defoliation regime (W1). Hence, 30 tillers in total, irrespective of replication, in W1 treatments were selected and marked with a plastic ring. All the leaves on each tiller were marked, and new leaves on the marked tillers were counted 6 days later, before imposing defoliation. Thus 180 tiller days were maintained in order to increase the probability of the appearance of new leaves within the week in order to calculate the average leaf appearance interval. For the W3 treatments, one tiller per treatment was randomly selected and marked with a plastic ring, all of the old leaves were spotted with a blue marker, and new leaves were counted daily during 1200-1300h until imposing the next defoliation. This process was repeated three times, with cycle one from 8 June to 28 June, two from 29 June to 19 July, and three from 20 July to 9 August 1998.

6.3.3 Statistical analysis

PROC GLM programme of SAS version 6.12 (SAS 1997) was used for all analyses. For Experiment 6.1, total dried mass of leaf, stem and root per plant were log transformed using the natural logarithm and regressed against time. The regression slope estimated mean relative growth rate (Hunt 1982). ANOVA was performed on regressed data to assess significance of differences in relative growth rate. For Experiment 6.2, residuals were examined for their normality, and appropriate transformation was carried out (SAS 1997) as indicated on the appropriate result table. The α level was set at 0.05. For all the tables NS denotes non significant at $P>0.05$.

6.4 Results

6.4.1 Experiment 6.1

6.4.1.1 Light environment

Mean PAR at noon in the three shade treatments was 486, 177, and 169 µmoles photons $m^{-2}s^{-1}$ resulting in 69, 25 and 24% ambient PAR respectively (Table 6.2). Mean PAR outside the glasshouse was 707 µmoles photons $m^{-2}s^{-1}$.

Table 6.2 Light environment and shade levels used in Experimental 6.1.

Shade	Mean PAR (µmoles photons $m^{-2}s^{-1}$)	% full sun light	R:FR ratio
0% shade, no shade cloth	486	69	1.36
50% shade cloth + natural R:FR	177	25	1.33
30% shade cloth + blue filter (low R:FR)	169	24	0.68

6.4.1.2 Above ground biomass

Aboveground biomass, leaf and stem dry mass (mg/plant) at each harvest under different PAR levels are presented in Table 6.3. There was a significant effect ($P<0.01$) of shade (except for 28 April), along with the differences in species ($P<0.001$), and the interaction ($P<0.01$) of shade and species for all the harvests (Table 6.3). Accordingly, both Nui and Wana produced their highest mass at 69% PAR and lowest at 24, and 25% PAR. Likewise, biomass of Nui was always higher ($P<0.001$) than Wana at each harvest, while mass of both species under 25% and 24% PAR was similar throughout the period (Table 6.3).

Table 6.3 Above ground mass for Grasslands Nui perennial ryegrass and Grasslands Wana cocksfoot under different PAR and R:FR levels.

Treatments	April 28 (0-14 days)	May 05 (14-21 days)	May 12 (21-28 days)	May 19 (28-35 days)	May 26 (35-42 days)	June 02 (42-49 days)	June 09 (49-56 days)
	Above ground mass (mg/plant)						
69% PAR, 0% shade							
Nui	1.0	8.0	31.0	95.0	231.0	426.0	785.0
Wana	0.4	1.0	10.0	33.0	96.0	206.0	368.0
25% PAR, natural R:FR							
Nui	1.0	4.0	9.0	32.0	75.0	101.0	174.0
Wana	0.4	1.0	3.0	11.0	37.0	72.0	137.0
24% PAR, low R:FR							
Nui	1.0	4.0	15.0	36.0	60.0	119.0	173.0
Wana	0.1	1.0	4.0	13.0	38.0	74.0	133.0
Analysis of variance							
Interactions (A*B)	**	*	**	***	*	***	**
SEM	0.08	0.6	1.0	2.0	16.0	13.0	35.0

* P<0.05, ** P<0.01, *** P<0.001, degrees of freedom: 2 for shade, 1 for species, and 2 for shade × species. A and B denotes shade and cultivars, respectively. SEM=standard error of the mean

Nui had greater below ground mass than Wana at 69% PAR, which was significantly higher (P<0.01) than that at 24 and 25% PAR for all harvests (Table 6.4). Nui had similar below ground mass under 24 and 25% PAR, as did Wana, but the mass of Nui was always higher (P<0.001) than that of Wana for all harvests.

Table 6.4 Below ground mass for Grasslands Nui perennial ryegrass and Grasslands Wana cocksfoot under different PAR and R:FR levels.

Treatments	April 28 (0-14 days)	May 05 (14-21 days)	May 12 (21-28 days)	May 19 (28-35 days)	May 26 (35-42 days)	June 02 (42-49 days)	June 09 (49-56 days)
	Below ground mass (mg/plant)						
69% PAR, 0% shade							
Nui	1.6	2.0	8.0	24.0	55.0	172.0	344.0
Wana	0.6	1.0	3.0	9.0	28.0	66.0	133.0
25% PAR, natural R:FR							
Nui	1.0	1.0	2.0	5.0	11.0	16.0	32.0
Wana	0.4	0.6	2.0	3.0	7.0	11.0	23.0
24% PAR, low R:FR							
Nui	1.0	1.0	2.0	6.0	8.0	15.0	31.0
Wana	0.5	0.7	1.0	3.0	7.0	12.0	24.0
Analysis of variance							
Interactions (A*B)	NS	NS	*	**	*	***	***
SEM	0.1	0.1	0.7	1.0	3.0	0.6	12.0

* P<0.05, ** P<0.01, *** P<0.001, degrees of freedom: 2 for shade, 1 for species and 2 for shade × species. A and B denotes shade and cultivars, respectively. SEM=standard error of the mean

6.4.1.3 Relative growth rate (RGR)

The total (above and below ground) relative growth rate of Nui and Wana increased, in general, with increase in ambient PAR. There was also a significant effect of shade (P<0.001) as well as differences in the species (P<0.001) in the relative growth rate of Nui and Wana (Figure 6.2).

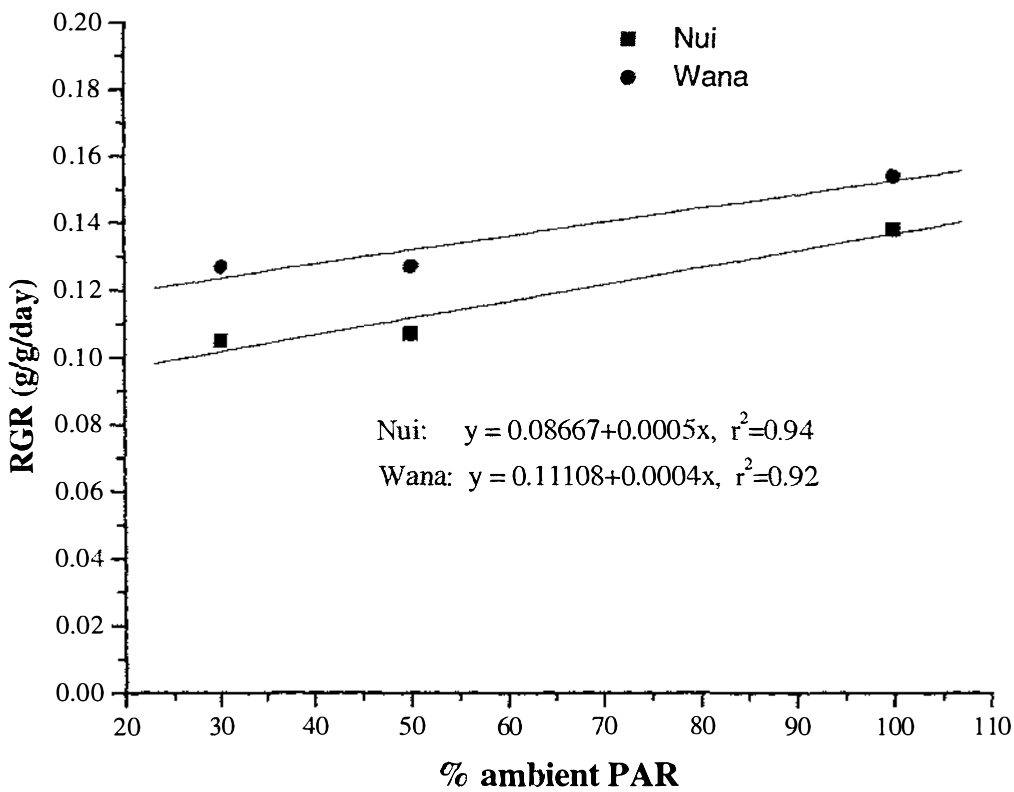


Figure 6.2 RGR of Wana and Nui grown under varied PAR levels and R:FR: ($P<0.01$) for PAR as well as species with NS for interaction of PAR × species. SEM of PAR and of species ± 0.001. Note that PAR levels on the x axis are adjusted to the shade rating of the Sarlon shade cloth: 30% PAR for the 24% PAR with low R:FR treatment, 50% PAR for 25% PAR with natural R:FR treatment, and 100% PAR (no shade cloth) for the 69%PAR with natural R:FR treatments.

Wana always had higher RGR than Nui at all PAR levels and R:FR ratios (Figure 6.2). RGR of Wana and Nui at both 24 and 25% PAR were similar. However, both Nui and Wana had higher RGR at 69% PAR compared with RGR at 24 and 25% PAR (Figure 6.2).

6.4.2 Experiment 6.2

6.4.2.1 Light environment

Mean PAR at noon in the shade treatments was 441, 153, and 149 μmoles photons $m^{-2}s^{-1}$ resulting in 71, 25 and 24% ambient PAR, hereafter called H/N, L/N and L/R, respectively, (Table 6.5). Mean PAR outside the glasshouse was 623 μmoles photons $m^{-2}s^{-1}$.

Table 6.5 Light environment and shade levels used in Experiment 6.2.

Shade	Mean PAR (μ moles photons $m^{-2}s^{-1}$)	% full sun light	R:FR ratio	Remarks
0% shade, no shade cloth	441	71	1.36	High PAR, natural R:FR (H/N)
50% shade cloth+ natural R:FR	153	25	1.34	Low PAR, natural R:FR (L/N)
30% shade cloth + blue filter (low R:FR)	149	24	0.68	Low PAR, reduced R:FR (L/R)

6.4.2.2 Shoot dry weight

Effects of PAR/RF, species, and defoliation on shoot dry weight per plant were all significant ($P<0.001$). Likewise interactions for PAR/RF×defoliation, species×defoliation and PAR/RF×species were also significant ($P<0.01$), but not the PAR/RF×species×defoliation. Both Nui and Wana had higher cumulative shoot dry weight at high PAR plus natural R:FR than at low PAR plus natural R:FR and low PAR plus reduced R:FR (Table 6.6). Between the species, Nui had higher cumulative shoot dry weight than Wana at high PAR plus natural R:FR while between the defoliation frequencies, W3 had higher cumulative shoot dry weight than W1. However, at low PAR and natural R:FR, Wana produced higher shoot dry weight than Nui under both defoliation frequencies.

Table 6.6 Effects of level of transmitted photosynthetically active radiation (PAR) and Red to Far red (R:FR) ratio: 71% PAR+ natural R:FR , 1.36 (H/N); 25%PAR + natural R:FR, 1.34 (L/N), and 24% PAR + reduced R:FR, 0.68 (L/R) under weekly (W1) and three weekly (W3) defoliation frequencies, on the cumulative herbage dry mass (g/plant; ln transformed [1]) of cocksfoot (Grasslands Wana) and perennial ryegrass (Grasslands Nui) at final harvest in glasshouse conditions, 1998.

Species/defoliation	% transmitted PAR and R:FR ratio (PAR/RF)		
	High PAR plus natural R:FR (H/N)	Low PAR plus natural R:FR (L/N)	Low PAR plus reduced R:FR (L/R)
Perennial ryegrass / W1	0.79 (2.20)	-1.22 (0.29)	-1.38 (0.25)
Perennial ryegrass / W3	1.72 (5.58)	0.12 (1.12)	0.04 (1.04)
Cocksfoot / W1	0.88 (2.41)	-0.45 (0.63)	-0.43 (0.65)
Cocksfoot / W3	1.57 (4.80)	0.34 (1.40)	0.30 (1.34)
SEM for PAR/R:FR	0.04	0.04	0.04
SEM for species = 0.03			
SEM for defoliation = 0.02			
Overall SEM = 0.06			

W1 = defoliated at 50 mm height in every week; W3= defoliated at 50 mm height in every three weeks;
[1] figures inside the parentheses are back transformed value. SEM=standard error of the mean

At low PAR plus reduced R:FR, shoot dry weight of both species was similar to that of low PAR plus natural R:RF, but effects of defoliation were more visible, particularly for weekly defoliation. Under the W1 regime, Nui had about 86% of its shoot dry weight at low PAR plus reduced R:FR compared to that at low PAR plus natural R:FR, while Wana had 100% or more of its shoot dry weight at low PAR plus reduced R:FR. However, this difference was not found under W3 defoliation where both Nui and Wana were similar (Table 6.6).

There were no significant differences between relative shoot dry weight per plant of Nui and Wana at low PAR plus reduced R:FR and low PAR plus natural R:FR compared to that of high PAR plus natural R:FR, although there were significant differences between species and defoliation frequencies ($P<0.001$) (Table 6.7). Nui had lower relative herbage production than Wana at both defoliation frequencies, while Wana had a similar proportion of production at both low PAR plus reduced R:FR and low PAR plus natural R:FR as well as W1 and W3 defoliation frequencies (Table 6.7).

Table 6.7 Effects of level of transmitted photosynthetically active radiation (PAR) and Red to Far red (R:FR) ratio: 25%PAR + natural R:FR, 1.34 (L/N), and 24% PAR + reduced R:FR, 0.68 (L/R) under weekly (W1) and three weekly (W3) defoliation frequencies on the % relative dry mass/plant (compared to that of 71% PAR+ natural R:FR , 1.36) of cocksfoot (Grasslands Wana) and perennial ryegrass (Grasslands Nui) at final harvest in glasshouse conditions, 1998.

Species/defoliation	% transmitted PAR and R:FR ratio (PAR/RF)	
	low PAR plus natural R:FR (L/N)	Low PAR plus reduced R:FR (L/R)
Perennial ryegrass / W1	14	11
Perennial ryegrass / W3	21	19
Cocksfoot / W1	26	27
Cocksfoot / W3	29	28
SEM for PAR/R:FR	0.78	0.78
SEM for species = 0.78		
SEM for defoliation = 0.66		
Overall SEM = 1.33		

W1= defoliated at 50 mm height in every week; W3= defoliated at 50 mm height in every three weeks.
SEM= standard error of the mean

6.4.2.3 Leaf area

Leaf area per plant was significantly affected by PAR/RF, species, and defoliation frequencies (P<0.001), and the following interactions: PAR/RF×defoliation (P<0.05), species×defoliation (P<0.01) and PAR/RF×species (P<0.05) (Table 6.8).

Both species had higher leaf area under high PAR plus natural R:FR than at low PAR plus natural R:FR and low PAR plus reduced R:FR, with the highest leaf area produced by Wana cocksfoot under W3 defoliation. Leaf area of both species under W1 defoliation was about half that of W3 at high PAR plus natural R:FR (Table 6.8).

Wana and Nui at low PAR plus natural R:FR, under both defoliation frequencies had higher leaf area than at low PAR plus reduced R:FR, except Nui at W3 defoliation which had higher leaf area at low PAR plus reduced R:FR. Leaf area of Nui under W3 defoliation at low PAR plus natural R:FR was only about 32% of Wana under W3 defoliation at low PAR plus natural R:FR, whereas this proportion was about 46 % in the case of low PAR plus reduced R:FR.

Table 6.8 Effects of level of transmitted photosynthetically active radiation (PAR) and Red to Far red (R:FR) ratio: 71% PAR+ natural R:FR , 1.36 (H/N); 25%PAR + natural R:FR, 1.34 (L/N), and 24% PAR + reduced R:FR, 0.68 (L/R) under weekly (W1) and three weekly (W3) defoliation frequencies on the leaf area (mm^2/plant) of cocksfoot (Grasslands Wana) and perennial ryegrass (Grasslands Nui) at final harvest in glasshouse conditions, 1998

Species/defoliation	% transmitted PAR and R:FR ratio (PAR/RF)		
	High PAR plus natural R:FR (H/N)	Low PAR plus natural R:FR (L/N)	Low PAR plus reduced R:FR (L/R)
Perennial ryegrass / W1	5380	1530	1100
Perennial ryegrass / W3	11730	4470	5780
Cocksfoot / W1	12220	6040	5590
Cocksfoot / W3	25100	14070	12530
SEM for PAR/R:FR	750	750	750
SEM for species = 610			
SEM for defoliation = 460			
SEM for PAR/RF ×defoliation = 800			
Overall SEM = 1133			

W1= defoliated at 50 mm height in every week; W3= defoliated at 50 mm height in every three weeks; SEM=standard error of the mean

On the other hand, W3 defoliation had higher leaf area than W1, and Wana had significantly higher leaf area than Nui in both low PAR plus natural R:FR and low PAR plus reduced R:FR as in the case of high PAR plus natural R:FR. (Table 6.8).

6.4.2.4 Leaf dry weight

PAR/RF significantly affected the leaf dry weight, as did defoliation ($P<0.001$) but not the species ($P>0.05$). Only the interaction of PAR/RF×defoliation was significant ($P<0.001$) (Table 6.9). Highest leaf dry weight was for Nui at W3 followed by Wana W3 defoliation under high PAR plus natural R:FR. Leaf dry weight of both species at W1 defoliation was only about 40% of W3 defoliation.

Table 6.9 Effects of level of transmitted photosynthetically active radiation (PAR) and Red to Far red (R:FR) ratio: 71% PAR+ natural R:FR , 1.36 (H/N); 25%PAR + natural R:FR, 1.34 (L/N), and 24% PAR + reduced R:FR, 0.68 (L/R) under weekly (W1) and three weekly (W3) defoliation frequencies on the leaf dry weight (g/plant) of cocksfoot (Grasslands Wana) and perennial ryegrass (Grasslands Nui) at final harvest in glasshouse conditions, 1998.

Species/defoliation	% transmitted PAR and R:FR ratio (PAR/RF)		
	High PAR plus natural R:FR (H/N)	Low PAR plus natural R:FR (L/N)	Low PAR plus reduced R:FR (L/R)
Perennial ryegrass / W1	0.36	0.06	0.04
Perennial ryegrass / W3	1.16	0.32	0.30
Cocksfoot / W1	0.46	0.16	0.15
Cocksfoot / W3	1.08	0.38	0.38
SEM for PAR/RF	0.03	0.03	0.03
SEM for species = 0.02			
SEM for defoliation = 002			
SEM for PAR/RF×defoliation = 0.03			
Overall SEM = 0.05			

W1= defoliated at 50 mm height in every week; W3= defoliated at 50 mm height in every three Weeks; SEM=standard error of mean

Leaf dry weight of both species at both defoliation frequencies under low PAR plus natural R:FR and low PAR plus reduced R:FR was similar. Wana W3 had similar leaf dry weight to Nui W3. W1 defoliation produced the lowest leaf dry weight for both species, but leaf dry weight of Nui under W1 defoliation at low PAR plus reduced R:FR, and low PAR plus natural R:FR, was only about 25 and 37% respectively of that of Wana W1 (Table 6.9).

6.4.2.5 Specific leaf area (SLA)

PAR/RF and species, but not defoliation, significantly affected SLA (P<0.01). There were no significant interactions of PAR/RF, species and defoliation on SLA. SLA of both Nui and Wana was greater at low PAR plus natural or reduced R:FR than at high PAR plus natural R:FR (Figure 6.3), whereas it was similar at low PAR plus natural R:FR and low PAR plus reduced R:FR for all the treatments, except Nui W3 which was higher at low PAR plus reduced R:FR than at low PAR plus natural R:FR.

SLA of Wana was always higher than that of Nui at each PAR/RF level. Nui had lower SLA at each PAR/RF level indicating that SLA of Nui was more affected by defoliation frequency than Wana (Figure 6.3). Considering all PAR/RF levels, Nui at W1 defoliation had about 58% of the SLA of Wana at W1 defoliation. Likewise, Nui at W3 defoliation had only about 45% of the SLA of Wana W3 defoliation.

SLA of Nui increased 141% from high PAR plus natural R:FR to low PAR plus natural R:FR, and increased further to 166% for low PAR plus reduced R:FR. SLA of Wana increased to 146% and 136% respectively for low PAR plus natural R:FR and low PAR plus reduced R:FR from that of high PAR plus natural R:FR (Figure 6.3).

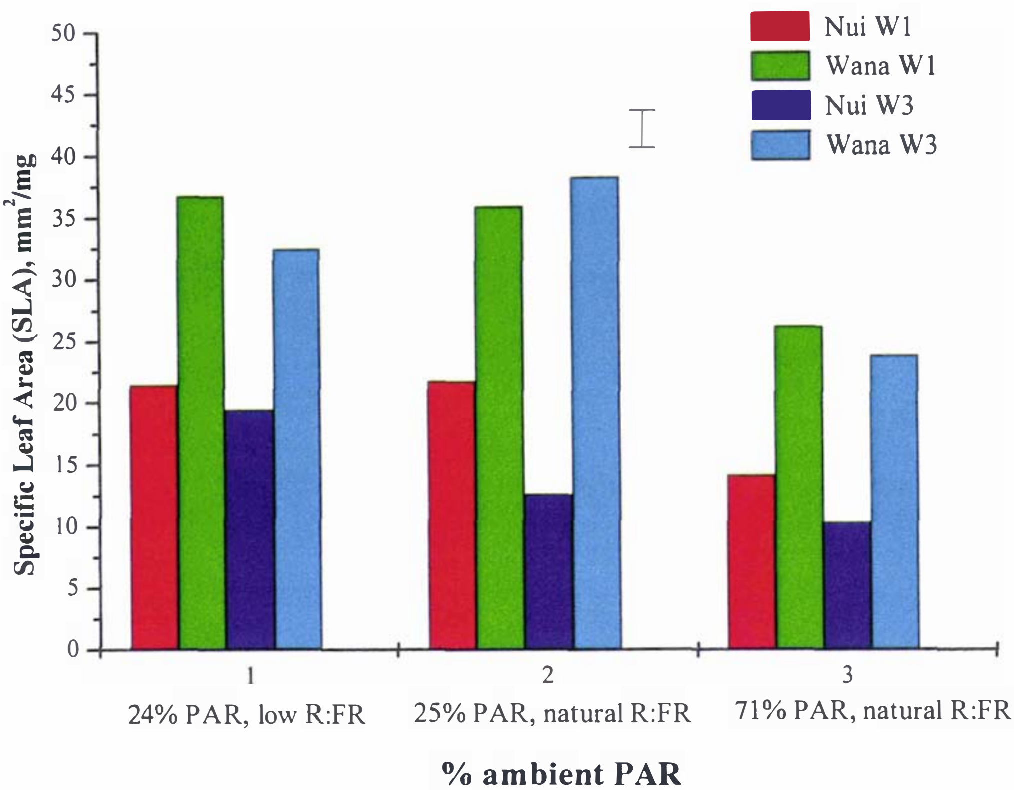


Figure 6.3 Specific leaf area (SLA) of Nui and Wana at different levels of PAR under two defoliation regimes of W1 and W3. Vertical bar represents standard error of the mean (SEM) for PAR/RF. SEM for species and defoliation were 1.23 and 1.24, respectively.

6.4.2.6 Tillers per plant

Effects of PAR/RF, species, and defoliation were significant ($P<0.001$) for tillers per plant at the final harvest in absolute terms as was the interaction of species×defoliation, and PAR/RF× species (Table 6.10). The highest number of tillers was produced by Nui W3 in high PAR plus natural R:FR followed by Wana , while Nui W1 produced the least number of tillers under the high PAR plus natural R:FR (Table 6.10).

Table 6.10 Effects of level of transmitted photosynthetically active radiation (PAR) and Red to Far red (R:FR) ratio: 71% PAR+ natural R:FR , 1.36 (H/N); 25%PAR + natural R:FR, 1.34 (L/N), and 24% PAR + reduced R:FR, 0.68 (L/R) under weekly (W1) and three weekly (W3) defoliation frequencies on the number of tillers/plant of cocksfoot (Grasslands Wana) and perennial ryegrass (Grasslands Nui) at final harvest in glasshouse conditions, 1998.

Species/defoliation	% transmitted PAR and R:FR ratio (PAR/RF)		
	High PAR plus natural R:FR (H/N)	Low PAR plus natural R:FR (L/N)	Low PAR plus reduced R:FR (L/R)
Perennial ryegrass / W1	34	6	5
Perennial ryegrass / W3	48	19	12
Cocksfoot / W1	41	30	23
Cocksfoot / W3	38	31	23
SEM for PAR/R:FR	1.28	1.28	1.28
SEM for species = 1.04			
SEM for defoliation = 0.7			
SEM for PAR/RF×defoliation = 1.0			
Overall SEM = 1.73			

W1= defoliated at 50 mm height in every week; W3= defoliated at 50 mm height in every three weeks; SEM= standard error of the mean

Nui and Wana both had significantly higher numbers of tillers at low PAR plus natural R:FR than at low PAR plus reduced R:FR for both defoliation frequencies, except Nui W1 which had the lowest number of tillers per plant (Table 6.10). Wana W1 and W3 both had almost similar number of tillers per plant at low PAR plus natural R:FR, which was about 75% of the number at high PAR plus natural R:FR, while Nui W3 had 40% and Nui W1 about 18% of the tillers per plant compared to that of Nui W3, and Nui W1, respectively at high PAR plus natural R:FR. Tiller numbers at low PAR plus reduced R:FR decreased to that of low PAR plus natural R:FR, but Wana, both at W1 and W3, at low PAR plus reduced R:FR had about 75% of the tillers of Wana W1 and W3 at low PAR plus natural R:RF, while the number of tillers for Nui W3 at low PAR plus reduced R:FR was only about 60% of that of Nui W3 at low PAR plus natural R:FR. However, tiller number per plant of Nui W1 at low PAR plus natural R:FR and at low PAR plus reduced R:FR were similar (Table 6.10).

Table 6.11 Effects of level of transmitted photosynthetically active radiation (PAR) and Red to Far red (R:FR) ratio: 71% PAR+ natural R:FR, 1.36 (H/N); 25%PAR + natural R:FR, 1.34 (L/N), and 24% PAR + reduced R:FR, 0.68 (L/R) under weekly (W1) and three weekly (W3) defoliation frequencies on root dry weight (g/plant; ln transformed [1]) of cocksfoot (Grasslands Wana) and perennial ryegrass (Grasslands Nui) at final harvest in glasshouse conditions, 1998

Species/defoliation	% transmitted PAR and R:FR ratio (PAR/RF)		
	High PAR plus natural R:FR (H/N)	Low PAR plus natural R:FR (L/N)	Low PAR plus reduced R:FR (L/R)
Perennial ryegrass / W1	-1.97 (0.13)	-4.02 (0.01)	-4.47 (0.01)
Perennial ryegrass / W3	-0.11 (0.89)	-2.84 (0.05)	-2.89 (0.05)
Cocksfoot / W1	-1.71 (0.18)	-3.57 (0.02)	-3.49 (0.03)
Cocksfoot / W3	-0.39 (0.67)	-2.32 (0.09)	-2.41 (0.08)
SEM for PAR/R:FR	0.08	0.08	0.08
SEM for species = 0.06			
SEM for defoliation = 0.08			
Overall SEM = 0.20			

W1= defoliated at 50 mm height in every week; W3= defoliated at 50 mm height in every three weeks; [1] figure inside the parentheses are the value of back transformed; SEM= standard error of the mean

6.4.2.7 Root dry weight

Effect of PAR/RF (P<0.001), species (P<0.01), and defoliation (P<0.0001) on per plant root dry weight at final harvest were significant. However, there was no interaction of PAR/RF, species, and defoliation frequencies (P>0.05). For both species, under both defoliation frequencies, root dry weight was higher at high PAR plus natural R:FR. Accordingly, Nui W3 had highest root dry weight followed by Wana W3. Root dry weight of Nui and Wana W1 at high PAR plus natural R:FR was similar (Table 6.11). Among low PAR levels, both Nui and Wana either at W1 or W3 defoliation frequency had similar root dry weight per plant, but Wana W3 had the highest root dry weight per plant and Nui W1 the lowest at both low PAR plus natural R:FR and low PAR plus reduced R:FR (Table 6.11).

6.4.2.8 Tiller site usage

Tiller site usage was higher for Wana W3 then Wana W1 at low PAR plus natural R:FR taking the whole experimental period. Site usage of Wana was also higher at low PAR plus reduced R:FR and high PAR plus natural R:FR, but site usage of Nui was very low particularly by Nui W1 at low PAR levels, both with natural and reduced R:FR (Figure 6.4d).

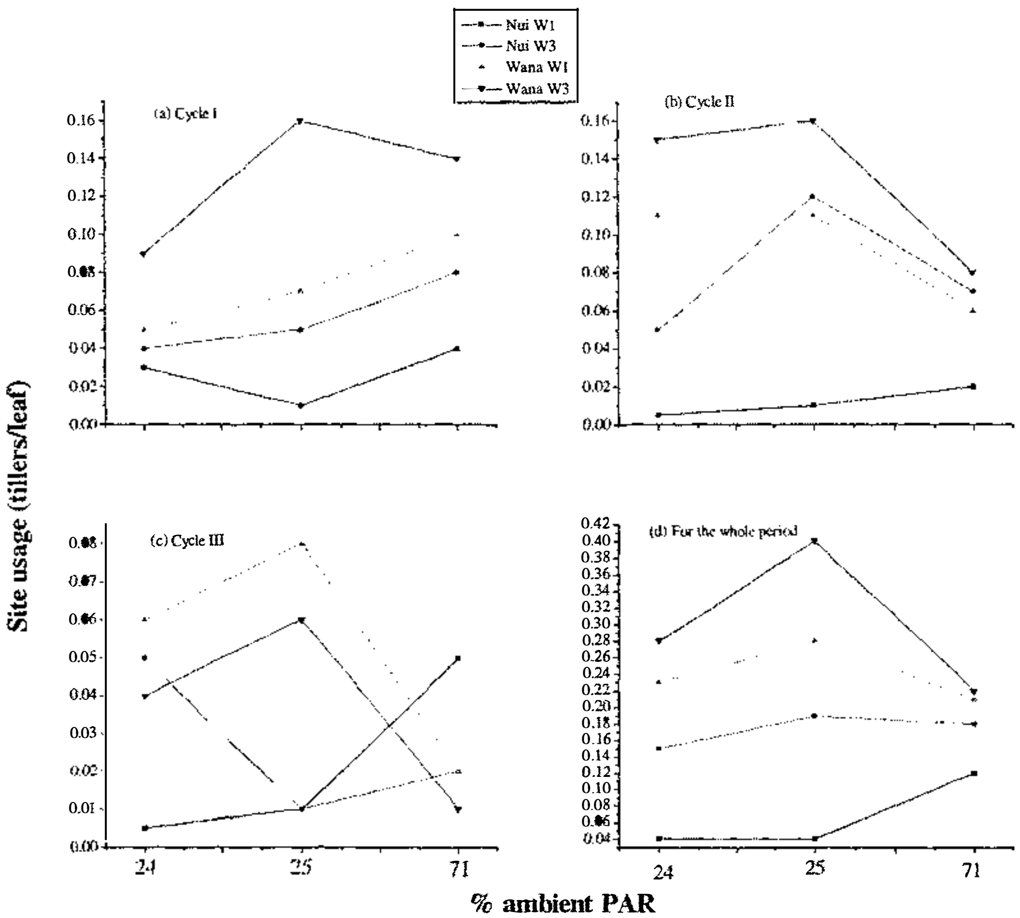


Figure 6.4 Site usage (tillers/leaf) of Nui and Wana under different PAR, R:FR and defoliation frequency: (a) cycle I (8 June-28 June), (b) cycle II (29 June-19 July), (c) cycle III (20 July-9 August), and (d) cycle IV (for the whole period of 8 June-9 August, 1998). Where, 24% PAR was with low R:FR, and 25% and 71% PAR were with natural R:FR light.

Results also indicated that the probability of a tiller appearing in Wana W3 at low PAR plus natural R:FR was almost one in two leaves, while for Nui W3, one tiller would have emerged for every five leaves.

There was a changing trend of site usage by both Nui and Wana in each cycle. For example, during the first cycle, site usage in all the treatments was lowest at low PAR and reduced R:FR, however, it increased in the second cycle in all treatments except, Nui W1 (Figure 6.4 a, b). All the treatments had higher site usage values at low PAR plus natural R:FR in both cycles, but Wana W3 had the highest site usage. In all cycles, Wana had a higher site usage than Nui, particularly Wana W3 which had the highest site usage at high PAR plus natural R:FR, except in cycle III, where Nui W1 was highest. However, Wana W3 and W1 both had higher site usage in all three cycles at low PAR plus reduced R:FR, except at cycle III (Figure 6.4). A similar trend was repeated at low PAR plus natural R:FR, except in cycle II, where Nui W3 was similar to Wana W3. Nui W1 had the lowest site usage overall, and in all cycles, except during cycle III at high PAR plus natural R:FR (Figure 6.4).

6.4.2.9 Leaf appearance interval

Leaf appearance interval was shorter for Wana than Nui at all PAR/RF levels (Table 6.12). Shortest duration for the appearance of a new leaf was at low as well as high PAR with natural R:FR for Wana W3 (Table 6.12). At high PAR plus natural R:FR, Nui W3 also had the shortest leaf appearance interval (cycle II, III). Overall, leaf appearance interval was greater at low PAR plus reduced R:FR (Table 6.12).

Table 6.12 Effects of level of transmitted photosynthetically active radiation (PAR) and Red to Far red (R:FR) ratio under different defoliation frequencies on the leaf appearance interval (days) of cocksfoot (Grasslands Wana) and perennial ryegrass (Grasslands Nui) in glasshouse conditions, 1998.

Species/defoliation	% transmitted PAR and R:FR ratio (PAR/RF)		
	High PAR plus natural R:FR (H/N)	Low PAR plus natural R:FR (L/N)	Low PAR plus reduced R:FR (L/R)
Cycle I (June 8-June28)			
Perennial ryegrass (Nui, W1)	8.3	13.3	11.9
Perennial ryegrass (Nui, W3)	7.2	10.3	10.6
Cocksfoot (Wana,W1)	6.7	7.2	7.9
Cocksfoot (Wana,W3)	4.9	5.1	6.0
Cycle II (June 29-July 19)			
Perennial ryegrass (Nui, W1)	8.2	11.1	13.1
Perennial ryegrass (Nui, W3)	5.6	7.3	7.5
Cocksfoot (Wana,W1)	7.3	7.3	7.2
Cocksfoot (Wana,W3)	5.1	5.3	5.5
Cycle III (July 20-August 9)			
Perennial ryegrass (Nui, W1)	7.2	10.6	11.7
Perennial ryegrass (Nui, W3)	6.6	6.8	9.3
Cocksfoot (Wana,W1)	7.1	6.9	7.6
Cocksfoot (Wana,W3)	7.0	4.7	7.0
Average of 3 cycles			
Perennial ryegrass (Nui, W1)	7.9	11.7	12.2
Perennial ryegrass (Nui, W3)	6.5	8.1	9.1
Cocksfoot (Wana,W1)	7.0	7.1	7.6
Cocksfoot (Wana,W3)	5.7	5.0	6.1

The pattern of leaf appearance interval for the species over all cycles were similar. Wana W3 required the least days in all cycles at all PAR levels, except at cycle III, high PAR plus natural R:FR, where Nui W3 was faster. Nui W1 had the longest leaf appearance interval in all cycles at all PAR/RF levels. The general trend for shortest to longest leaf appearance interval was Wana W3 < Wana W1 < Nui W3 < Nui W1 (Table 6.12).

6.5 Discussion

The RGR of Wana cocksfoot was always higher than that of Nui perennial ryegrass at all PAR/R:FR. RGR of Wana was less affected by reduced PAR/RF compared with Nui. Low PAR and reduced R:FR ratio had less affect on Wana than Nui, particularly under weekly defoliation. Wana produced higher biomass than Nui under both W1 and W3 defoliation regimes mainly due to its ability to produce higher leaf area, and higher leaf dry weight at low PAR plus natural or reduced R:F. Likewise, SLA of Wana was always higher than that of Nui at each PAR/RF level. Nui had the lowest SLA at each PAR/RF level indicating that SLA of Nui was more affected by defoliation frequency than Wana. Wana also had significantly more tillers per plant, higher site usage value, and a shorter leaf appearance interval than Nui under low PAR plus reduced R:FR. Shoot dry mass of Nui was comparatively low under low PAR/RF mainly due to the low tillering, and leaf area per plant. Low tiller site usage indicated that under low PAR/RF and defoliation conditions, Nui would have less chance of producing tillers, than Wana. Wana could continue to produce leaf area despite high defoliation frequency. This may be due to the higher SLA of Wana than Nui, suggesting that Wana could allocate more carbon to the leaves and thereby produce more tillers per plant. It was concluded that Wana is more tolerant of a high defoliation frequency than Nui, and can produce more shoot dry weight and tillers consistently under low PAR/R:FR.

Wana had a greater RGR than Nui in each PAR level irrespective of the light quality. Nui produced more aboveground shoot mass than Wana, but this could be due to bigger seed, faster germination and establishment compared to Wana cocksfoot. Genetic differences between plants and allocation of assimilates will also have a large impact on the relative growth rate of species (Zarrough *et al.* 1983). Sugiyama (1995) reported that carbohydrate availability could be closely related to the shoot growth rate. However, in relative growth rate terms, Wana was better than Nui, which suggests that Wana cocksfoot is more shade tolerant (Figure 6.2).

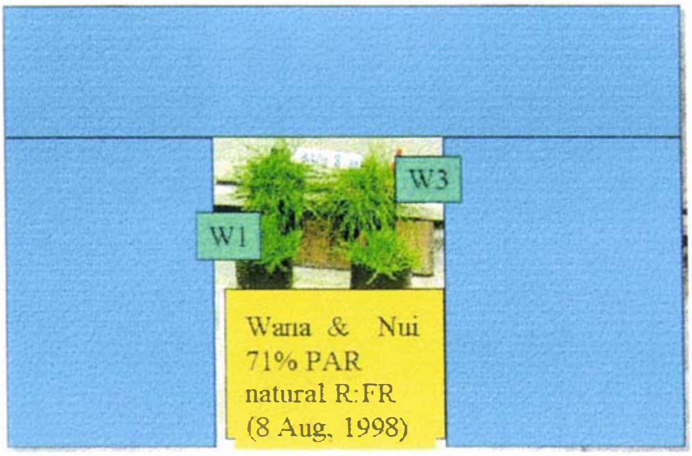
The higher shoot dry weight (Tables 6.6 and 6.7) of both Nui and Wana under W3 rather than W1 defoliation indicated that if a plant can receive more light and alter the allocation to leaves, this would be advantageous in terms of production and persistence (Caldwell 1987). Production is possible only when a plant is in a position to intercept light. The productivity of pasture can be rapidly altered by variation in defoliation management, particularly the frequency and height of the defoliation (Stockdale 1992; Fulkerson and Slack 1995; Rutkowska and Lewicka 1995; Harris *et al.* 1997; Sanderson *et al.* 1997; Turner *et al.* 1998) though the influence on plant growth depends on species, stage of growth and the degree of defoliation (Kang *et al.*1995; Havstad 1997; Donaghy *et al.* 1997). For these reasons the effects of defoliation have been interpreted largely in terms of competition for light (Remison *et al.* 1980).

Number of tillers per plant is also an important indicator of shade tolerance (Devkota *et al.* 1997), which also contributes to the productivity and persistence of the pasture species under continuous defoliation in the shade. This is because the growing region of the leaf is a strong sink that can deprive other sinks, such as tiller buds, when defoliated (Gautier *et al.* 1999). Removing the aboveground phytomass places a large stress on the stubble and roots (Sanderson *et al.* 1997). Moreover, tillering is well known to be sensitive to both defoliation and light environment (Gautier *et al.* 1999). Tillering was reduced for both Wana and Nui at low PAR plus reduced R:FR in this experiment (Table 6.10), but Nui was more sensitive than Wana in terms of tillering. Therefore, results of this study showed that as Wana can maintain higher tiller numbers per plant than Nui it could withstand low PAR and defoliation frequency.

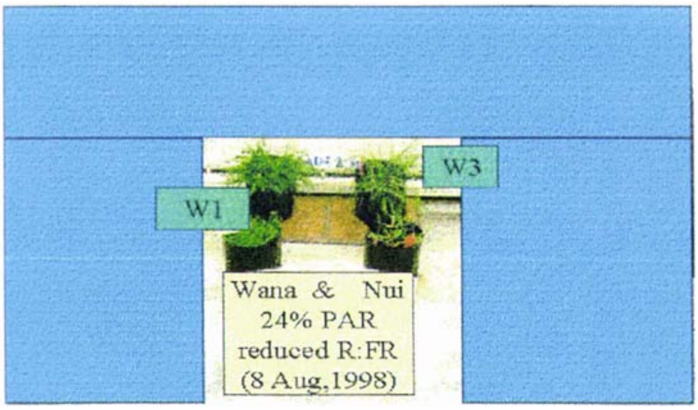
High SLA of pasture species at low PAR (heavy shade) appears to be an important morphological attribute that determines the ability of species to produce and persist. A high SLA enables species to allocate more carbon to leaf area and therefore intercept more of the available light in the shade (Sanderson *et al.* 1997; Dennis and Woledge 1983). Ultimately, a high SLA would also increase the chance of producing more tillers. Wana had better growth than Nui, especially at low PAR, mainly due to its ability to produce a higher leaf area (Table 6.8), and a higher leaf dry weight (Table 6.9). Higher leaf area of Wana contributed to higher site usage than that of Nui under weekly (W1) and three weekly defoliation (W3) (Figure 6.4) resulting in significantly more tillers per plant ($P<0.001$) for Wana than Nui at both low PAR plus reduced R:FR and low PAR plus natural R:FR (Table 6.10). These results were in line with an earlier screening experiment with grasses and legumes in pots in glasshouse conditions (Devkota *et al.* 1997).

In this study, Nui was more sensitive to defoliation frequency than Wana. In general, increasing the frequency of defoliation progressively reduces leaf size (Brock *et al.* 1996). Nui leaf area was more severely decreased by the weekly defoliation (Table 6.8). Thornton and Millard (1997) also reported that increasing the frequency of defoliation resulted in a reduction in the rate of growth of new leaves of Nui perennial ryegrass. The low level of biomass production by Nui at low PAR could also be associated with its reduced root dry weight under frequent defoliation (Table 6.11; Thornton and Millard 1997; Mawdsley and Bardgett 1997).

Cocksfoot is considered to be adapted to both shade and dry conditions (Hocking 1990), and also the tree shade of *Pinus radiata* (Seo *et al.* 1989) in New Zealand. The results of these experiments also showed that cocksfoot is adapted to heavy shade and intensive defoliation. Ward and Blaser (1961) reported that the rate of regrowth of cocksfoot following defoliation was largely due to the carbohydrate reserves in the stubble and the remaining leaf area. The carbohydrate reserves, or the remobilization of nutrients, of cocksfoot appear to enable it to produce relatively high leaf area and tiller numbers per plant in the shade. Wana cocksfoot is a particularly defoliation tolerant species that can be grown under heavy shade.



(a)



(b)

Figure 6.5 Effects of defoliation at weekly and three-weekly interval for Wana cocksfoot and Nui perennial ryegrass (a) under 71% PAR, natural R:FR, and (b) 24% PAR with reduced R:FR by using filters. Wana in background.

6.6 Conclusions

A study to determine the relative growth rate (RGR) of Wana cocksfoot and Nui perennial ryegrass at the seedling stage showed that the RGR of Wana was always higher than that of Nui in all PAR/R:FR treatments. RGR of Wana was also less affected by reduced PAR/R:FR compared with Nui. Likewise, effects of defoliation on the tillering and biomass producing ability of these species at low PAR/R:FR ratio revealed that Wana was a better species under frequent defoliation. Wana produced higher biomass than Nui under both W1 and W3 defoliation regimes mainly due to its ability to produce higher leaf area and higher leaf dry weight. Likewise, SLA of Wana was significantly higher ($P<0.0001$) than that of Nui at both W1 and W3 defoliation frequencies. Wana also had significantly higher tillers per plant, higher site usage value, and shorter leaf appearance interval than Nui under low PAR/R:FR conditions. Biomass yield of Nui was comparatively low in the heavy shade due mainly to the low tillering, and per plant leaf area. The low level of site usage value reflected that under heavy shade and defoliation, Nui would have least chance of producing tillers. Wana could continue to produce leaf even despite a high defoliation frequencies. Results from these studies, therefore, clearly indicated that under the experimental conditions Nui was particularly defoliation sensitive; the higher the defoliation frequency, the lower the biomass and tillering producing abilities. On the other hand, Wana was particularly defoliation insensitive, compared with Nui, and produced more biomass and tillers under a high frequency of defoliation and low PAR/R:FR ratio.

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7. Performance of pasture species under deciduous tree shade

Page

7.1 Summary

Deciduous trees are commonly used in silvo-pastoral systems to improve the stability of hill country. However, information on the effects of deciduous trees on understorey pasture production is scanty. There is a need for more information about management practices for deciduous based tree-pasture systems, especially in relation to performance of pasture species under different levels of shade.

A preliminary screening study on pasture species under glasshouse conditions showed that shade had a marked effect on tillering as well as on shoot dry weight accumulation. Mean tiller numbers per plant in the lowest PAR (photosynthetically active radiation) level was significantly higher for cocksfoot than for other species (Chapter 3). In this chapter, the results of an experiment conducted to validate the results obtained in the glasshouse study are reported. Perennial ryegrass (Grasslands Nui), Yorkshire fog (Massey Basyn), and cocksfoot (Grasslands Wana) with white clover (Grasslands Tahora) as the legume component in each sward, and also cocksfoot with lotus (Grasslands Maku), were examined under 11 year old alder trees (1197 stems/ha) in September, 1996 at Horticultural Research Centre, Aokautere, near palmerston North. A split-plot design with four replicate blocks was used. The main plot treatments were three levels of transmitted PAR (81%, 23%, and 12%; light, medium and heavy shade, respectively) created by pruning trees to different heights. The sub-plot treatments were combination of pasture species. The experiment ran from October 28, 1996 to May 28, 1998. Pasture plots were mowed monthly at 50mm aboveground. Pre-mowing herbage mass (g/m^2), and herbage harvested above 50mm were measured once in a month. Tillers/m^2 of the grass component, and number of growing points or branches (per m^2) for the legumes were counted.

In a subsidiary experiment, a grazing preference experiment was conducted at the same site in November 1998.

Herbage mass in heavy and medium shade was about 50% and 70%, respectively, of that in light shade ($P<0.0001$). Herbage mass was highest for cocksfoot, either with

lotus or white clover at all levels of light ($P<0.0001$), whereas herbage mass of ryegrass and Yorkshire fog was similar. Shade affected ryegrass more than cocksfoot and Yorkshire fog, especially at the lowest PAR level, which was consistent with the results obtained in the glasshouse study.

In the subsidiary experiment, observations were made on the distribution of grazing activity ($n=12$) across plots over periods of 2 hours in the afternoon on two successive days. There was no difference ($P>0.05$) in the number of observations of sheep grazing such plots of different pasture species in a 2 hour period. More sheep grazed in the light shade than in the heavy shade ($P<0.05$).

For a silvo-pastoral system based on alders at a high tree density, cocksfoot, in combination with either lotus or white clover was more productive and persistent than the other pasture species examined, supporting the results of the earlier glasshouse experiment. Further research on the long-term impact of shade on sustainable pasture production, however, is still required.

7.2 Introduction

Large areas of land used for agriculture in New Zealand are susceptible to soil erosion (Clough and Hicks 1993; Kelliher *et al.* 1995) mostly due to forest clearing for agriculture (Trustrum and Blaschke 1992). One technology to cope with this situation and to maintain pastoral farming has been the planting of conservation trees, particularly poplars and willows (Maclaren 1993; Anonymous 1995; NZMF 1995; Miller *et al.* 1996). High or low density planting of trees as an agroforestry system has also become a common land use practice in recent years, as a means of income diversification along with the erosion control (Pollock *et al.* 1994).

There are several published reviews on agroforestry which show the range of information on tree-crop systems (Wolters 1982; Cameron *et al.* 1989; Nair and Dagar 1991; Stür and Shelton 1991; Wilson and Ludlow 1991; Bird *et al.* 1992; Atta-Krah 1993; Ong 1996), but most of this information in New Zealand is associated only with *Pinus radiata* based systems (Knowles *et al.* 1991). Studies on *Pinus radiata* indicated that understorey herbage production decreases as crown density increases (Anderson and Batini, 1983, Pollock *et al.* 1994, Hawke and Knowles, 1997), and as there is an increase in age and slash from trees (Knowles *et al.* 1995; Hawke and Knowles 1997).

Shading is the most significant factor determining the output from pastures grown in plantations (Shelton *et al.* 1987). Some species like Yorkshire fog (*Holcus lanatus* L.), cocksfoot (*Dactylis glomerata* L.) and lotus (*Lotus uliginosus*) are more shade tolerant than other pasture species (Seo *et al.* 1989; West *et al.* 1991, Devkota *et al.* 1997; Chapters 3, 5). The results of a screening of pasture species under glasshouse conditions showed that shade had a marked effect on tillering as well as on shoot dry weight accumulation (Chapter 3; Devkota *et al.*1997). Mean tiller number per plant at the lowest PAR (photosynthetically active radiation) level was significantly higher for cocksfoot than for other species (Devkota *et al.* 1997). Lotus produced a higher number of branches at the lowest ambient PAR (14%) than did the other legumes (Chapter 3, Devkota *et al.*1997).

Poplars and other deciduous trees have the advantage of increasing soil organic matter and nutrient status on tilled (Jaswal *et al.* 1993; Thevathasan and Gordon 1997) and pastoral land (Bowersox and Ward 1977). Pasture production is decreased under deciduous trees (Ditschal *et al.* 1997), but less than under evergreen trees, and it can be managed better by pruning trees, by short rotations, or by coppice management (Treeby 1978; New 1985). However, detailed information on the effect of deciduous trees on understorey production by temperate pasture is scanty (Wall *et al.* 1997), despite some research on the impact of shade on the performance of pasture species (Eriksen and Whitney 1981; Samarakoon *et al.* 1990; Kephart and Buxton 1993). Particularly, the impact of shading by deciduous trees on the productivity and persistence of hill pastures has received little research attention (Hawke 1991; Knowles 1991; Pollock *et al.*1994). There is little objective information available on effects of a range of light intensities, particularly at the low levels of transmitted light (high levels of shade) found under mature stands of conservation trees (e.g. poplars, alders and willows), on the growth and morphology of pasture species.

An experiment was conducted to relate the results obtained in the glasshouse (Chapters 3, 4 and 5, Devkota *et al.* 1997) to the shade of deciduous trees. The experimental site used was the same as for Experiment 4.2, but in that experiment only alder tree shade was used as the main plot, and sub plots were cocksfoot selections and perennial ryegrass tested in pots under alder tree shade. In this experiment, perennial ryegrass (Grasslands Nui),Yorkshire fog (Massey Basyn), and cocksfoot (Grasslands Wana), with white clover (Grasslands Tahora) as the legume component in each sward, and also cocksfoot with lotus (Grasslands Maku) were grown to evaluate the effects of shade on tillering ability and biomass production of pasture under alders.

7.3 Materials and methods

7.3.1 Site description

The two experiments were conducted on a moist, lowland site at the Horticultural Research Institute's (HortResearch) field station at Aokautere, near palmerston North. The long term mean annual rainfall is 995 mm with dry months from January to April. The long term mean annual air temperature is 12.9^0 C (Oppong 1998). Mean monthly rainfall from September 1996 to November 1998, taken at the nearest Meteorological station (AgResearch, Palmerston North), was 71.4 ± 39.4mm (Figure 7.1). The mean global radiation was 403 ± 176.2 MJ/m^2/month (Figure 7.2). The soil is a Manawatu silt loam, fairly well drained with medium to poor fertility. For example, Olsen P was 11.4 (µg/g) at the beginning of the experiment, and soil pH was 5.5 (Table 7.1). The site had been established with evenly spaced (width between rows 3.0m and width within rows 4.0m, or 1197 stems/ha) Italian grey alder (*Alnus chordata*) trees with *Robinia* planted alternately in each row. Before the experiment began, all the *Robinia* trees were removed. The alder trees had been un-pruned until the experiment began.

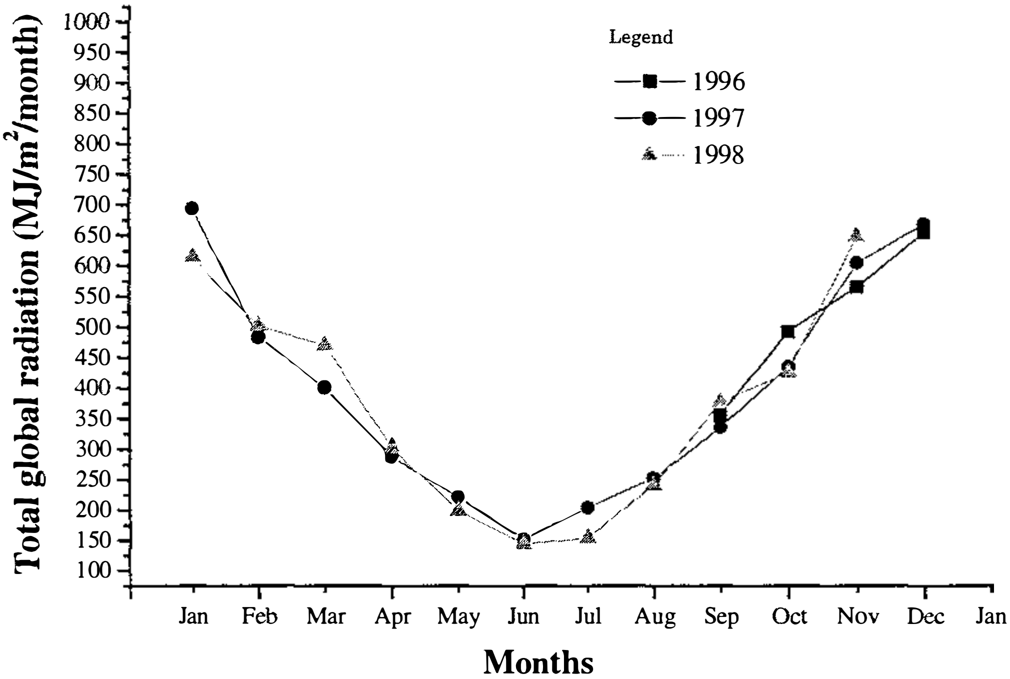

Figure 7.1 Monthly total global radiation (MJ/m^2/s), during the experiment period. Data from the nearest Meteorological Station (AgResearch, Palmerston North).

7.3.2 Experimental treatments, procedures and designs

7.3.2.1 Experiment 7.1

Experiment 7.1 was conducted from 14 October, 1996 to 28 May 1998 under 11 year old alder trees. Plots in the field were arranged in a split plot design with four replicate blocks (Appendix Figure 7.1). The main plots were shade treatments created by pruning trees to different heights from ground level, and subplots were mixed species swards. Pruning heights were to 2.5 m, 5.0 m and 7.0 m from the ground, which resulted in three different levels of transmitted PAR, hereafter called heavy, medium, and light shade respectively as determined by measuring PAR monthly (7 February, 19 March, 14 April, 22 November and 30 December in 1997, and 13 January, 11 February, 9 March, 7 April and 14 May 1998) on clear sky days between 1200-1300h using a LI-COR (Model LI-185) portable quantum sensor.

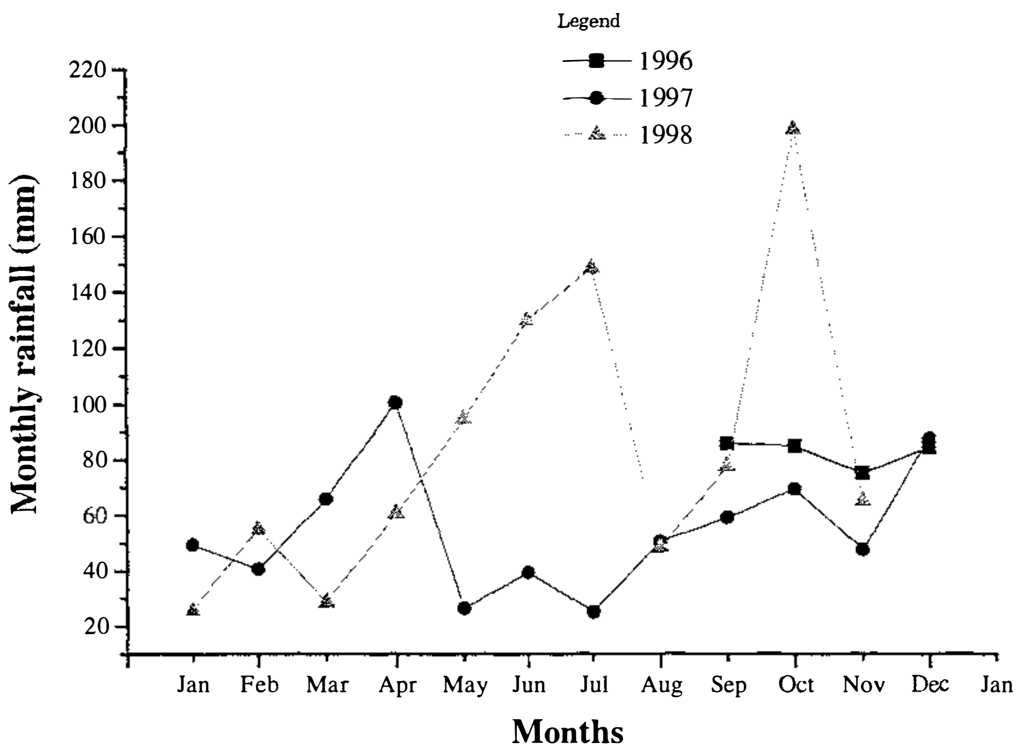

Figure 7.2 Monthly total rainfall distribution (mm) during the experiment period. Data from the nearest Meteorological Station (AgResearch, Palmerston North).

The R:FR ratio of the light was also measured monthly whenever possible (17 to 20 February, 23 to 25 March, 18 November, and 30 December in 1997, and 13 January, 7 April, and 20 May in 1998) with a Skye Sensor at just above the swards under the trees.

Soil temperature was recorded monthly at 100 mm depth in each treatment. Likewise, volumetric soil moisture (v/v%) was estimated using the Time Domain Reflectometry technique (TDR, Soil moisture Co. USA). Soil moisture was measured from 0-200mm depth randomly in each plot once a month using TDR probes of 200mm length.

The site was divided into three main plots (23 stems in one main plot of $12\times16m^2$, $192m^2$). Each main plot had four sub-plots, with $2 \times 4m$ of net cultivable area per sub-plot (by leaving 0.5m margin from the row of tree on both sides) used to grow understorey swards. Sub-plots were replicated four times (Figure 7.3).

Mean tree height in each main plot at the end of the experiment was 10.4 ± 0.4 m, 10.9 ± 0.5m, and 9.9 ± 1.3m for heavy, medium and light shade respectively. Mean diameter at breast height (DBH, at 1.4m) was 15.1 ± 2.3cm, 16.3 ± 1.8cm and 14.0 ± 1.4cm for heavy, medium and light shade, respectively. Mean leaf area index (LAI) of the trees was measured using a LAI 2000 Plant Canopy Analyser (Welles 1990; Welles and Norman 1991). LAI for heavy shade was 6.4 ± 0.7. Likewise, LAI of medium and light shade was 3.6 ± 0.7, and 1.7 ± 0.1, respectively, at the end of experiment.

The sub-plot treatments were pasture species in combination: perennial ryegrass (Grasslands Nui), Yorkshire fog (Massey Basyn), and cocksfoot (Grasslands Wana), were each grown with white clover (Grasslands Tahora) as the legume component in each sub-plot sward, and cocksfoot was also combined with lotus (Grasslands Maku) (Table 7.2). Before sowing, on 25 September 1996, all plots were sprayed with Roundup (glyphosate, 360g in 1 litre) to remove existing vegetation. After two weeks, on 8 October 1996, plots were ploughed by a rotary cultivator. Land was levelled, and the plots laid out on 10 October 1996. Seed was hand sown on 14 October 1996. Legume seeds were treated with appropriate Rhizobium cultures. Details of the pasture species and cultivars used are given in Table 7.2. After emergence, plots were hand weeded regularly from December 1996 to early January, 1997. Sprinkler irrigation was used twice, once in November and once in December, in order to help establishment of the swards. Irrigation was not used thereafter. There was no use of chemical or organic fertilizer. Plots were mowed monthly at 50mm height.

Pre-mowing herbage mass, and herbage harvested above the defoliation height of 50 mm were measured. The first harvest was on 25 March 1997 and the second harvest was on 24 April 1997. At each harvest a quadrat of 0.25 × 0.25m (0.0625 m^2) was used randomly in each plot. Plants were clipped to ground level with electric hand shears and washed carefully when necessary. All the clipped materials were separated into legume, grass, and other (flat weeds and dead materials) and dried at 70 ^{0} C for 24 hours, weighed, and added to the herbage mass. This information was also used to composition in each harvest. After quadrat cutting, a randomly selected $1.0m^2$ in each plot was mowed at 50mm height, and fresh weight was recorded. Representative samples of 150-200g from each plot were taken, dried at 70 ^{0} C for 24 hours, and weighed to determine herbage harvested above the defoliation height of 50mm (re-growth).

After the harvest on 24 April 1997, tree leaf fall began, and it was completed by the first week of June. The fallen leaves were completely raked away from the site, and sward harvests were not started again until trees had a full canopy of leaves. Therefore, the first harvest after the winter was on 28 October, 1997 and monthly harvests continued until May, 1998. From October, 1997 onwards, at each harvest, tillers/m^2 of the grass component, and number of growing points or branches (per m^2) for legumes were counted in small quadrats (10×10 cm). Counting was done in two randomly placed quadrat in each plot and the mean plot value calculated.

Figure 7.3 Field preparation to establish pasture under alder trees at Aokautere, September 1996.

Table 7.1 Soil nutrient levels at Aokautere site, sampled to 75mm depth before and at the end of the experiment.

Date/treatments	pH[a]	Olsen P (µg/g)	S[b] (µg/g)	Exchangeable cations (meq/100g)[c]		
				K	Ca	Mg
2/12/1996:						
Experimental area	5.4	11.4	5.8	0.5	5.0	1.3
5/10/1998						
Heavy shade						
Ryegrass + white clover	5.5	7.6	3.5	0.4	5.2	1.2
Yorkshire fog + white clover	5.6	6.7	3.3	0.4	5.1	1.2
Cocksfoot + white clover	5.5	7.1	2.8	0.3	4.6	1.1
Cocksfoot + lotus	5.6	7.1	2.5	0.3	5.0	1.2
Mean of dense shade	5.5	7.1	3.0	0.4	4.9	1.2
Medium shade						
Ryegrass + white clover	5.5	6.7	3.5	0.4	4.8	1.2
Yorkshire fog + white clover	5.5	7.1	2.8	0.4	4.8	1.2
Cocksfoot + white clover	5.5	6.2	3.0	0.4	4.8	1.1
Cocksfoot + lotus	5.5	6.9	3.9	0.4	4.9	1.2
Mean of medium shade	5.5	6.7	3.3	0.4	4.8	1.1
Light shade						
Ryegrass + white clover	5.5	7.1	4.0	0.5	6.4	1.4
Yorkshire fog + white clover	5.6	6.7	3.3	0.4	6.7	1.5
Cocksfoot + white clover	5.6	6.2	3.0	0.4	6.0	1.4
Cocksfoot + lotus	5.6	6.7	3.3	0.5	6.0	1.4
Mean of light shade	5.6	6.7	3.3	0.4	6.3	1.4

[a] Determined on a 1:2.5 soil : water suspension; [b] CaH_2PO_4 extractable SO_4-S; [c] 1*M* ammonium acetate, pH 7

Table 7.2 Pasture species and cultivars used in the Experiment 7.1.

Pasture species	Seed rate (kg/ha)
1. White clover (*Trifolium repens* L.) cv. Grasslands Tahora	3.0
2. Lotus (*Lotus uliginosus*) cv. Grasslands Maku	5.0
3. Cocksfoot (*Dactylis glomerata* L.) cv. Grasslands Wana	6.0
4. Yorkshire fog (*Holcus lanatus* L.) cv. Massey Basyn	2.0
5. Perennial ryegrass (*Lolium perenne* L.) cv. Grasslands Nui	12.0

7.3.2.2 Experiment 7.2

A grazing preference experiment was carried out at the same site as Experiment 7.1 with some modification. The plots of perennial ryegrass + white clover were destroyed by using Roundup (glyphosate, a.i. 360 g in 1 litre). Overall growth and performance of perennial ryegrass was poor in each plot compared with other swards, so it was removed to provide the homogeneity of swards to test diet selection.

The four replicates of Experiment 7.1 were partitioned into two replicates for ease of animal control. Battery operated electric fencing was used for this purpose. It was not possible to observe all replications at a time, hence observations were made in the afternoon of two successive days covering one partitioned area (two replications) a day over a period of 2 hours. Twelve dry ewes of mixed age (4-6 years) with an average weight of 60-70 kg were used for the observations. Sheep were allowed to graze in the morning in another paddock, then were transported to the site and penned in the afternoon until used for the grazing observations. Sheep were brought back to their pen overnight, allowed to graze in the next morning in another paddock, and then transported in the afternoon to record grazing observations in the remaining two replicates.

The number of sheep observed grazing at the end of each two-minute period was recorded for 2 hours. The position of each sheep in terms of treatment and replicate was also noted every two minutes. Recording was done by three people each responsible for the treatments in one main plot while hiding in the nearby bushes. A 2m transect was placed in each plot and five legumes (growing points or branches) and five grass tillers, in every 20cm distance were identified alternately and marked with plastic wire before grazing. Number of grazed marked tillers and marked legumes (out of 5 each), were recorded after grazing. The ratio of grazed tillers to legumes was also calculated.

7.3.3 Statistical analysis

The statistical significance for all the analyses was determined by analysis of variance using the PROC GLM procedure (SAS 1997). Residuals were examined for their normality and appropriate transformation was carried out when needed, and indicated on the appropriate results table. Tillers per- plant in Experiment 7.1 were also analyzed separately by the SAS GLM procedure using the model of repeated measures (SAS 1997) over the harvesting times. The significance level was set at α=0.05.

7.4 Results

7.4.1 Experiment 7.1

7.4.1.1 Light environment

The mean PAR as a % of unshaded PAR under the heavy, medium and light shade treatments was approximately 15, 25 and 75%, respectively (Table7.3a, b; Figure 7.4). Similarly, periodic R:FR measurements by instantaneous mode, or by data logger over 24 hours, found the range for R:FR was 0.7-1.0 under heavy shade, 0.9-1.1, under medium shade, and 1.3 under light shade (Table 7.3a, b, c).

Table 7.3a Levels of transmitted PAR (photosynthetically active radiation), and R:FR (red:far-red) ratios measured at various occasions under tree canopies at Aokautere, February to April 1997.

Shade	PAR (μmoles photons $m^{-2}s^{-1}$)					R:FR ratios		
	7 Feb 1997	19 Mar 1997	14 Apr 1997	Mean	Mean % full PAR	17-20 Feb 1997 (logged)	23-25 Mar 1997 (logged)	Mean
Heavy	131	121	245	166	17	0.9	1.0	1.0
Medium	227	174	383	262	27	1.2	1.2	1.2
Light	1050	527	702	759	77	1.4	1.3	1.4
Open	1265	750	919	978	-	1.5*	1.4*	1.5*

Logged: use of data logger for the given periods; * instantaneous reading

Figure 7.4 Establishment of experimental plots under light, medium and heavy shade from front to back, respectively, at Aokautere, February 1997.

Table 7.3b Levels of transmitted PAR (photosynthetically active radiation), measured at various occasions under tree canopies at Aokautere, November 1997 to May 1998.

Shade	PAR (µmoles photons $m^{-2}s^{-1}$)								
	22 Nov 1997	30 Dec 1997	13 Jan 1998	11 Feb 1998	9 Mar 1998	7 Apr 1998	14 May 1998	Mean	% full PAR
Heavy	420	33	42	55	208	261	259	183	12
Medium	774	63	86	171	405	532	491	360	23
Light	1791	1245	1152	1054	1352	1206	1045	1264	81
Open	1998	1816	1565	1460	1589	1337	1198	1566	-

Table 7.3c R:FR (red:far-red) ratios measured at various occasions under tree canopies with different shade levels at Aokautere, November 1997 to May 1998.

Shade	R:FR ratios							
	22 Nov 1997	30 Dec 1997	13 Jan 1998	10-13 Feb 1998 *	9 Mar 1998	7 Apr 1998	14 May 1998	Mean
Heavy	0.7	NA	NA	0.6	0.7	0.7	0.6	0.6
Medium	0.9	NA	NA	0.9	1.0	0.9	0.7	0.9
Light	1.5	NA	NA	1.4	1.3	1.1	1.1	1.3
Open	1.5	NA	NA	1.4	1.5	1.4	1.4	1.4

* Logged: use of data logger for the given period; NA, data not taken due to technical reason

7.4.1.2 Soil moisture

In the early phase of the experiment, there were significant differences ($P<0.01$) in % soil moisture content across the shade levels. However, moisture differences for species and interaction of shade and species were not significant, except in March, 1997 when species differences in % moisture were also found (Table 7.4a).

The trend in moisture content in those months revealed that a higher percentage of moisture was found under light shade followed by medium shade, then heavy shade. The soil moisture was higher in February and March than April and May (Table 7.4a). October, November, December, and May were the wettest months, while January to April were the driest months (Table 7.4b).

Table 7.4a Changes in % soil moisture to 200mm depth under different levels of shade at Aokautere during February to May 1997.

Shade/ treatments	Months			
	15 February 1997	7 March 1997	14 April 1997	8 May 1997
Heavy shade				
Mean value	19	22	11	14
Medium shade				
Mean value	21	24	11	15
Light shade				
Mean value	27	24	14	17
Analysis of variance				
Shade (A)	P<0.01	NS	P<0.001	P<0.001
SEM for shade (d.f.=2)	1.24	0.46	0.45	0.35
Species (B)	NS	NS	P<0.05	NS
SEM for species (d.f.=3)	0.63	0.52	0.44	0.42
Interactions (A*B)	NS	NS	NS	NS
SEM for A*B (d.f.=6)	1.09	0.90	0.76	0.73

NS= no significant differences at P<0.05, SEM=standard error of the mean ,d.f.=degrees of freedom

Soil moisture contents from October 1997 to May 1998 were greater in light than heavy shade (P<0.05) until January 1998. However, there was no effect of shade on the soil moisture content from February to May 1998 (Table 7.4b). There were no differences in soil moisture content between pasture species, except in January and March 1998. Likewise, the interaction between shade and species was also not significant for all the months, except November 1997 (Table 7.4b).

Table 7.4b Changes in % soil moisture to 200mm depth under different levels of shade at Aokautere during October 1997 to May 1998.

Shade/ treatments	29 Oct 1997	26 Nov 1997	22 Dec 1997	13 Jan 1998	11 Feb 1998	20 Mar 1998	8 Apr 1998	14 May 1998
Heavy shade								
Mean value	31	27	25	14	7	12	9	26
Medium shade								
Mean value	32	32	28	15	6	11	9	27
Light shade								
Mean value	35	34	30	19	7	10	9	25
Analysis of variance								
Shade (A)	P<0.05	P<0.001	P<0.05	P<0.01	NS	NS	NS	NS
SEM for shade (d.f.=2)	0.77	0.54	0.90	0.85	0.48	0.32	1.02	0.93
Species (B)	NS	NS	NS	P<0.05	NS	P<0.01	NS	NS
SEM for species (d.f.=3)	0.40	0.66	0.84	0.53	0.26	0.27	0.38	0.73
Interactions (A*B)	NS	P<0.01	NS	NS	NS	NS	NS	NS
SEM for A*B (d.f.=6)	0.70	1.15	1.46	0.92	0.46	0.48	0.66	1.26

NS= no significant differences at P<0.05, SEM=standard error of the mean , d.f.=degrees of freedom

7.4.1.3 Soil temperature

During the period February to May 1997, there was no variation (P>0.05) in soil temperature at 100mm depth under different shade levels, except in March (P<0.0001). Species differences in terms of soil temperature were also not significant, except for April (P<0.05) while there was no interactive effect of shade and species. Soil temperature ranged from 14 (April) to 20^{0}C (March) (Table 7.5a).

Table 7.5a Soil temperature at 100mm depth under different levels of shade at Aokautere from February to May 1997.

Shade/ treatments	Months			
	15 February 1997	7 March 1997	4 April 1997	8 May 1997
Heavy shade				
Mean value	17.1	18.0	16.5	13.8
Medium shade				
Mean value	17.5	18.9	15.5	14.0
Light shade				
Mean value	17.9	20.2	16.3	13.6
Analysis of variance				
Shade (A)	NS	P<0.0001	NS	NS
SEM for shade (d.f.=2)	0.22	0.09	0.59	0.10
Species (B)	NS	NS	P<0.05	NS
SEM for species (d.f.=3)	0.24	0.14	0.34	0.08
Interactions (A*B)	NS	NS	NS	NS
SEM for A*B (d.f.=6)	0.42	0.24	0.59	0.14

NS= no significant differences at P<0.05, SEM=standard error of the mean , d.f.=degrees of freedom

The effect of shade on soil temperature was significant for all months from October 1997 to May 1998, except during October 1997 and April 1998 (Table 7.5b). Species differences were only significant (P<0.05) for February and March 1998, while the interactive effect of shade and species was significant (P<0.05) only in November (Table 7.5b).

The highest soil temperature was under light shade for all the months. Soil temperature was highest in December 1997 and lowest in October 1997 and March 1998 (Table 7.5b).

Table 7.5b Soil temperature at 100mm depth under different levels of shade at Aokautere from October 1997 to May 1998.

Shade/ treatments	Months 28 Oct 1997	26 Nov 1997	22 Dec 1997	13 Jan 1998	27 Feb 1998	9 Mar 1998	8 Apr 1998	4 May 1998
Heavy shade								
Mean value	12.1	16.7	20.3	19.6	20.8	21.2	17.1	9.6
Medium shade								
Mean value	11.6	17.9	21.5	19.8	21.9	22.1	17.5	11.4
Light shade								
Mean value	12.0	20.1	23.7	21.2	22.4	22.6	18.6	11.0
Analysis of variance								
Shade (A)	NS	P<0.001	P<0.001	P<0.05	P<0.01	P<0.01	NS	P<0.001
SEM for shade (d.f.=2)	0.16	0.18	0.34	0.37	0.19	0.23	0.50	0.17
Species (B)	NS	NS	NS	NS	P<0.05	P<0.05	NS	NS
SEM for species (d.f.=3)	0.25	0.13	0.21	0.23	0.17	0.16	0.35	0.28
Interactions (A*B)	NS	P<0.05	NS	NS	NS	NS	NS	NS
SEM for A*B (d.f.=6)	0.43	0.22	0.37	0.40	0.30	0.28	0.61	0.49

NS= no significant differences at P<0.05, SEM=standard error of the mean, d.f.=degrees of freedom

7.4.1.4 Herbage mass

Pre-mowing herbage mass (HM) during the establishment period showed that there was a significant effect of shade for March (P<0.01) as well as April 1997 (P<0.0001), but not a difference between species. There was only a significant interactive effect of shade×species for the aboveground herbage mass during April 1997 (Table 7.6).

During March, herbage mass was highest in light shade followed by medium shade. Heavy shade had about 53% of the herbage mass (g/m^2) of that of light shade, compared to 66% under the medium shade. A similar trend was repeated during April harvest where the highest herbage mass was under light shade (239.9 g/m^2). However, under medium shade, it was increased, to about 74% of that of light shade, but under heavy shade it was down to 37% of light shade.

Table 7.6 Pre-mowing herbage mass (HM) (g/m^2) for March and April 1997 under different levels of shade at Aokautere.

Shade/ treatments	Pre-mowing herbage mass (HM) at each harvest (g/m^2)	
	25 Mar 1997	24 Apr 1997
Heavy shade		
RW	133.3	92.3
YW	122.5	60.0
CW	121.3	95.0
CL	139.5	111.8
Mean value	**129.1**	**89.8**
Medium shade		
RW	167.6	205.2
YW	187.0	149.2
CW	142.9	176.6
CL	152.3	175.5
Mean value	**162.5**	**176.6**
Light shade		
RW	251.9	217.2
YW	259.1	251.1
CW	242.0	240.8
CL	230.7	250.4
Mean value	**245.9**	**239.9**
Analysis of variance		
Shade (A)	P<0.01	P<0.0001
SEM for shade (d.f.=2)	14.75	8.80
Species (B)	NS	NS
SEM for species (d.f.=3)	9.75	6.88
Interactions (A*B)	NS	P<0.01
SEM for A*B (d.f.=6)	16.89	11.92

NS=no significant differences at P<0.05, SEM=standard error of the mean; RW=perennial ryegrass+white clover, YW=Yorkshire fog+white clover, CW=cocksfoot+white clover, and CL=cocksfoot+lotus, d.f.=degrees of freedom

Herbage mass (g/m^2) for 28 October 1997 to 28 May1998 are presented in Table 7.7. Effect of shade was always significant (P<0.01) from October 1997 to the end of the experiment, while differences between species were significant (P<0.01) only from December-January onwards. There were no interactive effects of shade × species for the whole experimental period.

Table 7.7 Pre-mowing herbage mass (HM) (g/m^2) for November 1997 to May 1998 under different levels of shade at Aokautere.

Shade/treatments	Pre-mowing herbage mass (HM) at each harvest (g/m^2)						
	24 Nov 1997	23 Dec 1997	23 Jan 1998	27 Feb 1998	27 Mar 1998	23 Apr 1998	28 May 1998
Heavy shade							
RW	241.7	152.4	77.0	98.3	64.8	40.4	93.8
YW	209.5	140.9	86.0	107.9	89.2	79.3	142.6
CW	223.0	173.6	142.6	114.0	126.8	99.7	173.8
CL	200.4	158.5	129.7	109.1	126.5	109.1	175.6
Mean value	218.6	156.39	108.8	107.3	101.8	82.1	146.4
Medium shade							
RW	328.2	222.4	164.2	138.2	113.1	58.1	146.2
YW	286.2	234.5	223.7	134.6	119.7	105.4	206.8
CW	264.7	254.1	206.1	150.3	174.1	163.1	237.8
CL	284.4	250.0	188.3	149.0	134.0	157.9	232.3
Mean value	290.9	240.3	195.6	143.0	135.2	121.1	205.8
Light shade							
RW	351.1	314.1	268.2	205.2	173.8	138.8	264.2
YW	360.6	369.4	271.5	203.6	220.8	174.2	262.6
CW	338.8	310.3	333.4	232.9	232.0	226.2	331.6
CL	439.6	327.6	270.7	258.3	251.6	232.3	305.7
Mean value	372.5	330.3	285.9	225.0	219.5	192.9	291.0
Analysis of variance							
Shade (A)	P<0.01	P<0.001	P<0.0001	P<0.01	P<0.0001	P<0.001	P<0.001
SEM for shade (d.f.=2)	26.90	12.39	11.94	14.63	2.84	9.64	10.44
Species (B)	NS	NS	P<0.01	NS	P<0.001	P<0.0001	P<0.0001
SEM for species (d.f.=3)	21.28	12.10	11.71	10.90	9.86	10.21	11.46
Interactions (A*B)	NS	NS	NS	NS	NS	NS	NS
SEM for A*B (d.f.=6)	36.86	20.97	20.29	18.89	17.0	17.69	19.85

NS=no significant differences at P<0.05, SEM=standard error of the mean; where RW=perennial ryegrass+white clover, YW=Yorkshire fog+white clover, CW=cocksfoot+white clover, and CL=cocksfoot+lotus, d.f.=degrees of freedom

Herbage mass (g/m^2) was always highest under light shade, and lowest under heavy shade. Herbage mass was highest during November and December harvests, 1997 (Table 7.7).

During November, above ground HM under medium shade was about 80% of that of light shade. HM under heavy shade was about 60% of that of light shade. This trend was repeated during December harvest, but % HM was about 73% and 47%, respectively, under medium and heavy shade relative to that of light shade. HM started to decrease from January-February but was similar in each shade level until the end of the experiment. For example, under medium shade, HM ranged from 62 (March harvest) to 71% (May harvest) of that of light shade, while under heavy shade it was consistently within the range of 45-50% of that of light shade (Table 7.7).

During January, HM of cocksfoot with lotus or white clover was highest under light shade, whereas HM of perennial ryegrass and Yorkshire fog, each with white clover, were similar and less than that of cocksfoot with lotus or white clover. Under the medium shade, HM of Yorkshire fog and cocksfoot, were also similar, but HM of perennial ryegrass with white clover was lower. Under the heavy shade, HM of cocksfoot, either with lotus or white clover, was significantly higher ($P<0.01$) than perennial ryegrass or Yorkshire fog (Table 7.7).

From February onwards, HM of cocksfoot either with white clover or lotus, was significantly ($P<0.001$) higher than any other pasture combinations in each shade level for each harvest, whereas HM of perennial ryegrass with white clover was the lowest, especially under heavy shade. For example, during March, HM of perennial ryegrass with white clover was about 80% of that of the mean HM for light shade, about 85% under the medium shade, and 64 % under the heavy shade. HM of Yorkshire fog with white clover under heavy shade was, however, inconsistent. For example, it was similar or slightly higher than perennial ryegrass with white clover during February to April, but was significantly higher than perennial ryegrass with white clover during May (Table 7.7).

7.4.1.5 Herbage harvested above the defoliation height of 50mm

Herbage harvested (g/m^2) above the defoliation height of 50mm (re-growth) at each month and the total of each month (g/m^2) for the whole experiment (212 days) is presented in Table 7.8.

There was a significant effect ($P<0.01$) of shade on the re-growth of the herbage understorey for all the harvests and also on the total re-growth (total herbage harvested over months). Similarly, there was a significant (P<0.01) difference between species for herbage re-growth, while the interactive effect of shade × species was not significant for all the harvests, except for March, 1998 (P<0.01) (Table 7.8).

Results showed a similar trend in re-growth of herbage harvest as for HM with the highest re-growth at the 28 October, 1997 harvest (Table 7.8).

For all the harvests highest re-growth was obtained under light shade, followed by medium shade. Re-growth of herbage harvest under the heavy shade was the lowest for all harvests and also for all the species combination.

Re-growth of cocksfoot, either with lotus or white clover, was always higher than the other species combinations at each harvest from November onwards. Re-growth of perennial ryegrass and Yorkshire fog each with white clover was similar and was lowest from February to May 1998 (Table 7.8).

Re-growth of perennial ryegrass with white clover was affected more under heavy shade than that of the other grass species. Relative to the mean re-growth of the other pasture species under heavy shade, perennial ryegrass with white clover had about 80% of its re-growth in November, December and February, and for the other months, it was within the range 70-75%. Under medium and light shade, however, re-growth of perennial ryegrass with white clover was well above 80% relative to the mean re-growth of the pasture species for most of the harvests (Table 7.8).

Total re-growth of herbage harvested was significantly affected by shade (P<0.0001). Differences between species were also significant (P<0.0001), but not the interactive effect of shade × species (Table 7.8). Light shade had the highest total re-growth followed by medium and the heavy shade. Highest total re-growth under light, medium and heavy shade was by cocksfoot with lotus followed by cocksfoot with white clover, while lowest total re-growth was by perennial ryegrass with white clover (Table 7.8).

Table 7.8 Herbage harvested above 50mm (re-growth) (g/m^2) at each month, and total herbage harvested (g/m^2) of over all months (October 28,1997 to May 28,1998) (212 days) under different levels of shade at Aokautere.

Treatments	Herbage re-growth above 50 mm at each harvest (g/m^2)								
	28 Oct 1997	24 Nov 1997	23 Dec 1997	23 Jan 1998	27 Feb 1998	27 Mar 1998	23 Apr 1998	28 May 1998	Total herbage over all month (g/m^2)
Heavy shade									
RW	63.5	43.5	39.2	31.1	31.5	37.6	22.5	28.5	297.7
YW	97.5	45.7	39.9	37.5	36.8	42.9	26.9	29.9	357.4
CW	83.8	54.9	54.6	62.8	46.5	60.7	40.0	44.7	448.4
CL	111.2	51.9	51.0	50.7	43.3	59.3	44.1	46.3	457.9
Mean value	89.0	49.0	46.2	45.5	39.5	50.1	33.4	37.3	390.4
Medium shade									
RW	115.2	55.3	62.5	64.2	40.7	62.8	29.5	35.8	466.4
YW	150.7	65.3	64.5	89.7	56.5	50.1	36.9	33.1	547.1
CW	132.6	70.4	82.2	94.8	58.7	57.9	45.6	47.1	589.7
CL	157.4	64.4	85.5	89.7	60.2	55.9	45.5	46.4	605.4
Mean value	139.0	63.8	73.7	84.6	54.0	56.6	39.4	40.6	552.1
Light shade									
RW	168.0	60.9	76.0	79.8	40.7	57.1	33.8	35.6	552.3
YW	202.4	67.0	103.1	104.1	30.7	54.6	37.3	34.4	633.9
CW	186.1	75.3	82.8	129.1	50.7	60.0	54.9	56.1	695.5
CL	227.6	68.1	107.0	101.2	60.8	57.6	55.9	57.1	735.8
Mean value	196.0	67.8	92.2	103.6	45.7	57.3	45.5	45.8	654.4
Analysis of variance									
Shade (A)	P<0.0001	P<0.05	P<0.01	P<0.001	P<0.01	NS	P<0.001	P<0.05	P<0.0001
SEM for shade (d.f.=2)	4.90	3.74	5.12	5.33	2.34	2.58	1.28	1.56	15.71
Species (B)	P<0.0001	P<0.01	P<0.01	P<0.0001	P<0.01	P<0.01	P<0.0001	P<0.0001	P<0.0001
SEM for species (d.f.=3)	6.82	2.62	4.17	3.99	4.09	2.28	2.30	2.21	11.55
Interactions (A*B)	NS	NS	NS	NS	NS	P<0.01	NS	NS	NS
SEM for A*B (d.f.=6)	11.82	4.53	7.23	6.91	7.09	3.96	4.00	3.83	20.00

NS=no significant differences at P<0.05, SEM=standard error of the mean; where RW=perennial ryegrass+white clover, YW=Yorkshire fog+white clover, CW=cocksfoot+white clover, and CL=cocksfoot+lotus, d.f.=degrees of freedom

7.4.1.6 Botanical composition

Distribution of grass, legumes, weeds and dead materials are presented as % botanical composition for each month from March 1997 to May 1998 (Appendix Table 7.1a,b).

The trend in botanical composition indicated inverse relationship between grass and legume components. The mean % grass of all shade levels increased from March 1997 to May 1998 so as the decreased in mean % legumes (Figure 7.5, 7.6). Higher percentage of grass in the composition during May 1998 resulted severe reduction in % legumes in all species, but with the maximum affect for legumes in a mixture with cocksfoot which was highest in the proportion than other grasses (Figure 7.6).

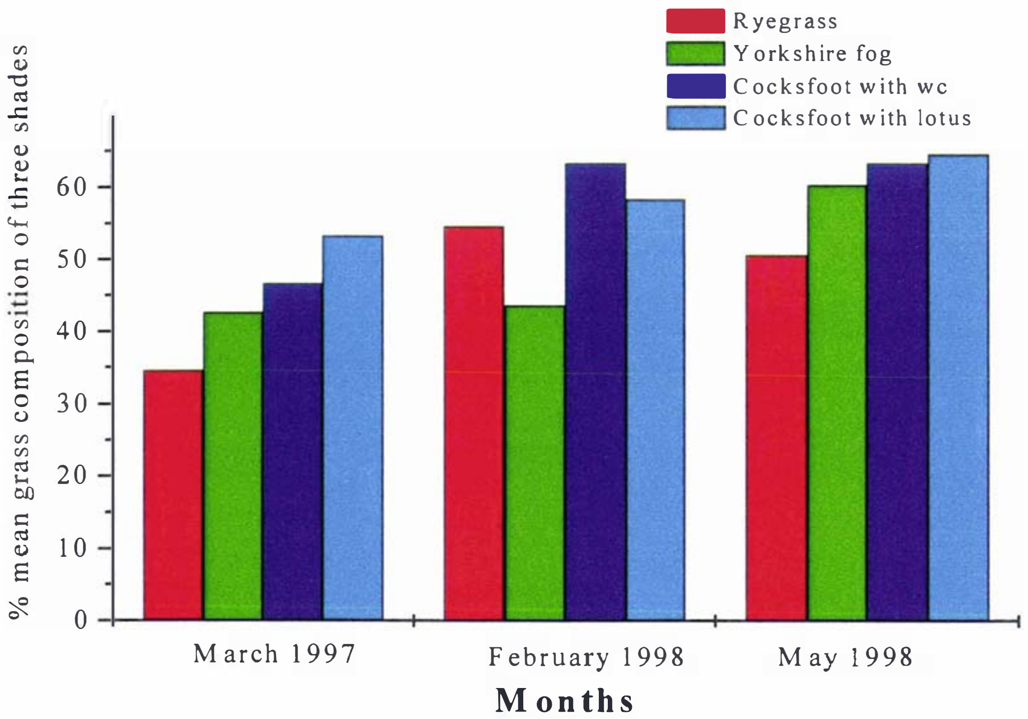

Figure 7.5 Percent mean grass composition of three shade levels on different grass-legumes combinations over selected months.

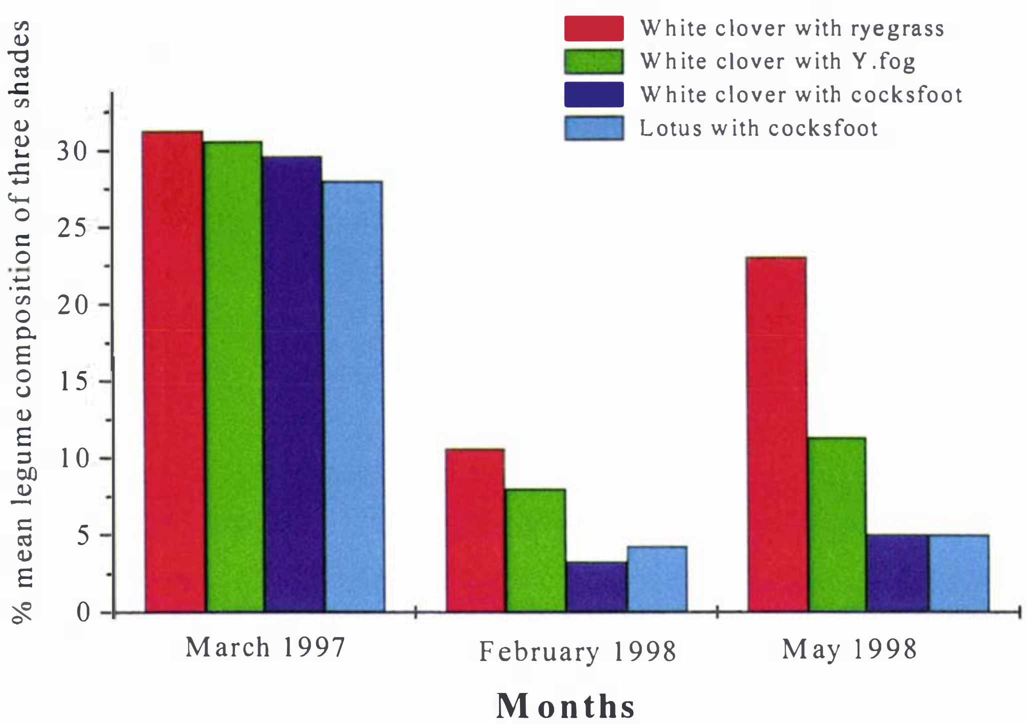

Figure 7.6 Percent mean legume composition for three shade levels on different grass-legume combinations over selected months.

Percent other materials that included dead materials and weeds in the botanical composition were more or less similar over time, except during some dry months, such as in February, where the proportion of dead material was nearly 50% in the composition, especially for Yorkshire fog. The percentage of dead material, however, dropped in the May once moisture contents in the soils improved (Figure 7.7).

In general botanical composition was similar during March, April, and May 1997. The grass component contributed a higher percentage in all shade levels for all species combinations. Cocksfoot's contribution was higher than for all other species in all shade levels. The highest % of legume, as well as dead material, was with perennial ryegrass, especially in heavy shade. The proportion of legume in the Yorkshire fog with white clover in combinations, particularly under light shade, was also high, while the % dead material was lowest with cocksfoot under all shade levels (Appendix Table 7.1a).

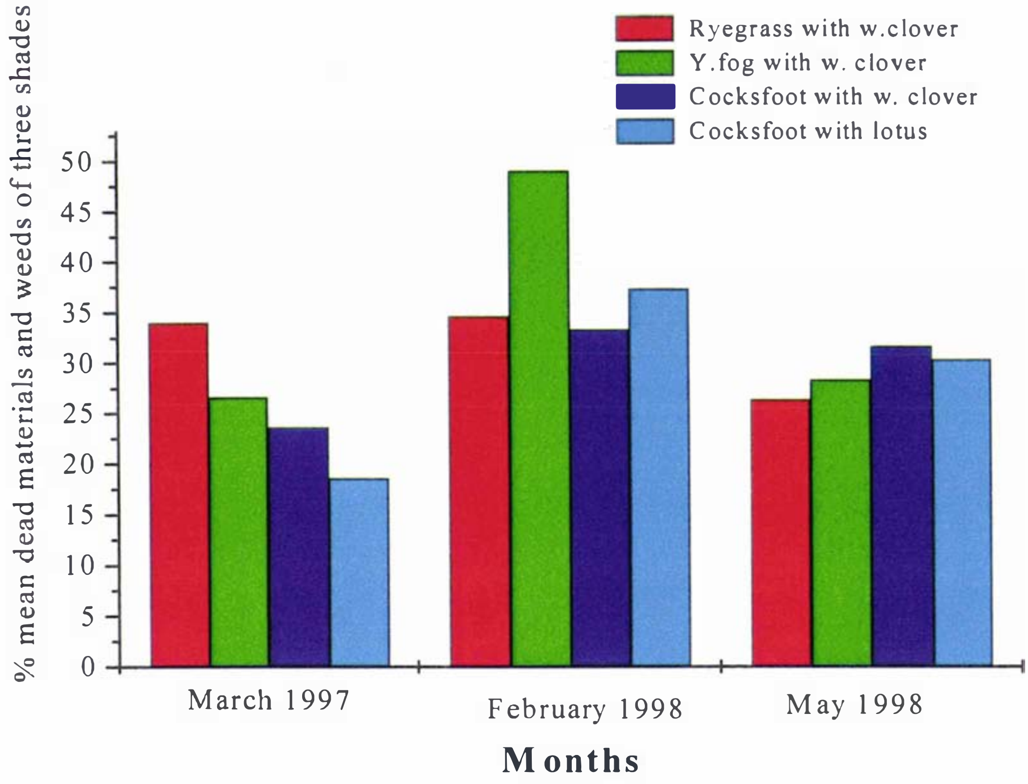

Figure 7.7 Percent mean other materials composition of three shade levels on different grass-legumes combinations over selected months.

January and February 1998 had decreased percentage of grass in the case of perennial ryegrass with white clover in combination, mainly under heavy shade, which was largely replaced by weeds as well as dead materials. During February, botanical composition was changed mainly in a mixture of Yorkshire fog with white clover where proportion of grass was dropped down to 35% of the composition, whereas proportion of dead material was increased up to 55% under the light shade. Likewise proportion of legumes with the cocksfoot mixture was decreased, with only about 1-2% in the case of lotus with cocksfoot under light shade, which was replaced by dead material. Proportion of weeds in a cocksfoot mixture was minimum (Appendix Table 7.1b)

7.4.1.7 Tiller density

Increased shade level significantly (P<0.001) reduced the number of tillers/m^2, which was also significantly different (P<0.001) between species from November 1997 to February 1998. However, the interactive effect of shade × species was not significant (Table 7.9a). Highest tiller number/m^2 was produced under light shade for all the months by all the species, followed by medium shade and then heavy shade. Under heavy shade cocksfoot always produced highest tiller number /m^2, while values for Yorkshire fog were highest under the light shade (Table 7.9a).

Table 7.9a Tiller density (number/m^2) of the grass component in grass-legume mixtures under three levels of tree shade at Aokautere from November 1997 to February 1998.

Treatments	Months			
	24 November 1997	20 December 1997	17 January 1998	21 February 1998
Heavy shade				
RW	2275	1850	1675	1925
YW	1675	2025	2350	2200
CW	2825	2275	2400	2500
CL	2675	2225	1750	2175
Mean value	2363	2094	2044	2200
Medium shade				
RW	2950	1875	2575	2175
YW	2275	3025	3600	2725
CW	3500	2800	2775	2675
CL	2850	2275	2625	2825
Mean value	2894	2494	2894	2600
Light shade				
RW	3700	2650	2975	2475
YW	3850	3900	4650	3500
CW	4075	3125	3700	3150
CL	3425	2975	2950	2850
Mean value	3763	3163	3569	2994
Analysis of variance				
Shade (A)	P<0.001	P<0.001	P<0.001	P<0.001
SEM for shade (d.f.=2)	129.95	94.99	131.62	77.81
Species (B)	P<0.01	P<0.001	P<0.0001	P<0.001
SEM for species (d.f.=3)	161.02	129.20	121.10	96.71

NS=no significant differences at P<0.05, SEM=standard error of the mean; where RW=perennial ryegrass+white clover, YW=Yorkshire fog+white clover, CW=cocksfoot+white clover, and CL=cocksfoot+lotus, d.f.=degrees of freedom

March, April, and May 1998 also had significant (P<0.001) effects of shade on tiller density where species differences were also significant (P<0.0001) for all the months but the interactive effects of shade × species were not significant. Light shade always produced highest tiller number/m^2 with the lowest under heavy shade (Table 7.9b).

Table 7.9b Tiller density (number/m^2) of the grass component in grass-legume mixtures under three levels of tree shade at Aokautere from March to May 1998.

Treatments	Months			
	March 20 1998	April 18 1998	May 20 1998	Repeated measures (Nov 24 to May 20)
Heavy shade				
RW	1575	1425	1575	1757
YW	3000	3300	2925	2496
CW	3200	3200	3150	2793
CL	3075	2975	3025	2557
Mean of shade	**2713**	**2725**	**2669**	**2401**
Medium shade				
RW	2125	2675	2250	2375
YW	3325	3925	4150	3289
CW	3350	3550	3775	3204
CL	3575	3625	3575	3050
Mean of shade	**3094**	**3444**	**3438**	**2979**
Light shade				
RW	2800	3075	3400	3011
YW	3875	4350	4575	4100
CW	3525	4125	4425	3732
CL	3450	3825	4175	3379
Mean of shade	**3413**	**3844**	**4144**	**3555**
Analysis of variance				
Shade (A)	P<0.01	P<0001	P<0.001	P<0.0001
SEM for shade (d.f.=2)	97.78	108.79	151.94	57.63
Species (B)	P<0.0001	P<0.0001	P<0.0001	P<0.0001
SEM for species (d.f.=3)	97.35	107.38	86.93	66.55
Interactions (A*B)	NS	NS	NS	P<0.05
SEM for A*B (d.f.=6)	168.61	185.99	150.57	115.27

NS=no significant differences at P<0.05, SEM=standard error of the mean; where RW=perennial ryegrass+white clover, YW=Yorkshire fog+white clover, CW=cocksfoot+white clover, and CL=cocksfoot+lotus, d.f.=degrees of freedom

Repeated measures of tiller density over seven occasions showed a significant effect (P<0.0001) of shade, species (P<0.0001) and the interaction of shade×species (P<0.05). Highest tiller density was under light shade by Yorkshire fog with white clover followed by cocksfoot with white clover. Tiller density of perennial ryegrass was lowest. This trend was repeated under the medium shade. Under heavy shade, however, highest tiller density was by cocksfoot either with white clover or lotus followed by Yorkshire fog. Perennial ryegrass had only about 73% of the tiller density relative to the mean value for heavy shade (Table 7.9b).

7.4.1.8 Legumes growing points or branches density

There was no effect of shade on the number of growing points (GP) of white clover or the number of branches of lotus for November and December 1997, but the effect was significant for January and February 1998 ($P<0.01$). There were also differences between species ($P<0.0001$) for all the months. However, interactive effects between shade and species were not significant (Table 7.10a).

Lotus always had higher density of branches under all levels of shade with the highest under light shade and for the months of November and December.

In general, white clover GP density was greater under heavy shade but often similar to that under medium shade (e.g. November). White clover GP density was highest with perennial ryegrass and lowest with a mixture of cocksfoot. For example, in February, white clover GP density under light shade with perennial ryegrass was 112% relative to the mean value of light shade, in comparison to 97% with Yorkshire fog and 60% with cocksfoot (Table 7.10a). Effects of shade on the number of GP of white clover or the number of lotus branches was significant ($P<0.0001$) for the months of April and May, and also for the repeated measurements (Table 7.10b). Similarly, differences between species were significant ($P<0.0001$) for these months. GP density of white clover with ryegrass component was similar in all shade levels, often greater under medium shade (April) which was highest than with the Yorkshire fog or the cocksfoot in mixture.

Repeated measures analysis revealed the significance of shade, species, and time with the interactive effects of shade $\times$ time and species $\times$ time for the GP density of white clover or the branches of lotus. Highest mean density was found under light shade followed by medium and heavy shade. Among the species, greater density was in a mixture with perennial ryegrass followed by Yorkshire fog and the lowest with cocksfoot (Table 7.10b).

Table 7.10a Density of growing points or branches (number/m^2) for white clover and lotus in grass-legume mixtures under different levels of tree shade at Aokautere from 24 November 1997 to 21 February 1998. (* ln transform, and value inside the parentheses are back transformed).

Treatments	Months			
	24 Nov 1997 *	20 Dec 1997	17 Jan 1998 *	21 Feb 1998
Heavy shade				
RW	6.10 (446)	350	5.91 (369)	400
YW	5.97 (392)	250	5.50 (245)	325
CW	5.67 (290)	250	5.39 (219)	250
CL	7.82 (2490)	1675	7.02 (1119)	450
Mean value	6.39 (596)	631	5.96 (388)	356
Medium shade				
RW	6.28 (534)	525	5.95 (384)	550
YW	6.37 (584)	375	6.05 (424)	500
CW	6.28 (534)	325	5.74 (311)	400
CL	7.89 (2670)	2200	7.44 (1703)	625
Mean value	6.71 (821)	856	6.29 (539)	519
Light shade				
RW	6.23 (508)	575	6.56 (706)	750
YW	6.28 (534)	450	6.14 (464)	650
CW	6.08 (437)	425	5.74 (311)	400
CL	7.76(2345)	2200	7.98 (2922)	875
Mean value	6.59 (728)	913	6.61 (743)	669
Analysis of variance				
Shade (A)	NS	NS	P<0.01	P<0.01
SEM for shade (d.f.=2)	0.07	72.49	0.08	54.64
Species (B)	P<0.0001	P<0.0001	P<0.0001	P<0.001
SEM for species (d.f.=3)	0.06	70.02	0.06	37.13

NS=no significant differences at P<0.05, SEM=standard error of the mean; where RW=perennial ryegrass+white clover, YW=Yorkshire fog+white clover, CW=cocksfoot+white clover, and CL=cocksfoot+lotus, d.f.=degrees of freedom

Table 7.10b Density of growing points or branches (number/m^2) for white clover and lotus in grass-legume mixtures under different levels of tree shade at Aokautere from 20 March to 20 May 1998.

Treatments	Months			
	20 Mar 1998	18 Apr 1998	20 May 1998	Repeated measures (Nov 24 to May 20)
Heavy shade				
RW	800	925	1000	614
YW	625	800	825	496
CW	425	500	500	350
CL	825	900	1225	1254
Mean value	**669**	**781**	**888**	**679**
Medium shade				
RW	750	1000	950	675
YW	775	950	875	646
CW	425	600	625	464
CL	850	1050	1600	1543
Mean value	**700**	**900**	**1013**	**832**
Light shade				
RW	825	975	1150	793
YW	775	1100	1075	725
CW	575	675	750	514
CL	1025	1475	1875	1836
Mean value	**800**	**1056**	**1213**	**967**
Analysis of variance				
Shade (A)	NS	P<0001	P<0.001	P<0.0001
SEM for shade (d.f.=2)	59.91	29.09	35.35	35.04
Species (B)	P<0.0001	P<0.0001	P<0.0001	P<0.0001
SEM for species (d.f.=3)	47.48	55.17	35.89	40.46
Interactions (A*B)	NS	NS	P<0.01	NS
SEM for A*B (d.f.=6)	82.24	95.56	62.17	70.08

NS=no significant differences at P<0.05, SEM=standard error of the mean; where RW=perennial ryegrass+white clover, YW=Yorkshire fog+white clover, CW=cocksfoot+white clover, and CL=cocksfoot+lotus,d.f.=degrees of freedom

7.4.2 Experiment 7.2

7.4.2.1 Diet selection by sheep

Diet selection by sheep was examined in terms of total number of sheep grazing, total number of observations of sheep grazing, grazed tillers and legume growing points, and the ratio of the grazed tillers to legumes (Table 7.11).

There was a significant difference between the shade levels ($P<0.05$) in terms of the total number of sheep grazing in two hours. More sheep grazed under light shade, followed by medium, and then heavy shade (Figure 7.8). Under medium shade, there were about 80% of the observations of sheep grazing relative to the mean sheep grazing observations under light shade, whereas under heavy shade there were 50% of the light shade grazing observations (Table 7.11). However, choice of pasture species, and the interaction between shade and species was not significant ($P>0.05$) for the total number of sheep grazing in two hours.

Figure 7.8 Sheep grazing under light shade.

Table 7.11 Total number of sheep grazing, total number of observations of sheep grazing, grazed tillers and growing points/branches of marked legumes, and the ratio of grazed tillers to legumes for Yorkshire fog with white clover, cocksfoot with white clover, and cocksfoot with lotus components of pastures grown under alder trees, at Aokautere, November 1998.

Treatments	Grazing and related attributes				
	Total number of sheep grazing	Total number of observations of sheep grazing	Number of tagged tillers grazed (out of 5)	Number of tagged legumes grazed (out of 5)	Ratio of grazed tillers to legumes
Heavy shade					
YW	12.2	6.2	2.0	1.7	1.4
CW	25.0	8.2	2.7	2.0	1.6
CL	19.0	6.7	2.2	3.0	0.7
Medium shade					
YW	33.0	12.0	3.7	2.2	1.7
CW	29.0	11.2	3.0	1.7	2.0
CL	26.5	13.2	3.5	3.0	1.1
Light shade					
YW	36.0	12.7	3.2	2.5	1.4
CW	38.5	15.0	3.2	2.7	1.2
CL	36.7	14.0	3.2	3.5	1.0
Analysis of variance					
Shade (A)	P<0.05	P<0.05	P<0.01	NS	NS
SEM (d.f.=2)	3.69	0.10	0.13	0.35	0.25
Species (B)	NS	NS	NS	P<0.01	P<0.01
SEM (d.f.=2)	2.36	0.07	0.17	0.19	0.13
Interaction (A*B)	NS	NS	NS	NS	NS
SEM (d.f.=4)	4.08	0.13	0.29	0.34	0.23

NS=no significant differences at P<0.05, SEM=standard error of the mean, YW=Yorkshire fog+white clover, CW=cocksfoot+white clover, and CL=cocksfoot+lotus,d.f.=degrees of freedom, d.f.=degrees of freedom

The number of tagged tillers that were grazed by sheep was significantly different (P<0.01) between the shade levels, but the species and the shade × species effects were not significant. Out of 5 marked tillers, 3.2 under light shade, 3.4 under medium shade and 2.3 under heavy shade were grazed (Table 7.11).

There was no significant difference (P>0.05) in the of number of tagged legumes that were grazed across the shade levels, but species differences (P<0.01) in grazing preference were found. Lotus was selected more than white clover in all shade levels in cocksfoot plots with the highest preference under light shade. Grazing of white clover was similar in the mixtures with Yorksire fog and with cocksfoot (Table 7.11).

For ratio of grazed tillers to legumes there was a significant difference between species (P<0.01) but not shade levels. Lotus was grazed more than white clover. The grass: legume ratio was smaller for cocksfoot with lotus in all shade levels, compared with Yorkshire fog with white clover, or cocksfoot with white clover (Table 7.11).

7.5 Discussion

7.5.1 Pasture species in the mixture and performance under deciduous tree shade

The greater the shade levels under the alders the lower the herbage production and the tiller density and the lower the grazing preference by sheep. There was a marked effect of shade on the herbage mass (HM), and also on the re-growth of herbage harvested above the defoliation height of 50mm. HM was always higher under the light shade and lowest under the heavy shade for all the experimental period. For example, HM in heavy and medium shade was only about 50% and 70%, respectively, of that in light shade. Differences between species were also markedly affected by shade; HM and tiller density of cocksfoot were always highest especially under heavy shade whereas perennial ryegrass and Yorkshire fog had the lowest HM and tiller density. Tiller density under heavy shade was only about 60% of that in light shade. There was no difference in the choice of understorey pasture species by sheep, while the number of observations of sheep grazing was about 50% higher under light shade than under heavy shade.

HM in heavy and medium shade was 50% and 70%, respectively, of HM in light shade for alders pruned to different heights. This suggested that understorey herbage production will be largely affected by increased shading at high density of trees if they are not pruned effectively (Braziotis and Papanastis 1995; Eastham and Rose 1998). Therefore pruning management could be an effective practice for deciduous trees. Shading is one of the most significant factors that determine the productive performance of understorey pastures (Shelton *et al.* 1987). Accordingly, the abilities of plants to regenerate leaf area to maximise interception of available radiation, and to generate tillers and stolons from main stems are the critical factors that determine production and persistence of pasture species under low irradiance (Chen 1993).

Cocksfoot either with lotus or white clover, always produced significantly higher HM or the re-growth above the defoliation height of 50mm in all shade levels compared with Yorkshire fog with white clover or perennial ryegrass with white clover. The higher HM of cocksfoot was supported by higher tiller density, except during January, (Tables 7.9a, b), and a higher proportion of the grass component in the botanical composition (Appendix Tables 7.1a, b; Figures 7.5-7.7), especially under heavy shade. Previous research results in the glasshouse conditions also supported this trend that higher numbers of tillers per plant was positively associated with higher shoot dry weight per plant (Devkota *et al.* 1997; 1998; Chapters 3, 4). High numbers of tillers, however, did not result in a high HM for Yorkshire fog in a mixture with white clover (Tables 7.9a, b). Previous research results (Chapters 3-6) also revealed that morphological characteristics of pasture species such as tiller numbers per plant, leaf area, and specific leaf area were important to sustain and produce higher shoot dry weight under heavy shade.

Significant differences between the species under shade from December/January onwards in HM indicated that there were differences in competition for water between trees and pasture during the dry period. Total moisture distribution across all months was not monitored in this experiment, but less water stress in the cocksfoot plots than other species was particularly visible during January 1998 (Table 7.4b). Miller *et al.* (1998) in a study of transpiration rates and canopy conductance of *Pinus radiata* growing with different pasture understories in Canterbury, New Zealand, reported that there was a reduction in mean transpiration flux density of *Pinus radiata* trees in the cocksfoot treatments, indicating the greater competition between *Pinus radiata* and cocksfoot than *Pinus radiata* and perennial ryegrass, enabling cocksfoot to grow better during a dry summer compared with perennial ryegrass. Montard *et al.* (1999) found strong competition for light, water and nutrients in an association of hazel trees and cocksfoot. Cocksfoot roots were predominant in the upper 20cm layer during dry periods, resulting in both water and N deficits for the trees.

Cocksfoot is the second most commonly sown grass species after perennial ryegrass in New Zealand farming (Moloney 1993). Relative to perennial ryegrass, cocksfoot provides reliable leafy summer growth free of endophyte and of moderate nutritive value, but with greater persistency in dryland (Rumball 1982; MacFarlane 1990; Woodman and Fraser 1991; Moloney 1993; Fraser and Hewson 1994). This experiment indicated that cocksfoot is also a good producer under heavy shade (PAR level about 200 μmoles photons m^{-2} s^{-1} or even lower) (Tables 7.3a, b; Chapters 3-6), even when fertility is low and with prolonged drought. Cocksfoot, 'Grasslands Wana' was also determined to be one of the most shade tolerant species in monoculture conditions (Devkota *et al.* 1997; 1998). Cocksfoot was equally shade tolerant in mixture with either white clover or lotus. However, legume abundance in dry months was particularly affected due to the presence of cocksfoot as a component species.

Low HM by perennial ryegrass, particularly in the heavy shade, could have been exacerbated by the poor soil fertility. Olsen P of the experiment plots was 11.4 μg/g with pH of 5.5 (Table 7.1). Low level of monthly rainfall during January to April with lowest in March 1998 (Figure 7.2) also suggests that perennial ryegrass was under stress not only due to shade but also from the low level of soil moisture, coupled with low fertility and high soil temperature (> 20^0C) (Tables 7.5a, b). However, production of perennial ryegrass under medium and light shade was not affected as much as under heavy shade, which indicates that perennial ryegrass could probably be managed under an intermediate level of shade (PAR level >200 μmoles photons m^{-2} s^{-1}) (Tables 7.3a, b; Chapters 3-6).

The proportion of legume in the pasture was always lower with cocksfoot than Yorkshire fog and perennial ryegrass, especially under light and medium shade (Figure 7.6). Moloney (1993) suggested that cocksfoot appeared to suppress white clover with its ability to compete faster for resources. This experiment also showed that there was a very small proportion of white clover and lotus in mixture with cocksfoot, especially during dry months under light shade.

West *et al.* (1988; 1991) reported that Yorkshire fog was one of the better performed species under shade. However, this experiment showed that Yorkshire fog was inferior to cocksfoot, and similar to perennial ryegrass in terms of HM in all the shade levels (Table 7.7). Yorkshire fog had a higher tiller density compared to other species in all the shade levels, but this did not lead to a higher level of HM. Yorkshire fog was particularly affected by the dry periods. Botanical composition revealed that % dead material in Yorkshire fog in all the shade levels was well above 50% during March 1998 (Appendix Table 7.1b).

There was no difference in the HM of cocksfoot with white clover or with lotus in all shade levels. Lotus was particularly seasonal in growth. For example, there was a significantly higher proportion of lotus in the mixture with cocksfoot during October and November in all shade levels compared with the other months, but the proportion from December onwards was progressively lower with almost none during March and April 1998. Gadgil *et al.* (1986), West *et al.* (1988), and West *et al.* (1991) all indicated that lotus is one of the most successful legumes under shade, and can be readily established on a range of sites. However, results of this experiment showed that lotus could be sensitive to the changes in season, and was also suppressed by the companion grass during a dry summer.

The proportion of white clover in all the shade levels was reasonably high until January (Appendix Table 7.1a, b). The contribution of white clover to the botanical composition was negligible from February to April, as in the case of lotus. White clover could have a lower level of photosynthesis in shade (Woldge and Parsons 1986), especially in a mixture of cocksfoot which was mowed only once in a month. This could be the one reason for the lower proportion of white clover during the dry period.

7.5.2 Diet selection by sheep under tree shade

Vigilant behaviour of sheep while grazing (Pulliam and Caraco 1984; Illius and Fitzgibbon 1994) could explain the sheep behaviour of selecting their diet more in light shade than under heavy shade. It is well known that vigilant behaviour of ruminants is the best defence against predators. It was noticed while monitoring the grazing that sheep mostly moved in a group and were most vigilant under heavy shade. Therefore, availability of more light under light shade and medium shade could be one of the reasons why sheep concentrated their grazing there. This was further supported by the sheep becoming indifferent to grazing across the shade levels after sunset, which was observed on both days of grazing.

Differences in pasture structure (Gordon and Lascano 1993) between the shade levels could have affected the differences in diet selection, as could have changes in texture (Vallentine 1990). Equally, differences in selection could have also been due to the animal response to variation in the vertical distribution between species (Hodgson 1981).

One important point to note is that the limited area available around the experimental site meant that the sheep could not be acclimatised to the conditions before observations started, so they had no preliminary experience of the plot lay out. However, there was no notable change observed in the behaviour of the sheep over the two days.

7.6 Conclusion

Cocksfoot was found to be the most shade tolerant pasture species, whether grown with white clover or lotus in a mixture, in the conditions of low soil fertility and moisture stress present during this experiment. The ability of cocksfoot to produce herbage mass under shade was associated with its relatively higher tiller production in heavy shade than for the other grass species. Cocksfoot was also defoliation tolerant. The ability of cocksfoot to regenerate leaf area to maximise interception of available radiation, and to generate tillers were critical factors that determined its production and persistence under low irradiance. On the other hand, Yorkshire fog was sensitive to shade, and drought. In Chapter 3 Yorkshire fog was one of the species that produced tillers under low irradiance in monoculture and it was assumed to be shade tolerant. Yorkshire fog also had high tiller numbers under the different shade levels under alders, but it could not produce a high biomass under the tree shade.

Perennial ryegrass was the most affected pasture species in all shade levels, particularly under heavy shade. The low level of herbage mass of perennial ryegrass under tree shade was directly related to its low tillering ability in the shade, and also, possibly, to the combined effects of low light, poor soil fertility and low soil moisture content. Production of perennial ryegrass was also affected under medium and light shade, but not as much as under heavy shade, which indicates that ryegrass could probably be managed under an intermediate level of shade. This agreed with findings of previous studies in the glasshouse (Chapters 3, 5 and 6) as well as under trees (Chapter 4).

It can be concluded that cocksfoot is the most shade tolerant pasture species which produced higher herbage mass, especially under heavy shade. This suggested the use of cocksfoot under heavy shade even when soils are limited with poor fertility and climatic stress such as summer drought. However, the moderate nutritive value of cocksfoot needs to be considered while trading-off between the scale of cocksfoot production for a silvo-pastoral system. The level of shade rather than the differences in the pasture species largely determined differences in the diet selection by sheep. Vigilant behaviour of sheep against dark (low light) under heavy shade could be an important factor for having a low level of grazing under heavy shade.

Cocksfoot was concluded to be the most shade tolerant pasture which produced higher herbage mass, especially under heavy shade. This suggested the use of cocksfoot under heavy shade even when soils are limited with poor fertility and climatic stress such as summer drought. However, the moderate nutritive value of cocksfoot needs to be traded off against its superior production in a silvo-pastoral system. Sheep grazing under alder trees indicated no differences in choice between pasture grass, but their preference to graze more under light shade needs further validation in a long-term study. Results suggested that pasture production is affected by shade but comparatively it can be managed by pruning trees. Pruning trees can be an equally effective way to conserve soil moisture content along with minimizing the effects of shade.

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8. Effect of tree shade on tissue turnover in perennial ryegrass/white clover, Yorkshire fog/white clover and cocksfoot/white clover pasture

Page

8.1 Summary

There are a large number of published research results on tissue turnover of temperate pastures species, but information on tissue turnover of pastures under tree shade is scanty. Previous studies of pasture production under tree shade show that cocksfoot, either with white clover or lotus, had higher biomass production than perennial ryegrass and Yorkshire fog throughout the seasons (Chapter 7).

A study was conducted on tissue turnover of pasture species under 11 year old alder trees during late spring and the early autumn at the Horticultural Research Institute's field station at Aokautere, near Palmerston North. A split-plot design with four replicate blocks was employed. The main plot treatments were three levels of shade created by pruning trees 2.5m, 5.0m and 7.0m from ground level, and the sub-plot treatments were pasture species in combination. Perennial ryegrass, Yorkshire fog, and cocksfoot were each combined with white clover, and cocksfoot was also combined with lotus (see Chapter 7: sections 7.3.1, 7.3.2 for detail). Leaf elongation and senescence were measured three times in both experiments; late spring/early summer (November-December 1997), and early autumn (March 1998) using the techniques of Birchman and Hodgson (1983) for grasses, and with some modifications (Williams *et al.* 1964) for white clover. Estimates of leaf weight per unit length (Hernandez-Garay *et al.* 1997a) together with the tiller population data (tillers/m^2), recorded routinely once each month by counting in two randomly chosen a 10×10 cm quadrats in each plot, were used to calculate net leaf expansion (mm/tiller/day), and weight change per tiller (mg/tiller/day), as well as weight change per unit of ground area (g/m^2/day). Leaf area, stolon and petiole length and dry weight of white clover were also measured to calculate net expansion per growing point and weight change per growing point, and per unit area.

The effect of shade on rates of net leaf expansion (mg/tiller/day) was not significant during November-December or March, while net leaf production (g/m^2/day) was only significantly ($P<0.01$) affected by shade during late spring/early summer. Likewise,

shade had no effect on net dry weight accumulation per growing point of white clover, but the effect was significant ($P<0.05$) on net dry weight per unit area during early spring/late summer. However, there was an effect of shade ($P<0.10$) on the net production during late spring/early summer, when species differences ($P<0.001$) were also observed between the treatments. Cocksfoot combined either with white clover or lotus had the highest leaf expansion per tiller, with the order being cocksfoot >Yorkshire fog > perennial ryegrass. Yorkshire fog had about 76% of the leaf expansion of the cocksfoot whereas perennial ryegrass had only about 70%.

Highest leaf production ($g/m^2/day$) was under light shade followed by medium and heavy shade. Under heavy shade, leaf production was highest for cocksfoot compared with Yorkshire fog or perennial ryegrass, where both perennial ryegrass and Yorkshire fog had similar production, which was about 62% of that of cocksfoot. Net accumulation of white clover was always higher when with perennial ryegrass in a mixture, and lowest with cocksfoot. This showed that white clover was particularly sensitive to the shade of the companion grass regardless of tree shade probably due to the higher level of competition by cocksfoot than with perennial ryegrass for light and moisture.

There was a seasonal difference in rates of net leaf expansion per tiller and net production per unit area. They were lower during autumn than in the late spring/early summer. Yorkshire fog and perennial ryegrass tissue dynamics were probably more affected by low soil moisture over summer and autumn than cocksfoot. Cocksfoot could also have a relative advantage of higher SLA and tiller numbers and thus higher tissue turnover, especially under heavy shade than perennial ryegrass.

8.2 Introduction

Leaves, tillers and other plant parts of swards are continuously emerging, growing and dying at different rates depending on environmental conditions and stage of development (Davies 1981; Hernandez-Garay *et al.* 1997a). In a given period the net change in the weight of living shoot material of a species is the result of the difference between the gross increase in weight brought about by the formation of new tissue and the gross decrease caused either by senescence and decomposition of older tissue, or by herbage intake (Birchman and Hodgson 1983; Carrere *et al.* 1997). The processes of growth and senescence are continuous in swards and they respond in different ways to variation in sward management (Hodgson 1981).

The rate of production of new tissue by individual tillers may be computed either in terms of the rate of increase of the weight of leaf laminae only, or of total above-ground parts (Davies 1981). Likewise, estimates of white clover growth and senescence can be based on measurement of length or area increments of petioles, stolons and laminae (Birchman and Hodgson 1983; Carrere *et al.* 1997).

To study the mechanisms affecting the abundance, and productivity of species, detailed swards measurements are required to estimate the growth, senescence and intake fluxes for each of the species (Carrere *et al.* 1997). Tiller dynamics under a range of sward managements have been determined. These include herbage production under different grazing managements, covering seasonal variation in tissue flows and tiller and growing point densities (Brereton *et al.* 1985; Grant *et al.* 1988; Xia *et al.* 1990; Hepp *et al.* 1996; Hernandez-Garay *et al.* 1997a; 1997b). These studies were all primarily concentrated on perennial ryegrass and white clover swards, but there have been studies on other pasture species (Xia *et al.* 1994). However, there is little or no information available on tiller or tissue dynamics of perennial ryegrass and white clover in silvo-pastoral system where pastoral plants are grown under tree shade. Moreover, information on the tissue dynamics of temperate species other than perennial ryegrass is also rare. The objective of this research was to determine tissue turnover of pasture species relevant to temperate silvo-pastoral systems based on deciduous trees.

Accordingly, perennial ryegrass, cocksfoot, Yorkshire fog, and white clover were monitored from late spring to early autumn.

8.3 Materials and methods

8.3.1 Site description

The experiment was conducted on a moist, lowland site at the Horticultural Research Institute's (HortResearch) field station at Aokautere, near Palmerston North and involved the same site and pasture species were used as used in Chapter 7. Details of the site have been described in Chapter 7, methodology (Section 7.3.1).

8.3.2 Experimental treatments and designs

The first measurement (Spring) was conducted from 28 November 1997 to 16 December 1997, and the second (Autumn) from 1 March 1998 to 22 March 1998. The field site was at the Horticultural Research Centre, Aokautere, near Palmerston North under 11 year old alder trees. Plots in the field were arranged in a split-plot design with four replicate blocks. The main plot treatments were three levels of shade created by pruning trees up to 2.5 m, 5.0 m and 7.0 m from the ground, which resulted in three different levels of transmitted PAR, hereafter called heavy, medium, and light shade, respectively (Chapter 7: section 7.3.1, 7.3.2). PAR was measured monthly on clear sky days between 1200 to 1300h using a LI-COR Model LI-185 Quantum Sensor. R:FR ratio of the light was also measured monthly with a Skye sensor at just above the swards under the trees.

The subplots were four mixed species swards: perennial ryegrass (Grasslands Nui), Yorkshire fog (Massey Basyn), and cocksfoot (Grasslands Wana), which were each combined with white clover (Grasslands Tahora), and cocksfoot was also combined with lotus (Grasslands Maku) (Table 8.2). Details of the experimental treatments and design have been described in Chapter 7, methodology (Section 7.3.2).

Table 8.1 Pasture species and cultivars used in the Experiment.

Pasture species	Seed rate (kg/ha)
1. White clover (*Trifolium repens* L.) cv. Grasslands Tahora	3.0
2. Lotus (*Lotus uliginosus*) cv. Grasslands Maku	5.0
3. Cocksfoot (*Dactylis glomerata* L.) cv. Grasslands Wana	6.0
4. Yorkshire fog (*Holcus lanatus* L.) cv. Massey Basyn	2.0
5. Perennial ryegrass (*Lolium perenne* L.) cv. Grasslands Nui	12.0

8.3.3 Tissue turnover

Leaf elongation and senescence were measured three times in both experiments; November/December (1997), and March (1998) using the techniques of Birchman and Hodgson (1983) for grasses, and with the modification of Williams *et al.* (1964) for white clover. At the beginning of each cycle, one 2-m long transect per plot was randomly placed on the plot after leaving one metre from each end. Four individual rooted grass tillers and four white clover stolons were selected at random at 20-cm intervals in each transect, but in alternate fashion of grass and white clover. The selected tillers and stolons were identified by tagging with short lengths of coloured split plastic tubing (2-5 mm diameter and 3-5 mm long) on day one (Hernandez-Garay *et al.* 1997a). The marked tillers and stolons were not changed until the measurements were completed.

Tissue turnover estimates were fitted within the re-growth period of pasture species since the measurements were started after a week of mowing. Since the total measurement period did not exceed 23 days, the turnover estimates period was well within the active re-growth of pasture species after mowing, and covered the period from one mowing to the next. Mowing was conducted only once per month.

Data on tiller density and density of white clover growing points from Chapter 7 were used in the tissue turnover study to calculate weight change per unit of ground area ($g/m^2/day$). This was done to avoid repetition of measurements since counting tillers and white clover growing points was a continuous part of the experiments, as described in Chapter 7.

8.3.3.1 Tissue turnover in grasses

For all grass tillers, the length of the lamina was recorded to a precision of 1 mm for each leaf of each tiller on three occasions over 19 days (days 1, 9 and 18) in spring measurements, and over 23 days (days 1, 13 and 22) in autumn measurements. The leaf lengths were measured as the distance from the point of insertion (ligule) to the tip of the leaf or, in senescent leaves, to the base of the chlorotic tissue. The lengths of all laminae, and the length of the pseudostem of vegetative tillers were measured. There were no reproductive tillers during both measurements. Leaf elongation of young leaves (mm/tiller/day) was calculated from the length data. Senescence was also determined similarly for mature leaves, and net elongation was calculated as elongation minus senescence. At the end of the measurement period 10 tillers per replicate were randomly harvested and the relationship between leaf length (mm) and leaf weight (mg) was determined. Estimates of leaf weight per unit length were then used (Hernandez-Garay *et al.* 1997) together with the tiller population data (tillers/m^2), recorded each month by counting them in two random 10×10 cm quadrats in each plot, to calculate net leaf expansion per tiller (mm/tiller/day) and weight change per tiller (mg/tiller/day), as well as weight change per unit of ground area (g/m^2/day). Tiller population data used were as described in Table 7.9a: 24 November 1997, and Table 7.9b: 20 March,1998. Note that tiller population data in these tables are mean values of all replications, but while calculating weight change per unit of ground area (g/m^2/day), tiller population of the respective plot was used for more accuracy.

Net accumulation was calculated as:

Gross tissue growth (G) = Δ in leaf weight

Senescence (S) = loss in leaf weight

Net accumulation (NA) = (G-S) +Δ in pseudostem weight

8.3.3.2 Tissue turnover in white clover

Petiole elongation and leaf expansion were estimated from measurements from four stolons per plot on the same three occasions as the grasses. Elongation measurements of white clover petiole were made from the stipule to the tip or the lower edge of the senescent region (Hernandez-Garay *et al.* 1997a). Stolon length was measured up to the tip of the growing point. Likewise, leaf lamina expansion was determined according to visual assessment of leaf area in cm^2 using standard scores (Williams *et al.* 1964). To estimate the relationship between leaf area expansion, stem length and petiole length to their mass, 10 stolons were randomly collected at the end of the measurements and separated into leaf, stolon and petiole. Leaf area, stolon and petiole lengths were measured. The components were separately oven dried for 24 hours at 70^0C, and dry weight was taken to calculate net (net stolon + net petiole + net leaf) expansion per growing point (mm/growing point per day for stolon and petiole, and cm^2/growing point/day for leaf area) and weight change per growing point (mg/growing point/day), and per unit area (g/m^2/day). Density of white clover growing points data was used as described in Table 7.10a: 24 November 1997, and Table 7.10b: 20 March,1998 to calculate weight change per unit area. Note that density of white clover growing points data in these tables are mean values of all replications, but while calculating weight change per unit of ground area (g/m^2/day), density of white clover growing points of the respective plot was used for more accuracy.

8.3.4 Statistical analysis

The statistical significance for all the analyses was determined by analysis of variance using PROC GLM procedure (SAS 1997). Residuals were examined for their normality. No transformation of data was necessary. The significance level was set at α=0.05.

8.4 Results

8.4.1 Light environment

Measurements of PAR on 22 November 1997 showed that the mean µmoles photons m^{-2} s^{-1} under heavy, medium, and light shade were 420, 774, 1791 respectively. PAR measured in the open area was 1998 µmoles photons m^{-2} s^{-1}. On the 9th March 1997, PAR levels under heavy, medium and light shade were 208, 405, and 1352 µmoles photons m^{-2} s^{-1}, respectively, compared with 1589 µmoles photons m^{-2} s^{-1} in the open (Chapter 7, Table 7.3b). Similarly, the R:FR ratio on 22 November 1997 was 0.7, 0.9 and 1.5 under heavy, medium and light shade, respectively. R:FR ratio in the open was also 1.5 (Chapter 7, Table 7.3c).

8.4.2 Tissue turnover

8.4.2.1 Spring measurements

8.4.2.1.1 Net leaf expansion and net leaf production of grasses

The effect of shade on the rates of net leaf expansion per tiller during late spring/early summer (November-December) was not significant whereas shade had a significant effect ($P<0.01$) on net leaf production ($g/m^2/day$) (Table 8.2). However, species differences were significant ($P<0.0001$) for per tiller expansion (mg/tiller/day) as well as for net leaf production ($g/m^2/day$) during the same period (Table 8.2).

Cocksfoot either with white clover or lotus had the highest leaf expansion per tiller compared with perennial ryegrass and Yorkshire fog with white clover during 28 November to 16 December, 1997. Accordingly, relative to the leaf expansion rate of cocksfoot, Yorkshire fog was about 80% and perennial ryegrass 70%. This trend was repeated during 28 November to 16 December as well, where Yorkshire fog had about 76% of the leaf expansion of cocksfoot and perennial ryegrass about 70% (Table 8.2).

Leaf production (g/m^2/day) was highest under the light shade followed by medium and heavy shade in both periods of measurements during November/December. Cocksfoot, either with white clover or lotus, and also the Yorkshire fog with white clover had the highest production under light shade during 28 November- 16 December. Perennial ryegrass had only 55% of the leaf production of cocksfoot with white clover under the light shade. A similar trend was repeated under the medium shade where perennial ryegrass had about 73% of the leaf production of cocksfoot and Yorkshire fog (Table 8.2).

From November 28 to December 16 production of perennial ryegrass was down to about 50% relative to the leaf production of cocksfoot in the cocksfoot/white clover mixture under the medium shade. Under the heavy shade, leaf production was higher for cocksfoot than for Yorkshire fog or perennial ryegrass, with both perennial ryegrass and Yorkshire fog producing about 62% of that of cocksfoot (Table 8.2).

Table 8.2 Rates of net leaf expansion per tiller (mg/tiller/day) and net leaf production ($g/m^2/day$) of the grass components of ryegrass-white clover (RW), Yorkshire fog-white clover (YW), cocksfoot-white clover (CW) and cocksfoot-lotus (CL) swards under different levels of shade at Aokautere, 1997.

Net leaf expansion/ production	Treatments [1]												Significance		
	Heavy shade				Medium shade				Light shade				shade	species	interactions [2]
	RW	YW	CW	CL	RW	YW	CW	CL	RW	YW	CW	CL			
Nov. 28-Dec.6, 97															
Per tiller (mg)	1.02	1.18	1.29	1.52	1.16	1.54	1.66	1.47	1.13	1.42	1.80	1.50	NS	P<0.01	NS
SEM													0.08	0.07	0.12
Per m^2 (g)	1.88	2.38	2.96	3.39	2.19	4.63	4.62	3.40	3.03	5.52	5.59	4.50	P<0.01	P<0.0001	P<0.10
SEM													0.29	0.25	0.43
Nov.28-Dec.16,97															
Per tiller (mg)	0.99	0.87	1.23	1.24	1.05	1.20	1.59	1.31	0.95	1.14	1.68	1.52	NS	P<0.0001	NS
SEM													0.07	0.07	0.12
Per m^2 (g)	1.73	1.73	2.81	2.79	2.13	3.60	4.41	2.99	2.52	4.40	5.29	4.46	P<0.01	P<0.0001	P<0.10
SEM													0.27	0.20	0.35

NS no significant differences at P=0.05

[1] RW = Ryegrass + white clover; YW = Yorkshire fog + white clover; CW = cocksfoot + white clover, and CL = cocksfoot + lotus
[2] Interactions tests for treatment responses with differences in shade, SEM = standard error of the means

8.4.2.1.2 Net production of grasses

There was a significant effect of shade ($P<0.10$) for November 28 to December 6 and for November 28 to December 16 ($P<0.05$) on the net production (leaves plus stems) per tiller. Species differences ($P<0.001$) were also observed between the treatments in both periods. An interactive effect of shade and species for net production per tiller was also observed (Table 8.3). Effects of shade were also significant for the net production per unit area ($g/m^2/day$) for both periods and differences in the species were also significant ($P<0.01$).

There was a similar performance of species in terms of net production per tiller (mg/tiller/day) under different shade levels in both periods, but the effect of shade was more obvious during November 28 to December 16, 1997. Accordingly, the highest net production was under light shade by cocksfoot in the cocksfoot/white clover mixture followed by cocksfoot in the cocksfoot/lotus mixture. Net production per tiller of perennial ryegrass was lower than cocksfoot under light shade, but was similar under medium and heavy shade. Perennial ryegrass net production per tiller under heavy shade was about 78% of that of cocksfoot under heavy shade compared with only about 66% in the case of Yorkshire fog (Table 8.3).

In terms of net production per unit area ($g/m^2/day$), the species were similar under shade for both periods. Cocksfoot and Yorkshire fog had higher production per unit area compared with perennial ryegrass, except for Yorkshire fog under heavy shade (Table 8.3). Under heavy shade, production of Yorkshire fog was lower than perennial ryegrass during 28 November-16 December, and was only about 66% of that of cocksfoot in the mixture with white clover or lotus under heavy shade. Cocksfoot always had the highest net production per unit area ($g/m^2/day$) even under the heavy shade (Table 8.3). Net production per m^2 of cocksfoot mixed with white clover, was higher than for cocksfoot with lotus under all shade levels, except under heavy shade during 28 November to 6 December, 1997 (Table 8.3).

Table 8.3 Rates of net production (stem+leaf) per tiller (mg/tiller/day) and per m^2 ($g/m^2/day$) of the grass components of ryegrass-white clover (RW), Yorkshire fog-white clover (YW), cocksfoot-white clover (CW), and cocksfoot-lotus (CL) swards under different levels of shade at Aokautere, 1997.

Net production	Treatments[1]												Significance		
	Heavy shade				Medium shade				Light shade				shade	species	inter-actions[2]
	RW	YW	CW	CL	RW	YW	CW	CL	RW	YW	CW	CL			
Nov. 28-Dec.6, 97															
Per tiller (mg)	1.19	1.30	1.55	1.82	1.34	1.80	1.97	1.68	1.41	1.69	2.17	1.79	P<0.10	P<0.01	NS
SEM													0.10	0.08	0.15
Per m^2 (g)	2.20	2.63	3.56	4.09	2.52	5.41	5.46	4.11	3.83	6.56	6.76	5.34	P<0.01	P<0.0001	P<0.10
SEM													0.32	0.31	0.54
Nov. 28-Dec.16,97															
Per tiller (mg)	1.19	0.99	1.51	1.51	1.35	1.38	1.94	1.74	1.28	1.57	2.15	1.92	P<0.05	P<0.0001	NS
SEM													0.09	0.07	0.13
Per m^2 (g)	2.10	1.96	3.46	3.38	2.55	4.54	5.36	3.97	3.41	6.11	6.77	5.70	P<0.01	P<0.0001	P<0.10
SEM													0.31	0.25	0.44

NS no significant differences at P=0.05

[1] RW = Ryegrass + white clover; YW = Yorkshire fog + white clover; CW = cocksfoot + white clover, and CL = cocksfoot + lotus

[2] Interactions tests for treatment responses with differences in shade, SEM = standard error of the means

8.4.2.1.3 Net dry weight per growing point, and net dry weight per m^2 of white clover

Shade had no effect on the rate of net dry weight accumulation per growing point (mg/growing point/day) of white clover during 28 November-6 December. Also, there was no difference in the rate of net accumulation of white clover in mixture with the three grasses, and there was no interaction between shade and species (Table 8.4). However, shade had a significant effect ($P<0.05$) on the net dry weight per growing point of white clover during 28 November-16 December. There were also differences between white clover in the mixtures ($P<0.05$) and a weak ($P<0.10$) interactive effect of shade and species (Table 8.4).

In terms of rate of net dry weight accumulation per growing point during 28 November-16 December, white clover mixed with perennial ryegrass had the highest production followed by white clover with Yorkshire fog. White clover with cocksfoot had the lowest production, and was 75% of that of white clover in the mixture with perennial ryegrass (Table 8.4). Net dry weight per growing point of white clover was highest under light shade and lowest under heavy shade. Under heavy shade net dry weight per growing point of white clover was about 70% of that of light shade, but not significantly different (Table 8.4).

In terms of net dry weight production per unit area ($g/m^2/day$), there was a similar performance of white clover in mixture with grass species for both periods, with highest production of white clover with perennial ryegrass, followed by with Yorkshire fog and then with cocksfoot (Table 8.4). White clover production per unit area with cocksfoot was only about 60% of that of white clover with perennial ryegrass. Similarly, in both periods, highest production per unit area ($g/m^2/day$) was under light shade, while under heavy shade production was only 50% of that under light shade (Table 8.4).

Table 8.4 Rates of net dry weight accumulation (net stolon+net petiole+net leaf) per growing point (mg/growing point/day), and per unit area (g/ m^2/day) of the white clover component of ryegrass-white clover (RW), Yorkshire fog-white clover (YW), and cocksfoot-white clover (CW) swards under different levels of shade at Aokautere, 1997.

Net production	Treatments [1]									Significance		
	Heavy shade			Medium shade			Light shade			shade	species	interactions [2]
	RW	YW	CW	RW	YW	CW	RW	YW	CW			
Nov. 28-Dec.6, 97												
Per growing point (mg)	1.99	1.65	1.62	2.11	1.80	1.56	2.07	2.30	1.96	NS	NS	NS
SEM										0.16	0.20	0.36
Per m^2 (g)	0.69	0.43	0.45	1.21	0.74	0.52	1.17	0.98	0.83	P<0.10	P<0.10	NS
SEM										0.12	0.12	0.20
Nov. 28-Dec.16,97												
Per growing point (mg)	1.93	1.31	1.08	2.63	1.99	1.70	1.99	2.44	2.11	P<0.05	P<0.05	P<0.10
SEM										0.18	0.13	0.23
Per m^2 (g)	0.67	0.33	0.27	1.41	0.70	0.57	1.13	1.04	0.90	P<0.05	P<0.01	NS
SEM										0.11	0.09	0.15

NS no significant differences at *P*=0.05

[1] RW = Ryegrass + white clover; YW = Yorkshire fog + white clover; CW = cocksfoot + white clover, and CL = cocksfoot + lotus
[2] Interactions tests for treatment responses with differences in shade, SEM = standard error of the means

8.4.2.2 Autumn measurements

8.4.2.2.1 Net leaf expansion and net leaf production of grasses

There was no effect of shade on net leaf expansion per tiller (mg/tiller/day) or net leaf production per unit area (g/m^2/day) during early autumn (March 1998), while species differences were significant for all the periods of measurement ($P<0.01$). There was no interactive effect of shade and species (Table 8.5).

Net leaf expansion per tiller (mg/tiller/day) of the grasses was higher for early (1-13), than mid March (13-22). Cocksfoot always had a higher leaf expansion rate than Yorkshire fog and perennial ryegrass. In terms of leaf expansion, Yorkshire fog was most affected followed by perennial ryegrass. Yorkshire fog had only about 31% of the net leaf expansion of that of cocksfoot during March 13-22, compared with 52% by perennial ryegrass (Table 8.5).

Similarly to net leaf expansion, net leaf production per unit area (g/m^2/day) was higher during early (1-13) than mid-March (13-22). Leaf production per unit area was highest for cocksfoot compared with the other grasses, while cocksfoot from the cocksfoot/lotus mixture had the highest production in each period. During early March (1-13), perennial ryegrass leaf production per unit area was lowest with Yorkshire fog intermediate, but leaf production of Yorkshire fog decreased and was the lowest in mid-March. Overall March (1-22), leaf production of Yorkshire fog was about 20% of that of cocksfoot in the cocksfoot/lotus mixture, and 25% of that of perennial ryegrass (Table 8.5).

Table 8.5 Rates of net leaf expansion per tiller (mg/tiller/day) and net leaf production (g/m²/day) of the grass components of ryegrass-white clover (RW), Yorkshire fog-white clover (YW), cocksfoot-white clover (CW), and cocksfoot-lotus (CL) swards under different levels of shade at Aokautere, 1998.

Net leaf expansion / production	Treatments [1]												Significance		
	Heavy shade				Medium shade				Light shade				shade	species	interactions [2]
	RW	YW	CW	CL	RW	YW	CW	CL	RW	YW	CW	CL			
March 1-13, 98															
Per tiller (mg)	0.52	0.40	0.80	1.37	0.49	0.34	0.96	1.36	0.31	0.22	1.28	1.32	NS	P<0.0001	NS
SEM													0.07	0.10	0.18
Per m^2 (g)	0.85	1.22	2.58	4.21	1.08	1.14	3.24	4.84	0.88	0.88	4.45	4.61	NS	P<0.0001	NS
SEM													0.30	0.34	0.59
March 13-22, 98															
Per tiller (mg)	0.31	0.27	0.46	0.66	0.21	0.10	0.59	0.64	0.36	0.14	0.47	0.74	NS	P<0.0001	NS
SEM													0.07	0.06	0.11
Per m^2 (g)	0.53	0.82	1.48	2.02	0.43	0.30	2.07	2.30	1.03	0.54	1.62	2.61	NS	P<0.0001	NS
SEM													0.24	0.21	0.37
March 1-22, 98															
Per tiller (mg)	0.45	0.25	0.68	1.06	0.38	0.18	0.63	1.09	0.35	0.16	0.92	1.09	NS	P<0.0001	NS
SEM													0.06	0.08	0.14
Per m^2 (g)	0.75	0.79	2.18	3.26	0.82	0.61	2.15	3.88	1.03	0.60	3.14	3.80	NS	P<0.0001	NS
SEM													0.24	0.25	0.44

NS no significant differences at P=0.05

[1] RW = Ryegrass + white clover; YW = Yorkshire fog + white clover; CW = cocksfoot + white clover, and CL = cocksfoot + lotus,
[2] Interactions tests for treatment responses with differences in shade, SEM = standard error of the means

8.4.2.2.2 Net production of grasses

Net production per tiller (mg/tiller/day) and per unit area ($g/m^2/day$) of the grass components of the swards was unaffected by shade in March (Table 8.6). However, the net production of the grass species was significantly different ($P<0.001$, Table 8.6). There was no interaction between shade and grass species.

Highest net production per tiller was by cocksfoot in the cocksfoot/lotus mixture followed by cocksfoot in the cocksfoot/white clover mixture, while Yorkshire fog produced the least. For example, net production per tiller under light shade during March (1-22) for Yorkshire fog was about 20% of that of cocksfoot mixed with lotus, followed by perennial ryegrass which produced 37% of that of cocksfoot mixed with cocksfoot (Table 8.6).

Similarly, the highest net production per unit area was also by cocksfoot in the cocksfoot/lotus mixture followed by cocksfoot in the cocksfoot/white clover mixture (Table 8.6). Net production per unit area of perennial ryegrass and Yorkshire fog was usually about 20% of that of cocksfoot, while production of perennial ryegrass was slightly higher than Yorkshire fog, especially during 1-22 March (Table 8.6).

Table 8.6 Rates of net production (stem+leaf) per tiller (mg/tiller/day) and per m^2 ($g/m^2/day$) of the grass components of ryegrass-white clover (RW), Yorkshire fog-white clover (YW), cocksfoot-white clover (CW), and cocksfoot-lotus (CL) swards under different levels of shade at Aokautere, 1998.

Net production	Treatments [1]												Significance		
	Heavy shade				Medium shade				Light shade				shade	species	interactions [2]
	RW	YW	CW	CL	RW	YW	CW	CL	RW	YW	CW	CL			
March 1-13, 98															
Per tiller (mg)	0.61	0.45	0.92	1.64	0.57	0.35	1.23	1.56	0.4	0.27	1.46	1.71	NS	P<0.0001	NS
SEM													0.09	0.12	0.20
Per m^2 (g)	0.97	1.37	2.96	5.02	1.24	1.18	4.14	5.53	1.15	1.10	5.05	5.95	NS	P<0.0001	NS
SEM													0.36	0.39	0.67
March 13-22, 98															
Per tiller (mg)	0.43	0.38	0.64	0.81	0.32	0.19	0.86	1.03	0.49	0.24	0.90	1.05	NS	P<0.0001	NS
SEM													0.11	0.07	0.13
Per m^2 (g)	0.72	1.17	2.06	2.49	0.66	0.62	2.89	3.70	1.39	0.93	3.18	3.68	NS	P<0.0001	NS
SEM													0.40	0.27	0.47
March 1-22, 98															
Per tiller (mg)	0.56	0.31	0.82	1.27	0.47	0.23	0.89	1.37	0.47	0.24	1.21	1.43	NS	P<0.0001	NS
SEM													0.08	0.09	0.16
Per m^2 (g)	0.90	0.99	2.64	3.88	1.02	0.77	3.02	4.88	1.35	0.94	4.15	4.97	NS	P<0.0001	NS
SEM													0.33	0.30	0.51

NS no significant differences at P=0.05

[1] RW = Ryegrass + white clover; YW = Yorkshire fog + white clover; CW = cocksfoot + white clover, and CL = cocksfoot + lotus
[2] Interactions tests for treatment responses with differences in shade, SEM = standard error of the means

8.4.2.2.3 Net dry weight per growing point and net dry weight/m^2 of white clover

There was a marginally significant effect of shade on net dry weight per growing point (mg/growing point/day) of white clover for early March (1-13, P<0.1), and also during March (1-22, P<0.1), but not for mid-March (13-22). On the other hand, white clover was significantly different in the three grass species for those two periods (P<0.05), but not for March 13-22 (Table 8.7). Net dry weight accumulation per unit area was affected by shade only during March 1-13 (P<0.1). Species differences were significant (P<0.001) for all the periods. There was no interactive effect of shade and species for all the periods for net dry weight in terms of per growing point or per unit area of land (Table 8.7).

For the net dry weight per growing point all the periods had similar results, with white clover with perennial ryegrass always highest followed by white clover with Yorkshire fog. White clover with cocksfoot had the lowest dry weight per growing point. For all periods, white clover under light shade had the highest dry weight per growing point followed by medium shade and then heavy shade which produced about 65% of the white clover per growing point that was produced under light shade. However, this effect of shade on white clover growth per growing point during March was only marginally significant (P<0.10) except during 13-22 March where shade had no effect (Table 8.7).

Similarly, white clover dry weight per unit area (g/m^2/day), for all the periods, was highest for white clover with perennial ryegrass followed by with Yorkshire fog and with cocksfoot. White clover with cocksfoot had only about 45-50% of the dry weight per unit area of that of white clover with perennial ryegrass (Table 8.7). White clover production was always highest under light shade in all the periods, followed by under medium shade and then under heavy shade. Production under heavy shade was about 66% of that under light shade (Table 8.7). This was, however, statistically not significant except for a marginal effect of shade (P<0.10) during early March (1-13).

Table 8.7 Rates of net dry weight accumulation (net stolon+net petiole+net leaf) per growing point (mg/growing point/day), and per m^2 area (g/ m^2/day) of the white clover component of ryegrass-white clover (RW), Yorkshire fog-white clover (YW), and cocksfoot-white clover (CW) swards under different levels of shade at Aokautere, 1998.

Net production	Treatments [1]									Significance		
	Heavy shade			Medium shade			Light shade			shade	species	interactions [2]
	RW	YW	CW	RW	YW	CW	RW	YW	CW			
March 1-13, 98												
Per growing point (mg)	1.27	1.08	0.80	1.44	1.06	0.80	1.63	1.67	1.21	P<0.10	P<0.05	NS
SEM										0.03	0.02	0.22
Per m^2 (g)	1.03	0.67	0.37	1.01	0.85	0.39	1.31	1.28	0.63	P<0.10	P<0.0001	NS
SEM										0.10	0.07	0.13
March 13-22, 98												
Per growing point (mg)	1.27	1.06	0.80	1.38	1.21	1.05	1.36	1.31	1.65	NS	NS	NS
SEM										0.13	0.11	0.19
Per m^2 (g)	1.03	0.71	0.36	1.00	0.95	0.45	1.16	1.02	0.96	NS	P<0.001	NS
SEM										0.15	0.07	0.12
March 1-22, 98												
Per growing point (mg)	1.25	1.04	0.79	1.45	1.05	0.80	1.51	1.51	1.32	P<0.10	P<0.01	NS
SEM										0.10	0.09	0.15
Per m^2 (g)	1.02	0.67	0.36	1.03	0.83	0.37	1.24	1.16	0.72	NS	P<0.001	NS
SEM										0.11	0.05	0.08

NS no significant differences at *P*=0.05

[1] RW = Ryegrass + white clover; YW = Yorkshire fog + white clover; CW = cocksfoot + white clover, and CL = cocksfoot + lotus
[2] Interactions tests for treatment responses with differences in shade, SEM = standard error of the means

8.5 Discussion

8.5.1 Effect of shade on tissue turnover

Species differences were more apparent than level of shade effects on tissue net herbage accumulation in this study (Tables 8.2-8.7). Effect of shade on the net leaf expansion per tiller was not significant for both seasons, and hence significant differences in the rates of net production per tiller and also per unit area during late spring/early summer must be associated with the number of tillers.

Previous research also supported the finding that tiller population density (numbers/m^2) was significantly different ($P<0.01$) across the shade levels during November and December, 1997 (early spring), and in March 1998 (late autumn/early summer). Tillers per unit area under heavy shade were significantly lower than under medium and light shade in both seasons (Chapter 7: section 7.4.1.6, Tables 7.9 a, b). Similarly, SLA was found to be positively correlated with higher dry weight per plant of pasture species under heavy shade (Chapters 3-6). The high SLA of cocksfoot in heavy shade resulted in a higher leaf area per unit area available for photosynthesis and therefore greater likelihood of tiller formation. Perennial ryegrass always had a smaller SLA than cocksfoot, and under heavy shade its tiller numbers and shoot dry weight per plant decreased relatively more than for cocksfoot (Chapters 3-6). Increased herbage accumulation rate has been associated with a greater tiller population (Hernandez- Gary *et al.* 1993) and higher growth per tiller (Xia *et al.* 1990), while tillering ability of plants is particularly dependent on carbohydrate supply (Cooper and Tainton 1968).

Tissue flow of white clover was seasonal and was more affected by shade during autumn than late spring (Tables 8.4, 8.7). On the other hand, the consistent significant differences in net dry weight accumulation per growing point as well as per unit area for white clover mixed with grass species during both late spring/early summer as well as early autumn (Tables 8.4, 8.7), indicated that white clover was more affected by the shade or some other form of competition by the companion grass than by tree shade. For example, under heavy shade white clover production per unit area with cocksfoot was only about 60% of that of white clover with perennial ryegrass.

Grazing management practices affect tillering, tissue flows and thereby the production of the swards (Birchman and Hodgson 1983; Hemandez-Garay *et al.* 1997a, b). Similarly, changes in the light spectra reaching the understorey sward are a critical aspect of tree canopy management that affects the tissue flows in the swards in silvo-pastoral system. Shelton *et al.* (1987) reported that shading is one of the major factors that determines the productive performance of understorey pastures. Decreased irradiance reduces the growth of pasture species and can affect morphological attributes of pasture species that may impact on productive performance (Kephart and Buxton 1993).

8.5.2 Tissue turnover and production of grasses under tree shade

The tissue turnover of the three grass species differed, and was also affected by season. Rates of net leaf expansion and net production per tiller for all the grass species were reduced more during autumn than in the late spring/early summer. Perennial ryegrass and Yorkshire fog were the most affected in terms of net leaf expansion per tiller as well as production per unit area during early autumn and late spring/early summer. Net leaf expansion per tiller and net production per unit area of Yorkshire fog were especially affected during early autumn (Tables 8.5 and 8.6). During autumn, net leaf expansion per tiller and net production per unit area for perennial ryegrass were also decreased, especially under light shade. However, this effect later disappeared during the period of 1-22 March for perennial ryegrass, but not for Yorkshire fog (Tables 8.5 and 8.6).

An increase in both tiller population density and leaf growth per tiller enhance pasture production of perennial ryegrass-white clover pasture under spring grazing management and conventional farm practice in New Zealand (Hernández-Garay *et al.* 1997a). In general, under a conventional management system, growth rate of herbage is greater on relatively tall than short swards of perennial ryegrass, while senescence rates are similar (Hepp *et al.* 1996). In Experiment 7.1 (Chapter 7), total above ground herbage accumulation per unit area during the establishment period was similar for perennial ryegrass, cocksfoot, and Yorkshire fog when soil moisture content was not limited, and soil nutrient content was reasonable (Chapter 7: section 7.4.1.4, Table 7.6).

The prolonged period of low soil moisture (February-April) decreased the tissue turnover of Yorkshire fog and perennial ryegrass more than that cocksfoot. Low soil moisture resulted in Yorkshire fog and perennial ryegrass having an increased rate of leaf senescence. The rates of net leaf expansion and production of these species were not affected during late spring/early summer due to the higher soil moisture during that period. Lower rates of net leaf expansion per tiller and production per unit area for perennial ryegrass could also have resulted due to the low level of soil fertility. Olsen P of the experiment plots was 11.4 μg/g with a pH of 5.5 (Chapter 7: section 7.3.1, Table 7.1). Bradshaw *et al.* (1960) reported that perennial ryegrass is adapted to fertile habitats and it shows a marked growth response to increasing phosphate levels. Therefore, the low production of perennial ryegrass could have been due to the combined effects of shade, low fertility, and moisture stress.

Net flows of tissues of cocksfoot were consistently higher than for the other species throughout the experiment and it was comparatively less affected by the period of low soil moisture. Cocksfoot is known to be adapted to moderate soil fertility and short periods of drought (Moloney 1993; Woodman and Fraser 1991; MacFarlane 1990; Rumball 1982).

8.5.3 Tissue turnover and production of white clover under tree shade

The rate of net dry weight accumulation of white clover per growing point, as well as per unit area, was significantly different for the grass species and white clover mixtures for both periods of the experiment (Tables 8.4, 8.7). Net dry weight accumulation per growing point, and per unit area, was always higher for white clover with perennial ryegrass, and with Yorkshire fog in mixture than it was for white clover in a mixture with cocksfoot (Tables 8.4, 8.7,8.7).

One of the reasons for the net dry weight accumulation per growing point and per unit area of white clover being highest with perennial ryegrass and lowest with cocksfoot could be the competitive effects of the companion grass on white clover. Perennial ryegrass had a lower tissue flow and lower tiller density than cocksfoot. Consequently, there was less shading of the companion white clover by perennial ryegrass, or

Yorkshire fog, compared with cocksfoot. Accumulation of herbage reduces the amount of light reaching the bottom layer of the sward (Thomas and Davies 1978; Orr *et al.* 1988) which will affect white clover growth. Similarly, Moloney (1993) suggested cocksfoot suppressed white clover growth. Dear *et al.* (1998) showed that the growth of subterranean clover was mainly decreased by the companion perennial grass reducing light, along with competition for water and nutrients.

8.6 Conclusions

Shade did not affect rates of net leaf expansion per tiller of three perennial grass species. However, shade decreased the net leaf production per tiller and per unit area which indicated the effect of shade on herbage accumulation was a decrease in tiller numbers. Rates of net leaf expansion per tiller and net production per unit area were lower during autumn than in the late spring/early summer for all the species. Perennial ryegrass net leaf expansion per tiller and production per unit area decreased more than the other grass species from late spring/early summer to autumn. Yorkshire fog and perennial ryegrass tissue dynamics were probably affected more negatively by low soil moisture over summer and autumn than was cocksfoot. Net accumulation of white clover was always higher when with perennial ryegrass in a mixture, intermediate with Yorkshire fog, and lowest with cocksfoot. This was probably due to the higher level of competition by cocksfoot, than perennial ryegrass and Yorkshire fog, for light and moisture.

Cocksfoot's tissue turnover was probably higher due to its higher SLA and higher number of tillers per unit area than perennial ryegrass. Cocksfoot maintains a higher SLA than perennial ryegrass, and a greater number of tillers per plant that enables cocksfoot to produce more leaf area per unit area compared with perennial ryegrass.

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9. General discussion and conclusions

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9.1 Introduction

Large areas of New Zealand pastoral hill country are susceptible to soil erosion (Clough and Hicks 1993; Kelliher *et al.* 1995). The planting of selected trees has, therefore, become a common land-use practice to counter the negative impact of erosion and to diversify farm income (Pollock *et al.* 1994; Anonymous 1995; Miller *et al.* 1996). Understorey pasture productivity is affected principally by the tree shade, which in turn depends upon the degree of canopy closure and characteristics of the tree canopy. Despite important past experience in the use of trees for soil conservation (Miller *et al.* 1996), detailed information associated with the effects of deciduous trees on understorey pasture production is scanty (Wall *et al.* 1997). There is a need to understand the effect of a range of light intensities (particularly low levels of transmitted light) on morphological attributes of common pasture species. Also, there is a need to understand the management of shade levels in deciduous tree-pasture systems. A series of glasshouse and field experiments were conducted to determine the morphological attributes of pasture species that are associated with shade tolerance, and to determine appropriate grazing management practice. The responses of pasture species to a range of light intensities, to the quality of light, and to different defoliation frequencies were determined in Chapters Three to Six. Chapters Seven and Eight determined responses of selected pasture species under different levels of shade imposed by tree pruning. This Chapter focuses on a general discussion of the findings in previous Chapters and implications for the management of deciduous tree-pasture systems.

9.2 Evaluation of experimental procedures

9.2.1 PAR measurements

A range of PAR levels was created in the glasshouse and in the field experiments. The lowest levels of PAR were 14% (Chapter 3) to 17% of incident radiation (Experiment 4.2: section 4.4.2.1), while it was 24% in one experiment (Experiment 4.1: section

4.4.1.1), equivalent to the range 60-200 (μmoles photons m^{-2} s^{-1}). This variation was mainly due to seasonal fluctuations while conducting the experiments. For example, some experiments were conducted during winter (Chapters 3 and 5), while others were conducted during spring and summer (Experiments 4.1 and 4.2), and the field experiment (Experiment 7.1) ran all year round. Similarly, variation at the lowest level of transmitted PAR was also due to reductions in light quality (R:FR ratio) by the use of filters (Lee *et al.*1994) to simulate the natural tree canopy environment (section 5.4.1).

Obtaining actual PAR measurements is often difficult. In all the experiments, the % of transmitted PAR was measured using a single, but the same Licor quantum sensor. Still, there is a question about the accuracy of measurements (Smith 1982), especially when in the field under natural conditions. The variable geometry of plant parts clearly makes it impossible to specify a single photodetector arrangement (Smith 1994). Yet, PAR is very relevant to plant growth studies (Wilson and Ludlow 1991). In practice, it appears that a spectral error of ± 20% is not uncommon (McCree 1981).

All the experiments conducted in a glasshouse had about 20% transmitted PAR (130 μmoles photons m^{-2} s^{-1}) at the low PAR level (Table 9.1). Similarly, the field experiment under the alder trees that ran all year round also had an average of 12% of the transmitted PAR in the heavy shade, and the mean transmitted PAR was about 180 μmoles photons m^{-2} s^{-1}. Results from the glasshouse experiments at low PAR, therefore, ought to provide comparable information to the results under the heavy shade of the alders in the field experiment.

9.2.2 Field tests

Results showed differences between cocksfoot selections in terms of tiller numbers and cumulative shoot dry weight per plant at low PAR. Repeating of these studies under other deciduous trees such as poplars would be beneficial to draw clear conclusions on broad-leaved tree pasture management, but it was not possible here due to time, budget, and technical constraints.

9.2.3 Research needs

Frequent defoliation markedly affected shoot dry weight and tiller numbers per plant for perennial ryegrass, while cocksfoot was relatively less affected. This should be tested in field experiments under tree shade in terms of grazing management studies. R:FR ratio did not significantly affect the performance of plants. However, studies with further low levels of R:FR ratios would be beneficial to quantify the effects of light quality. Likewise, the feeding value of cocksfoot under tree shade should be determined. More research on the morphological and physiological adaptations of perennial pasture species, including *Poa trivialis* and browntop, under shade are necessary.

9.3 General discussion of results

Shade markedly decreased tillering as well as shoot dry weight for all grass species but mean tiller number per plant at low PAR was significantly higher for cocksfoot than for other species. Yorkshire fog was also tolerant of heavy shade in glasshouse conditions, but not under tree shade. Browntop and Poa trivialis were intolerant of heavy shade, but had higher shoot dry weight than cocksfoot and legumes in medium shade, especially when plants were not defoliated. Perennial ryegrass was more affected than the other pasture species under heavy shade, but was on par with cocksfoot under medium shade in terms of shoot dry weight. When defoliated at weekly or three weekly intervals, cocksfoot produced higher shoot dry weight per plant than perennial ryegrass, mainly due to the higher tiller numbers and leaf area per plant. Likewise, lotus produced a higher number of branches at low PAR than the number of stolons produced by white clover. The R:FR ratio had no effect on cumulative shoot dry weight per plant. Likewise, the diet selection of sheep under tree shade showed no difference in preference for alternative grasses but more sheep grazed in light than heavy shade.

Tiller number per plant, leaf area, specific leaf area (SLA), root dry weight per plant and leaf appearance intervals were identified in this thesis as the important morphological attributes related to shade tolerance of common pastoral plants used in New Zealand hill country. Tables 9.1-9.3 summarise the attributes of cocksfoot and perennial ryegrass as determined under heavy shade at the lowest PAR reported in this thesis. General discussions of the results obtained are presented in the following sections.

Table 9.1 Summary of properties of cocksfoot and perennial ryegrass as determined under heavy shade or at low PAR in a series of experiments.

Properties	Indication: Cocks-foot	Indication: Perennial ryegrass	Mean % PAR as determined by measuring daily light	Remarks
(a) Plant growth				
Cumulative shoot dry weight	↓	↓↓	14% (60 µmoles m^{-2} s^{-1})	Grown fully under shade
	↓	↓↓	24% (234 µmoles m^{-2} s^{-1})	Initially established under full sunlight
	↓	↓	16% (78 µmoles m^{-2} s^{-1})	Grown without defoliation
	↓	↓↓	24% (149 µmoles m^{-2} s^{-1})	Defoliated at one and three week intervals
	↓	↓↓	12% (183 µmoles m^{-2} s^{-1})	Under tree shade of alder, 2.5m pruning
Net leaf expansion	↓	↓↓	12% (183 µmoles m^{-2} s^{-1})	Under tree shade of alder, 2.5m pruning
(b) Tillering				
Tiller number/plant	↓	↓↓↓	14% (60 µmoles m^{-2} s^{-1})	Grown fully under shade
	↓	↓↓	24% (234 µmoles m^{-2} s^{-1})	Initially established under full sunlight
	↓↓	↓	16% (78 µmoles m^{-2} s^{-1})	Grown without defoliation
	=	↓↓↓	24% (149 µmoles m^{-2} s^{-1})	Defoliated at one and three week intervals
	↓	↓↓	12% (183 µmoles m^{-2} s^{-1})	Under tree shade of alder, 2.5m pruning
Tiller weight	=	=	16% (78 µmoles m^{-2} s^{-1})	Grown without defoliation
(c) Leaf area	↓↓↓	↓↓↓	14% (60 µmoles m^{-2} s^{-1})	Grown fully under shade
	↓	↓↓↓	24% (234 µmoles m^{-2} s^{-1})	Initially established under full sunlight
	↓	↓	16% (78 µmoles m^{-2} s^{-1})	Grown without defoliation
	↓	↓	24% (149 µmoles m^{-2} s^{-1})	Defoliated three weekly
	↓	↓↓↓	24% (149 µmoles m^{-2} s^{-1})	Defoliated weekly
(d) Leaf dry weight	↓	↓↓	24% (234 µmoles m^{-2} s^{-1})	Initially established under full sunlight
	↓	↓	16% (78 µmoles m^{-2} s^{-1})	Grown without defoliation
	↓↓	↓↓	24% (149 µmoles m^{-2} s^{-1})	Defoliated weekly and three weekly
(e) Specific leaf area (SLA)	=	↑	14% (60 µmoles m^{-2} s^{-1})	Grown fully under shade
	↑↑	↑	24% (234 µmoles m^{-2} s^{-1})	Initially established under full sunlight
	↑	↑	16% (78 µmoles m^{-2} s^{-1})	Grown without defoliation
	↑↑	↑	24% (149 µmoles m^{-2} s^{-1})	Defoliated in one and three week interval
(f) Root dry weight	↓↓	↓↓↓	24% (234 µmoles m^{-2} s^{-1})	Initially established under full sunlight
	↓↓	↓↓↓	16% (78 µmoles m^{-2} s^{-1})	Grown without defoliation
	↓↓	↓↓↓	24% (149 µmoles m^{-2} s^{-1})	Defoliated in one and three week interval
(g) Leaf appearance interval	=	↑↑	24% (149) µmoles m^{-2} s^{-1}	Defoliated weekly
	=	↑	24% (149 µmoles m^{-2} s^{-1})	Defoliated three weekly
(h) General				
Defoliation tolerance	✔✔	✔		
Sensitivity to light quantity	✔	✔✔		
Sensitivity to light quality	✔	✔✔		
Tolerance to heavy shade	✔✔	✔		
Compatibility with legume	✔	✔		

Key : =, maintained ~ to that of no shade; ↓, reduced up to 50%; ↓↓, up to 70%, and ↓↓↓, > 80%.; ↑, increased up to 50%, ↑↑, 50% and above to that of no shade. ✔, indicates relatively low, and ✔✔, indicates relatively high.

Table 9.2 Tolerance index of perennial ryegrass and cocksfoot as indicated by cumulative shoot dry weight/plant at different PAR levels.

% transmitted PAR levels	% tolerance index of cocksfoot for different PAR levels	% tolerance index of perennial ryegrass for different PAR levels	% tolerance index of cocksfoot to that of perennial ryegrass at each PAR level
(a) Screening pasture species in range of light intensities, grown fully under shade (Chapter 3)			
73	100	100	60
43	55	54	61
27	25	17	89
18	10	6	106
14	3	2	90
(b) Screening with selected PAR: Initially established under full sunlight (Chapter 4)			
73	100	100	81
32	62	46	109
24	49	26	158
(c) Grown without defoliation (Chapter 5)			
38, natural R:FR	100	100	68
39, reduced R:FR	96	95	69
16, natural R:FR	63	48	95
17, reduced R:FR	54	42	87
(d) Weekly defoliated (Chapter 6)			
71, natural R:FR	100	100	110
25, natural R:FR	26	13	217
24, reduced R:FR	27	11	260
(e) Field conditions, under alder trees (Chapter 7)			
Light shade	100	100	116
Medium shade	73	68	124
Heavy shade	53	44	138

Table 9.3 Tolerance index of perennial ryegrass and cocksfoot as indicated by tiller number/plant at different PAR levels.

% transmitted PAR levels	% tolerance index of cocksfoot for different PAR levels	% tolerance index of perennial ryegrass for different PAR levels	% tolerance index of cocksfoot to that of perennial ryegrass at each PAR level
(a) Screening pasture species in range of light intensities, grown fully under shade (Chapter 3)			
73	100	100	75
43	78	67	88
27	67	21	240
18	39	13	233
14	22	4	400
(b) Screening with selected PAR: Initially established under full sunlight (Chapter 4)			
73	100	100	90
32	85	73	105
24	78	5	124
(c) Grown without defoliation (Chapter 5)			
38, natural R:FR	100	100	80
39, reduced R:FR	95	103	74
16, natural R:FR	59	62	76
17, reduced R:FR	37	54	55
(d) Weekly defoliated (Chapter 6)			
71, natural R:FR	100	100	121
25, natural R:FR	73	18	500
24, reduced R:FR	56	15	460
(e) Field conditions, under alder trees (Chapter 7)			
Light shade	100	100	124
Medium shade	86	79	135
Heavy shade	75	58	159

9.3.1 Pasture species under range of shade

In all experiments, shade markedly affected the cumulative shoot dry weight per plant (Figure 3.2, Tables 4.3, 4.9, 5.2, 6.6, 7.6, 7.8) for all pasture species. The highest cumulative shoot dry weight was always produced at the highest level of PAR. However, pasture species responded differently over a range of shade. In terms of shoot dry weight per plant, some species ranked best at lowest PAR, while others ranked well at medium levels of PAR.

Cocksfoot was the best species for all shade levels including heavy shade (Chapters 3 to 7). Cumulative shoot dry weight of perennial ryegrass was similar to cocksfoot at 27% or 32% PAR (section 3.3.2), under enclosed shade cloth and even at 17% PAR when not defoliated (section 5.4.2), or in 25% PAR under tree shade (Experiment 7.1: section 7.4.1.4). However, when plants were defoliated at weekly intervals then cumulative shoot dry weight of perennial ryegrass was similar to the cocksfoot only at 70% PAR (Experiment 6.2: section 6.4.2.2).

Poa trivialis and browntop had the lowest shoot dry weight per plant of the grass species examined at low levels of PAR (section 3.3.2). However, they produced the highest number of tillers per plant (section 5.4.3), but not the highest shoot dry weight per plant (section 5.4.2) when plants were not defoliated (section 5.4). There is a possibility of successfully growing these species under medium or intermediate tree shade.

The cumulative shoot dry weight and tiller number per plant of Yorkshire fog under heavy shade were similar to cocksfoot in the glasshouse experiments (sections 3.3.2, 3.3.5, 5.4, 5.4.2, and 5.4.3), but in the field under heavy tree shade its performance was similar to that of perennial ryegrass (Experiment 7.1: sections 7.4.1.4, 7.4.1.5).

Lotus was less affected than white clover under heavy shade in terms of shoot dry weight production, and also number of branches per plant, or branches per m^2 area (sections 3.3.5; 5.4.3; experiment 7.1: sections 7.4.1.4, 7.4.1.7). White clover was more sensitive to changes in the intensity of light than lotus, as white clover could not produce any stolons at 14% PAR (section 3.3.5). It was also more affected by the companion grass species than lotus (Experiment 7.1: section 7.4.1.7).

Pasture species that maintained high shoot dry weight per plant, due to maintaining higher tiller numbers per plant or a high leaf area per plant, ranked best at either the lowest or the highest available PAR (Devkota *et al.* 1997).

There were distinct differences between the cocksfoot selections in terms of shoot dry weight and tiller number per plant. Wana (tetraploid) cocksfoot had higher shoot dry weight, leaf area, and tiller number per plant compared with the other selections of tetraploid cocksfoot (sections 3.3.2; Experiment 4.1: section 4.4.1.2; section 5.4.2, experiment 6.2: sections 6.4.2.2, 6.4.2.6; Experiment 7.1: sections 7.4.1.4, 7.4.1.6). However, the cumulative shoot dry weight per plant of PG 74 (diploid) cocksfoot was also similar or even better than Wana cocksfoot in the glasshouse (Experiment 4.1: sections 4.4.1.2, 4.4.1.3), but not under tree shade (Experiment 7.1: sections 4.4.2.2, 4.4.2.3). Wana also had higher SLA at low levels of PAR. This clearly suggests that even within the tetraploid selections of cocksfoot, some are better at low levels of PAR, and thus are tolerant of heavy shade.

Cocksfoot could have the morphogenetic capacity to increase its light capture to increase carbon for leaf growth, as in the case of *Dichanthium aristatum* (Cruz 1997). In a field experiment Brook *et al* (1996) found cocksfoot had 50% higher total dry weight, and 150% heavier stem components (basal + connective stem) than perennial ryegrass. In mixed species stands, the competitive ability of cocksfoot root was greater than perennial ryegrass (Remison and Snaydon 1980). Cocksfoot can provide reliable leafy summer growth (Rumball 1982; Moloney 1993), and is moderately tolerant of drought and low fertility (MacFarlane 1990; Woodman and Fraser 1991; Fraser 1994; Fraser and Hewson 1994; Lolicato and Rumball 1994). Cocksfoot can be grown as an understorey crop in New Zealand (Hocking 1990) and is regarded as one of the most shade tolerant grass species (Seo *et al.* 1989; Pollock *et al.* 1997).

Tetraploid cocksfoot is found in contrasting climates of Galicia, Spain, either in the area of highest rainfall, or summer drought (Lindner and Garcia 1997). This wide adaptability of tetraploid cocksfoot is thought to be related to the higher number of alleles (genetic buffering) and to higher heterozygosity (Lindner and Garcia 1997). Galician diploid cocksfoots were found in shady habitats and in perennial meadows, but with shorter, fewer and wider leaves (Lindner and Garcia 1997). Fewer as well as wider leaves on diploid cocksfoot (PG 74) were also observed in the glasshouse and field experiments. Perhaps for these reasons, PG 74 was also one of the most heavy shade tolerant cocksfoot selections (Experiment 4.1: section 4.4.1.2 and Experiment 4.2: section 4.4.2.2).

9.3.1.1 Light intensity versus quality under shade

Only PAR had a significant effect on the shoot dry weight per plant of the pasture species in this thesis. However, research results indicate that plants are able to detect change in light quality (reduced R:FR ratio) via the phytochrome family of photoreceptors and respond morphologically (Smith 1982; Smith 1994; Maliakal *et al.* 1999). The common morphological responses are reduced tillering, or branching (Deregibus *et al.* 1985; Solangaarachchi and Harper 1987; Casal *et al.* 1987; Assmann 1992; Hay *et al.* 1997). The effects of light quality on pastoral plants, therefore, could be photomorphogenic via regulation of photosynthate allocation (Kasperbauer and Hunt 1998), and could stimulate morphological changes such as increased plant height, and reduced tillering or branching, but may not affect the shoot dry weight production. However, the differences between individual species were more important than those in response to light levels for the performance of pasture species in the shade. That is, differences between species in attributes that affect the plant's performance in shade like tillering and SLA were largely due to inherent differences between species rather than due to a response to light quality (R:FR). This could also be an indication that morphological responses such as reduced tillering, branching or stem elongation are not potentiated only by a low R:FR (Assmann 1992), but also by other variables including light intensity, leaf temperature and humidity (Maliakal *et al.* 1999).

The significant effect of PAR on all the parameters studied (Chapter 5) showed that the ability of a plant species to tolerate low light has its root in photosynthesis (Corré 1983). The allocation of biomass to plant organs can be considered as a strategy used to improve survival (Lee *et al.* 1994), and hence light quantity might have its greatest effect on shoot dry weight. There is a threshold level of PAR for plant species to grow. Assmann (1992) found that *Commelina communis,* a shade tolerant plant, was able to flower and set seed with 13 hours daily of 25 ± 5 μmoles photons m^{-2} s^{-1}white light, which could be the threshold of light quantity for that species. The lowest level of PAR maintained in the experiments reported in this thesis was 60 μmoles photons m^{-2} s^{-1} (Chapter 3) and 78 μmoles photons m^{-2} s^{-1} (Chapter 5), which may be near to the threshold value to these pasture species. Since some species could not produce any tillers at 60 μmoles m^{-2} s^{-1}, it is postulated that this could be the heaviest shade under which these plants could be grown.

Light quantity, rather than quality, was the important factor determining photosynthetic capacity for white clover (Dennis and Woledge 1983). Light demanding plants have high rates of respiration, and there can be a great variation in the extent to which the respiration rate is reduced in heavy shade (Grubb *et al.* 1996). However, to determine the respiration rates of species under various levels of shading was not within the scope of this thesis.

The level of transmitted PAR affected the relative growth rate (RGR) of cocksfoot and perennial ryegrass, where the RGR of cocksfoot was less affected by reduced PAR compared with perennial ryegrass. However, the RGR of both species was not affected by a reduced R:FR. This further suggests that light quantity was more important than light quality (R:FR ratio) for plants grown under shade (experiment 6.1: sections 6.4.1.2 and 6.4.1.3). There was also no effect of reduced R:FR ratio on the shoot dry weight per plant of cocksfoot and perennial ryegrass under weekly and three-weekly defoliation in the glasshouse (Experiment 6.2: section 6.4.2.2).

In glasshouse experiments, the reduced R:FR ratio was maintained at 0.57 (section 5.4) and 0.68 (Experiment 6.1: section 6.4.1.1) which were similar to values of 0.4-0.6 found under dense tree canopies by Wilson (1997). In the field experiment (Experiment 7.1) the R:FR under heavy shade was 0.66 (Experiment 7.1: section 7.4.1.1), which was similar to levels measured by Smith (1982) for deciduous wood lots (ranging from 0.36-

0.97). This means that the reduction of R:FR along with the reduction in transmitted PAR in the glass house was in a manner similar to natural light filtering through an overstorey canopy (sections 5.4.2-5.4.6; Experiment 6.1: sections 6.4.1.2, 6.4.1.3; Experiment 6.2: sections 6.4.2.2-6.4.2.7). However, these results should be interpreted with caution and should not be extrapolated since R:FR can be down to 0.2 under deep shade in tropical forest (Lee *et al.* 1994).

Shade is an ever-present factor in crop production, be it in agriculture or agroforestry (Smith 1981). Shade tolerant species concentrate their efforts into leaf development in the shade, and appear to principally perceive the light quantity aspect of shade rather than light quality (Smith 1981).

9.3.1.2 Defoliation and plant growth under shade

Perennial ryegrass was more affected than cocksfoot by defoliation and shade, in terms of growth related attributes (Experiment 6.1: sections 6.4.2.2-6.4.2.9). When plants were established under full sunlight and not defoliated until final harvest (sections 5.3, 5.4), shoot dry weight and tiller number per plant of perennial ryegrass was higher than cocksfoot (Table 9.3). But weekly defoliation greatly reduced the tiller number per plant of perennial ryegrass relative to the cocksfoot (Table 9.3).

Increased frequency of defoliation or shorter re-growth periods results in a reduction in the rate of growth of new leaves, and in the leaf size of perennial ryegrass (Brock *et al.* 1996; Faurie *et al.* 1996; Thornton and Millard 1997). Defoliation also significantly reduces root dry weight (Experiment 6.1: section 6.4.2.7; Mawdsley and Bardgett 1997). For these reasons defoliated perennial ryegrass had poor shoot dry weight and tiller number per plant at low levels of PAR. In contrast, cocksfoot had relatively higher cumulative shoot dry weight and tiller number per plant under weekly defoliation at low PAR compared with perennial ryegrass (Experiment 6.1: sections 6.4.2.2, 6.4.2.6). This superiority of cocksfoot was mainly due to its higher leaf area (Table 6.8), higher leaf dry weight (Table 6.9), higher SLA (Figure 6.2) and higher tiller number per plant (Table 6.10).

Cocksfoot can tolerate more frequent defoliation in the shade than perennial ryegrass. If perennial ryegrass is managed to maintain optimum LAI under shade, then it will be able to intercept sufficient light and alter the allocation of assimilates to leaves for production and persistence (Caldwell 1987). Also, the re-growth potential of perennial ryegrass could be based more on the total amount of water-soluble carbohydrates in the stubble (Fulkerson and Slack 1995). In comparison, cocksfoot is less sensitive to LAI, and keeps on allocating a high proportion of its photosynthates to the leaves even under frequent defoliation. This is perhaps due to a higher level of soluble carbohydrates in the bases of expanding leaves, and a more efficient photosynthesis system (Davidson and Milthorpe 1966).

9.3.1.3 Morphological attributes in relation to shade tolerant pasture species

The morphological responses of plants to shade are a complex phenomenon (Thompson 1993). Some research has shown that morphological responses of plants are based only on light quality (Corré 1983), but most studies have focused on the effects of light quantity and quality in relation to the morphological adaptations of plants in shade (Monteith 1981; Kephart and Buxton 1993; Callan and Kennedy 1995; Wilson 1997; Sanderson *et al.* 1997). However, it is difficult to determine which morphological attribute(s) is the most important contributor to the productive performance of pasture species in shade.

Morphological responses of plants growing under shade include: increased leaf-area ratio, increased shoot-to-root ratio, increased specific leaf area, increased plant height, and reduction in vegetative shoots (Cooper and Tainton 1968; Park *et al.* 1988; Stür 1991; Kephart *et al.* 1992; Lambers and Poorter 1992; Grubb *et al.* 1996; Sanderson *et al.* 1997; Wilson 1997; Nassiri and Elgersma 1998; Wan and Sosebee 1998). Tillers per plant, specific leaf area and leaf area were also found to be associated with the more productive pasture species under heavy shade reported in this thesis (sections 4.4.1.6, 4.4.1.7).

Absolute or relative number of tillers or branches per plant were the most influential attributes affecting shoot dry weight at low PAR in all the experimental conditions presented in this thesis (section 3.3.5; Experiment 4.1: section 4.4.1.3; Experiment 4.2: section 4.4.2.3; section 5.4.3; Experiment 6.2: section 6.4.2.6; Experiment 7.1: section 7.4.1.6). In shade all the components of plant growth are depressed by a low energy input, and tillering ability of the plant is mainly dependent on carbohydrate supply (Cooper and Tainton 1968). In this sense, persistence of pasture species under low PAR could best be evaluated on their ability to continue to tiller or branch (Devkota *et al.* 1997).

The defoliation experiment (Experiment 6.2) demonstrated that under heavy shade and defoliation, only a species that can continue to produce leaf under intense defoliation was able to produce tillers in the shade. The relative index of perennial ryegrass and cocksfoot as indicated by tiller number per plant also summarized the importance of tiller number as a determinant of plant performance under shade (Table 9.3). Number of leaves per tiller and axillary tiller formation are greater in Wana cocksfoot than Nui perennial ryegrass even in unshaded field conditions with intensive grazing management (Brock *et al.* 1996).

Plants grown under a low PAR generally have a higher SLA and thinner leaves, which is also associated with less non-structural carbohydrate (Lambers and Poorter 1992) invested in leaves (Nassiri and Elgersma 1998). High SLA is interpreted as adaptation to shade in that for each unit weight of leaf dry matter, a greater area of leaf is able to intercept the available light (Dennis and Woledge 1983; Grubb *et al.* 1996; Sanderson *et al.* 1997). In this thesis, species that produced the greatest shoot dry weight per plant and tiller number per plant usually also had the highest SLA at low PAR. For example, SLA of perennial ryegrass was always lower than Yorkshire fog and cocksfoot (Figure 3.3, Tables 4.1.1, 4.5, 5.10), and SLA of Wana cocksfoot was always higher than Nui perennial ryegrass at a range of PAR and defoliation levels (Figure 6.3).

Shade tolerant pasture species appear to allocate more assimilates to leaf growth and to increase SLA. In this way photosynthetic capacity per plant will increase, which creates a positive feed back system since more assimilates will be available for leaf growth due to the higher photosynthesis per plant. Increased total plant photosynthesis results in increased tiller number per plant, which will also have a positive feed back to a larger leaf area via increased SLA (Ward and Blaser 1961; Solhaug 1991). Thus, successful grass plants in shade will increase in shoot dry weight mainly due to tiller production. The mechanism of increased leaf area and SLA influencing maintenance of tillering leading to increased dry weight per plant for shade tolerant grass is illustrated in Figure 9.1. Cocksfoot appears to have the mechanism for SLA maintained increased tillering shown in Figure 9.1 to result in higher number of tillers per plant. Solhaug (1991) found increased leaf area and SLA resulted in increased leaf area ratio in cocksfoot in response to a range of different photoperiods and temperatures. Conversely Eagles (1973) showed for a natural population of cocksfoot there was a negative relationship between SLA and increased light.

There are two hypotheses that could explain the greater biomass accumulation of cocksfoot in heavy shade as suggested by Ballaré (1991) in the case of elongated plants: (1) efficient at capturing light or (2) greater light conversion into biomass. Since photosynthesis measurements were not carried out in this thesis, the physiological mechanism governing these adaptations is not fully explained. However, larger leaf area or higher SLA, and maintenance of tillering and shoot dry weight by cocksfoot, as demonstrated in this thesis, suggested increased proportional investment in leaves by cocksfoot as discussed by Maliakal *et al.* (1999) in their work with *Impatiens capensis.*

Like cocksfoot, perennial ryegrass also had a higher leaf area ratio (LAR), due to its high SLA, in a mixture of perennial ryegrass with white clover under conditions of low N and high temperature (Davidson and Robson 1986). However, in this study perennial ryegrass always had lower SLA in the heavy shade than cocksfoot, and thus was unable to produce the shoot dry weight of cocksfoot. Ong and Marshall (1979) reported that tillers of ryegrass severely stressed by heavy shade were unable to survive.

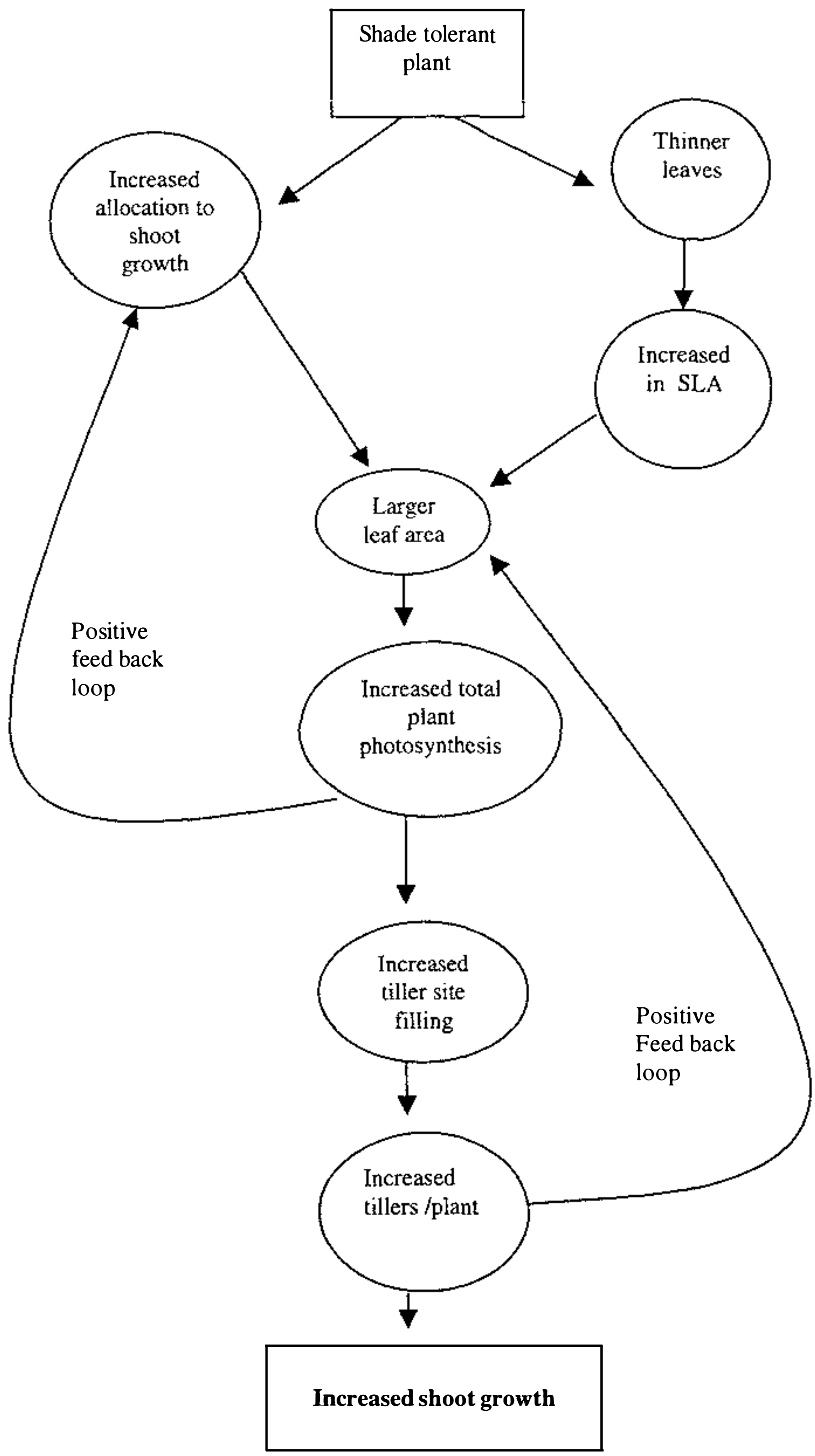

Figure 9.1 Mechanism of leaf area/SLA maintenance of tillering and shoot dry weight for shade tolerant grass species.

9.3.2 Pasture production and management under a deciduous tree-pasture system

Pasture production under deciduous trees is higher than that under younger *Pinus radiata* agroforest at a similar tree density (Hawke and Knowles 1997), and also than under widely spaced as well as closed plantations of *Pinus radiata* (Miller *et al.* 1996). Pasture production under trees decreases basically due to the competition of trees and associated pasture understorey for light, water, and mineral nutrients (Cameron *et al.* 1989). For these reasons, the management of trees in terms of density, species, canopy management and the understorey (mainly in terms of pasture species introduction, defoliation and mixture of companion grass species and legumes) are an important part of silvo-pastoral systems.

Deciduous trees such as alders, poplars and willows are primarily planted in New Zealand hill country for soil erosion control (DeRose *et al.* 1993; Miller 1996). Understorey pasture production is reduced by deciduous trees (Ditschal *et al.* 1997), but comparatively it can be better managed via practices like tree pruning or short rotations (New 1985). In this thesis, for the tree density of 1197 stems/ha (PAR level of around 180 and 360 μmoles photons m^{-2} s^{-1}, respectively, for heavy and medium shade; Experiment 7.1: sections 7.3.1, 7.3.2) with 11 year old alders, herbage mass in heavy and medium shade was about 50 and 70% respectively of that in light shade (section 7.4.1.4). Pasture production in a wide spaced (37 stems/ha) mature poplar-pasture system in a hill environment (PAR level 122 μmoles photons m^{-2} s^{-1} during December) in New Zealand was 60% of that of open pasture (Guevara-Escobar *et al.* 1997). The pasture was dominated by browntop, with a mixture of other perennial grasses and legumes (Guevara-Escobar *et al.* 1997). However, the canopy allowed sunflecks due to the wide tree spacing, and so browntop probably dominated for that reason although the measured PAR level was less than 200 μmoles photons m^{-2} s^{-1} (Guevara-Escobar *et al.* 1997).

Reduction of understorey pasture production appeared to be mainly associated with the shading effects of trees. However, there could be other limiting factors as well, for example, there were differences in competition for water between trees and pasture during the dry period; less water stress in cocksfoot plots than other species. Pasture species such as perennial ryegrass were under stress from low fertility, high soil temperature, coupled with a low level of soil moisture (Chapter 7:section 7.5.1). Soil moisture and nutrients were also limiting in a poplar-cereal crop system as reported by Thevathasan and Gordan (1997).

There is always a trade-off between tree production and understorey pasture production but the results suggest pasture production can be maintained at a reasonable level by pruning the trees (Experiment 7.1: sections 7.3.1, 7.3.2), or widely spacing the trees (Guevara-Escobar *et al.* 1997).

9.3.2.1 Canopy management of trees by pruning

As the alders were at the same spacing over the site, but pruned to different heights, it was possible to make some conclusions on the pruning management of trees. From a practical point of view, it was noted that pruning all but the last whorl (light shade) was not an appropriate practice since in some cases the tree's top whorl was broken off due to swinging in high wind. Likewise, pruning only the lower 2-3 branches (heavy shade) did not greatly reduce the canopy shading effect since it resulted in PAR levels of less than 200 µmoles photons m^{-2} s^{-1} and depressed pasture production to about half of that of light shading. Pruning half way up the trees (medium shade; 5m pruned) would be an appropriate practice, as it resulted in a canopy of understorey PAR levels about 360 µmoles photons m^{-2} s^{-1} that depressed understorey pasture production by only about 30% relative to light shade. However, the objectives and purpose of the particular tree-pasture system would affect the pruning decision. Deciduous trees only use available resources for part of the year, thus allowing resource use by pasture with minimal competition (Newman 1997), for about 25% of the year in the case of alders.

9.3.2.2 Shade tolerant pasture species and the options for management

The impact of spaced trees on understorey pasture production increases as the tree canopy develops (Guevara-Escobar *et al.* 1997; McGregor *et al.* 1999). As the canopy becomes closed, light, then the soil moisture contents under the trees, would be the main limiting factors determining total pasture dry matter accumulation (Power *et al.* 1999).

The tree density, tree species, and degree of canopy closure therefore, largely determine introduction of appropriate pasture species under tree shade.

Cocksfoot, particularly Wana was identified as the grass species most tolerant of heavy shade in this thesis. Yorkshire fog was also a shade tolerant pasture species in the glasshouse conditions, but not under the shade of the alder trees. Unlike cocksfoot, Yorkshire fog is not a common species under tree shade apart from as a weed in a condition when pasture species are not well defoliated, or managed by grazing. Among legumes, lotus was more tolerant of heavy shade than white clover, as also indicated by other research results (Gadgil *et al.* 1986; West *et al.*1988; West *et al.*1991). However, both lotus and cocksfoot have some disadvantages. Lotus can not tolerate frequent defoliation. Long rotations are required to maintain a persistent sward of lotus (Harris *et al.* 1997). For cocksfoot, Barker *et al.* (1985) discussed disadvantages that include reduced palatability when rank, and slow establishment. Total nitrogen and crude protein of cocksfoot were also reported to be lower than for perennial ryegrass (Woodman and Fraser 1991), but metabolizable energy and digestibility were ranked as high in cocksfoot as in perennial ryegrass (Woodman and Fraser 1991). In this thesis when grown under 27% ambient PAR (Chapter 3), *in vivo* organic matter digestibility of perennial ryegrass and cocksfoot were about 82 and 71%, respectively, (data not presented in the chapter). Further nutrient analyses of pasture species were outside the scope of this thesis. Nevertheless, if cocksfoot is managed to maintain the sward in an actively growing state, animal production is within expectations from other grass pasture species (Fraser and Rowarth 1994).

A conclusion from this thesis is that a cocksfoot based pasture, preferably with lotus, is likely to be the most persistent and productive under heavy tree shade (PAR <200 µmoles photons m^{-2} s^{-1}). Additionally, cocksfoot and lotus are both tolerant of the low to medium soil fertility and seasonal dry periods likely to be encountered on hill country where deciduous trees are used for erosion control.

Under medium shade, however, the opportunity exists to manage the light environment by pruning trees rather than introducing pasture species tolerant of heavy shade. As indicated by the results in this thesis, perennial ryegrass and browntop with white clover, can be grown under a medium level of shade if the PAR level is well above 200 µmoles photons m^{-2} s^{-1}. As perennial ryegrass, browntop and white clover are used traditionally in hill country pastures, management of these species under a medium shade by pruning trees is perhaps a cheaper option than establishing a new pasture species like cocksfoot.

Pruning of trees is a major way to benefit understorey pastures, by reducing above-ground competition between trees and pastures (Noordwijk and Purnomosidhi 1995). Pruning trees can be an equally effective way to conserve soil moisture contents (Tables 7.4a, b). The results of this study indicate that canopy management of deciduous trees to maintain medium shade is very important in order to improve understorey pasture productivity.

9.4 Conclusions

This thesis has provided important information for deciduous based tree-pasture systems, particularly with respect to the performance of pasture species in a range of % transmitted PAR. Suitable pasture species for use in heavy and medium levels of shade were identified as well as some effective options for pasture management under trees.

The overall conclusions from this thesis on the effect of a range of light intensities and variation in light quality on the growth and morphology of pasture species are summarized below.

(1) Shade had a marked effect on regeneration from main stems as well as on shoot dry weight accumulation. However, pasture species responded differently to shade. Cocksfoot was the best species for heavy shade and can be grown either with lotus or white clover in a mixture, even under low levels of soil fertility and moisture. Cocksfoot should be the choice for a tree-pasture system if PAR level is less than 200 µmoles m^{-2} s^{-1}, while perennial ryegrass, browntop, or Poa are suitable pasture species for medium shade with PAR levels more than 200 µmoles photons m^{-2} s^{-1}. Yorkshire fog was not suitable for growth under heavy shade. Lotus is preferable to white clover under heavy

shade, but white clover can be grown with any of the above grass species under a medium level of shade.

(2) Wana (tetraploid), and PG 74 (diploid) were the most shade tolerant cultivars of cocksfoot. Tetraploids and diploids could be equally suited for heavy shade. PG lines of cocksfoot, other than PG 74, were similar in performance, but were not promising under heavy shade. Cocksfoot produced the highest shoot dry weight in heavy shade, and thus can be recommended for use under a dense tree canopy, but its long-term persistence under tree shade requires further study.

(3) Wana cocksfoot performed better than Nui perennial ryegrass under intense defoliation in the shade. Wana produced higher biomass than Nui ryegrass under both weekly (W1) and three-weekly (W3) defoliation intervals due mainly to its ability to produce higher leaf area, higher leaf dry weight, and higher specific leaf area (SLA). Wana also had significantly more tillers per plant, a higher tiller site usage value, and a shorter leaf appearance interval than Nui ryegrass at both low PAR and low R:FR conditions. In contrast, perennial ryegrass production was poor under the combination of heavy shade and defoliation mainly due to its low tillering and leaf area per plant, and also due to its low tiller site usage value. Relative growth rate (RGR) of Wana was always higher than Nui at all PAR levels. RGR of both species was not affected by low R:FR.

(4) Nui perennial ryegrass is not adapted to silvo-pastoral systems where the degree of shading is heavy, i.e. less than 200 μmoles photons m^{-2} s^{-1}. There was a consistency in the results of field and glasshouse studies. However, there could be variation in the shade tolerance of cultivars of perennial ryegrass, and further research would be required to determine the extent of any shade tolerance within perennial ryegrass.

(5) Tillers per plant, specific leaf area, and leaf area, were the morphological attributes that mainly influenced the performance of pasture plants under heavy shade. Net flows of tissues were also consistently higher for the plants that performed well under shade. The ability to regenerate leaf area to maximise the interception of available radiation,

and to generate new tillers were the critical factors that determined production and persistence of pasture species under low irradiance.

(6) The level of shade rather than differences between the pasture species largely determined the diet selection by sheep that were inexperienced in grazing under trees, with the least grazing in the heaviest shade level.

(7) Shade is the most significant factor determining the production from pastures grown under trees. However, the decrease in pasture production due to shading can be managed by pruning lower branches from trees.

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APPENDICES

Appendix 3.1 Effects of shade on pasture species tiller or branch number per plant, and their relative values (to that of 73% ambient PAR) at different harvest dates under glasshouse conditions, 1996.

PAR/spcies	Absolute tillers or branches per plant		Relative tillers or branches per plant	
	9 August	23 August	9 August	23 August
73% ambient PAR				
White clover	4	5	-	-
Lotus	5	10	-	-
Sub.clover	4	5	-	-
Browntop	9	19	-	-
Cocksfoot	5	8	-	-
Yorkshire fog	13	22	-	-
Tall fescue	4	7	-	-
Plantain	0	2	-	-
Perennial ryegrass	8	13	-	-
Poa trivialis	7	14	-	-
43% ambient PAR				
White clover	3	5	88	82
Lotus	5	8	91	82
Sub.clover	3	5	93	84
Browntop	4	9	51	50
Cocksfoot	4	8	70	88
Yorkshire fog	7	13	56	59
Tall fescue	3	4	66	59
Plantain	0	2	0	67
Perennial ryegrass	4	7	51	51
Poa trivialis	5	11	69	80
27% ambient PAR				
White clover	2	3	59	54
Lotus	3	6	61	59
Sub.clover	2	3	52	50
Browntop	3	4	32	22
Cocksfoot	3	5	64	56
Yorkshire fog	5	8	35	36
Tall fescue	2	3	53	37
Plantain	0	0	0	0
Perennial ryegrass	2	3	27	23
Poa trivialis	4	6	50	41
18% ambient PAR				
White clover	0	2	0	41
Lotus	2	5	44	47
Sub.clover	0	0	0	0
Browntop	0	2	0	13
Cocksfoot	3	4	53	45
Yorkshire fog	3	6	25	26
Tall fescue	2	2	50	30
Plantain	0	0	0	0
Perennial ryegrass	2	3	28	20
Poa trivialis	2	4	34	25
14% ambient PAR				
White clover	0	0	0	0
Lotus	2	3	44	35
Sub.clover	0	0	0	0
Browntop	0	0	0	0
Cocksfoot	0	3	0	38
Yorkshire fog	3	3	19	14
Tall fescue	0	0	0	0
Plantain	0	0	0	0
Perennial ryegrass	0	2	0	16
Poa trivialis	0	2	0	16
Analysis of variance				
Shade P (A)	<0.0001	<0.0001	<0.0001	<0.0001
SEM (d.f.=4)	0.18	0.18	1.30 (d.f.=3)	1.33 (d.f.=3)
Species P (B)	<0.0001	<0.0001	<0.0001	<0.0001
SEM (d.f.=9)	0.14	0.20	1.56	1.51
Interactions P (A*B)	<0.0001	<0.0001	<0.001	NS
SEM (d.f.=36)	0.32	0.46	3.13 (d.f.=27)	3.02 (d.f.=27)

SEM= standard error of the mean, d.f.= degrees of freedom, NS= non significant at P<0.05. Note that relative tillers are the mean of four replications, calculated first for each replication, and then the mean value. This also implies to the Appendix table 3.2.

Appendix 3.2 Effects of shade on mean specific leaf area (SLA, m^2/kg) of the pasture species ,and their relative values (to that of 73% ambient PAR) at different harvest dates under glasshouse conditions, 1996.

	Absolute			Relative		
PAR/spcies	**9 August**	**23 August**	**6 September**	**9 August**	**23 August**	**6 September**
73% ambient PAR						
White clover	45.48	42.98	40.87	-	-	-
Lotus	54.21	47.94	42.89	-	-	-
Sub.clover	38.29	36.24	37.19	-	-	-
Browntop	28.68	29.08	27.68	-	-	-
Cocksfoot	34.84	31.48	33.96	-	-	-
Yorkshire fog	41.25	41.41	44.67	-	-	-
Tall fescue	28.55	28.83	30.46	-	-	-
Plantain	31.62	31.31	30.38	-	-	-
Perennial ryegrass	27.51	30.15	27.13	-	-	-
Poa trivialis	28.25	30.26	36.91	-	-	-
43%ambient PAR						
White clover	48.78	43.70	42.30	107	101	103
Lotus	62.57	52.43	51.60	115	109	120
Sub.clover	40.46	36.93	40.67	106	102	109
Browntop	37.64	33.52	32.07	131	115	116
Cocksfoot	37.17	37.64	41.68	107	119	123
Yorkshire fog	48.40	47.81	51.02	117	115	113
Tall fescue	32.67	33.98	35.62	114	118	117
Plantain	36.42	35.93	36.88	115	115	121
Perennial ryegrass	29.05	29.14	30.16	105	96	111
Poa trivialis	39.18	39.89	35.96	138	132	97
27% ambient PAR						
White clover	51.92	49.54	54.97	132	115	134
Lotus	48.09	61.93	68.56	88	129	160
Sub.clover	43.35	42.27	41.59	113	116	111
Browntop	37.80	50.18	32.91	132	172	119
Cocksfoot	44.11	45.03	42.39	127	143	125
Yorkshire fog	51.76	46.74	55.41	125	113	124
Tall fescue	37.10	38.37	33.86	130	133	111
Plantain	45.90	40.42	43.40	145	129	143
Perennial ryegrass	35.90	36.94	31.72	130	122	117
Poa trivialis	37.39	46.05	35.99	132	152	97
18% ambient PAR						
White clover	51.76	57.01	57.13	113	132	139
Lotus	56.92	69.56	71.14	105	145	166
Sub.clover	43.21	45.23	45.88	113	124	123
Browntop	37.00	42.75	36.27	129	147	131
Cocksfoot	38.41	45.45	46.25	110	144	136
Yorkshire fog	56.02	50.12	55.58	136	121	124
Tall fescue	39.75	44.26	41.77	139	153	137
Plantain	47.57	47.57	44.84	150	152	148
Perennial ryegrass	38.17	43.70	38.52	138	145	142
Poa trivialis	40.94	48.06	37.93	145	159	102
14% ambient PAR						
White clover	57.39	59.88	55.86	126	139	136
Lotus	55.21	72.92	82.78	102	152	193
Sub.clover	43.50	45.26	49.69	114	124	133
Browntop	39.36	43.94	28.74	137	151	104
Cocksfoot	47.53	46.33	46.86	136	147	138
Yorkshire fog	67.94	60.03	64.47	164	145	144
Tall fescue	34.99	46.24	44.39	122	160	146
Plantain	47.62	49.57	45.92	150	158	151
Perennial ryegrass	48.59	50.64	41.07	176	168	151
Poa trivialis	40.59	40.85	31.09	143	135	84
Analysis of variance						
Shade P (A)	P<0.0001	P<0.0001	P<0.0001	P<0.0001	P<0.0001	P<0.0001
SEM (d.f.=4)	0.75	0.74	0.44	2.01(d.f.=3)	2.38 (d.f.=30	1.43 (d.f.=3)
Species P (B)	P<0.0001	P<0.0001	P<0.0001	P<0.0001	P<0.0001	P<0.0001
SEM (d.f.=9)	0.57	0.61	0.53	2.25	2.17	1.75
Interactions P (A*B)	P<0.0001	P<0.0001	P<0.0001	P<0.0001	P<0.0001	P<0.0001
SEM (d.f.=36)	1.28	1.38	1.20	4.50 (d.f.=27)	4.35 9d.f.=27)	3.50 (d.f.=27)

SEM= standard error of the mean, d.f.= degrees of freedom

Appendix 3.3 Effects of shade on mean plant height (cm) of the pasture species at different harvest dates under glasshouse conditions, 1996.

PAR/spcies	10 July	25 July	9 August	23 August	6 September	Repeated measures
73% ambient PAR						
White clover	3.85	5.56	7.51	9.68	9.91	8.16
Lotus	3.11	4.72	9.33	10.21	11.33	8.90
Sub.clover	5.93	7.14	6.88	8.25	8.84	7.78
Browntop	6.17	10.58	14.27	18.53	20.00	15.84
Cocksfoot	8.33	11.74	11.71	12.29	19.13	13.72
Yorkshire fog	9.63	15.99	20.49	14.51	15.94	16.73
Tall fescue	6.38	21.90	23.24	21.31	22.85	22.33
Plantain	7.04	10.11	12.79	14.88	14.12	12.98
Perennial ryegrass	16.78	23.51	25.05	23.14	23.32	23.75
Poa trivialis	6.45	10.65	11.69	15.31	17.64	13.82
43%ambient PAR						
White clover	4.86	6.68	7.78	10.16	9.87	8.62
Lotus	3.84	4.37	10.57	11.45	13.04	9.86
Sub.clover	7.78	8.57	8.39	8.66	9.46	8.77
Browntop	7.25	11.98	15.70	20.38	22.27	17.58
Cocksfoot	8.39	13.41	12.76	18.19	20.12	16.12
Yorkshire fog	12.89	19.69	19.89	21.11	22.34	20.76
Tall fescue	17.32	26.07	24.24	23.25	25.32	24.72
Plantain	7.98	9.53	12.31	11.78	15.03	12.16
Perennial ryegrass	19.99	26.15	26.41	27.05	29.20	27.20
Poa trivialis	8.57	12.26	13.42	15.69	18.05	14.85
27% ambient PAR						
White clover	5.69	7.48	9.98	10.73	9.17	9.34
Lotus	3.97	4.57	7.78	9.71	10.95	8.25
Sub.clover	9.00	10.47	8.74	9.50	9.75	9.62
Browntop	9.28	14.60	12.68	20.50	19.61	16.85
Cocksfoot	9.77	17.79	15.81	18.13	18.24	17.49
Yorkshire fog	13.26	19.18	21.75	21.72	21.69	21.08
Tall fescue	18.80	25.45	23.19	20.56	23.81	23.25
Plantain	8.32	9.37	11.99	12.35	14.70	12.10
Perennial ryegrass	21.90	26.48	24.73	24.92	25.54	25.41
Poa trivialis	8.69	12.94	14.34	14.81	19.57	15.42
18% ambient PAR						
White clover	5.39	6.34	8.29	8.82	10.02	8.37
Lotus	4.01	4.27	6.53	8.67	9.43	7.23
Sub.clover	7.58	10.01	8.51	8.08	9.67	9.07
Browntop	7.98	13.25	12.52	17.17	17.28	15.05
Cocksfoot	10.42	14.18	15.13	16.02	16.81	15.53
Yorkshire fog	14.36	18.70	17.44	17.11	19.99	18.31
Tall fescue	19.32	24.64	19.64	20.85	24.34	22.37
Plantain	7.91	8.71	8.93	12.98	12.28	10.72
Perennial ryegrass	21.04	26.71	21.94	23.66	26.43	24.69
Poa trivialis	8.49	11.19	11.33	10.63	16.14	12.32
14% ambient PAR						
White clover	4.36	4.74	6.04	7.27	7.53	6.39
Lotus	3.44	3.78	5.50	6.25	8.16	5.92
Sub.clover	8.09	9.12	8.62	8.58	8.36	8.67
Browntop	7.42	10.68	12.69	14.03	15.72	13.28
Cocksfoot	10.80	14.35	15.24	11.29	14.41	13.82
Yorkshire fog	12.52	16.72	16.98	16.06	16.88	16.66
Tall fescue	19.23	21.03	16.02	20.84	22.41	20.08
Plantain	7.17	6.97	6.90	7.77	10.56	8.05
Perennial ryegrass	18.10	21.59	18.67	18.78	21.63	20.17
Poa trivialis	8.57	10.73	11.05	9.67	13.41	11.21
Analysis of variance						
Shade P (A)	P<0.0001	P<0.0001	P<0.0001	P<0.0001	P<0.0001	P<0.0001
SEM (d.f.=4)	0.54	0.21	0.24	0.29	0.22	0.11
Species P (B)	P<0.0001	P<0.0001	P<0.0001	P<0.0001	P<0.0001	P<0.0001
SEM (d.f.=9)	0.12	0.12	0.18	0.15	0.20	0.08
Interactions P (A*B)	P<0.0001	P<0.0001	P<0.0001	P<0.0001	P<0.0001	P<0.0001
SEM (d.f.=36)	0.28	0.28	0.42	0.34	0.46	0.19

SEM= standard error of the mean, d.f.= degrees of freedom

Appendix 3.4 Effects of shade on mean leaf/petiole length (cm) of the pasture species at different harvest dates under glasshouse conditions, 1996.

PAR/spcies	10 July	25 July	9 August	23 August	6 September	Repeated measures
73% ambient PAR						
White clover	2.72	3.89	5.84	6.19	7.61	5.88
Lotus	0.24	0.27	0.38	0.49	0.54	0.42
Sub.clover	3.92	4.93	4.72	5.21	7.13	5.50
Browntop	5.42	8.69	11.38	12.43	12.97	11.37
Cocksfoot	6.32	8.92	11.08	11.77	13.37	11.28
Yorkshire fog	8.75	12.03	15.65	12.84	11.80	13.08
Tall fescue	12.32	16.36	15.83	14.78	16.60	15.89
Plantain	6.10	8.38	10.18	11.67	11.54	10.44
Perennial ryegrass	12.73	18.16	15.44	16.37	16.38	16.59
Poa trivialis	4.61	8.05	9.31	10.43	11.28	9.77
43% ambient PAR						
White clover	3.33	4.41	4.98	7.05	7.96	6.10
Lotus	0.24	0.27	0.37	0.44	0.59	0.41
Sub.clover	4.49	5.65	4.42	6.08	7.65	5.90
Browntop	5.75	9.76	9.94	12.81	13.28	11.45
Cocksfoot	6.34	10.72	10.44	12.63	15.15	12.23
Yorkshire fog	8.80	11.03	14.46	13.82	14.91	13.56
Tall fescue	11.73	18.17	15.22	15.03	18.05	16.61
Plantain	6.38	7.03	9.81	10.27	13.02	10.03
Perennial ryegrass	13.60	17.38	19.26	18.17	18.56	18.34
Poa trivialis	7.03	7 90	9.91	10.79	13.07	10.42
27% ambient PAR						
White clover	3.46	4.04	5.51	6.12	7.18	5.71
Lotus	0.23	0.23	0.32	0.38	0.50	0.36
Sub.clover	4.52	6.06	5.39	6.16	6.83	6.11
Browntop	6.32	9.80	12.34	11.21	14.51	11.96
Cocksfoot	6.89	11.60	10.41	11.01	13.50	11.63
Yorkshire fog	10.53	13.65	15.00	13.52	15.53	14.42
Tall fescue	12.23	16.83	13.18	12.59	15.88	14.62
Plantain	5.57	7.80	8.71	9.68	11.72	9.48
Perennial ryegrass	13.24	19.23	14.85	15.92	17.90	16.97
Poa trivialis	6.78	9.21	10.90	10.69	12.46	10.81
18% ambient PAR						
White clover	2.77	4.13	4.51	6.55	6.68	5.46
Lotus	0.15	0.17	0.32	0.34	0.38	0.30
Sub.clover	4.83	5.50	5.66	5.92	6.71	5.95
Browntop	6.52	8.41	8.67	11.12	10.10	9.57
Cocksfoot	7.58	9.93	9.72	10.55	13.45	10.91
Yorkshire fog	11.21	13.32	12.32	12.40	14.87	13.23
Tall fescue	14.90	14.63	11.07	14.14	15.95	13.95
Plantain	4.75	6.12	6.24	8.02	8.94	7.33
Perennial ryegrass	14.11	16.90	15.76	14.57	16.48	15.93
Poa trivialis	6.80	8.10	8.86	9.16	10.87	9.25
14% ambient PAR						
White clover	3.14	3.08	3.98	4.95	5.31	4.33
Lotus	0.31	0.10	0.22	0.29	0.29	0.22
Sub.clover	6.11	4.79	6.34	6.02	5.50	5.66
Browntop	5.73	7.03	8.99	9.68	8.19	8.47
Cocksfoot	9.25	9.99	10.32	9.22	10.66	10.05
Yorkshire fog	10.04	9.61	10.94	7.78	12.85	10.30
Tall fescue	14.39	14.80	10.36	8.80	10.44	11.10
Plantain	4.66	5.61	6.27	6.64	6.58	6.28
Perennial ryegrass	14.68	12.84	14.97	9.70	13.51	12.75
Poa trivialis	7.28	7.76	8.52	7.01	8.79	8.02
Analysis of variance						
Shade P (A)	P<0.0001	P<0.0001	P<0.0001	P<0.0001	P<0.0001	P<0.0001
SEM (d.f.=4)	0.08	0.12	0.19	0.17	0.15	0.09
Species P (B)	P<0.0001	P<0.0001	P<0.0001	P<0.0001	P<0.0001	P<0.0001
SEM (d.f.=9)	0.15	0.20	0.19	0.21	0.17	0.10
Interactions P (A*B)	P<0.0001	P<0.0001	P<0.0001	P<0.0001	P<0.0001	P<0.0001
SEM (d.f.=36)	0.34	0.45	0.42	0.48	0.38	0.23

SEM= standard error of the mean, d.f.= degrees of freedom

Appendix 7.1a Percent mean botanical composition under different levels of shade at Aokautere, 25 March 1997 to 24 November 1997.

Treatments/ % mea composition	25 March 1997	24 Apr l 1997	28 May 1997	28 October 1997	24 November 1997
Heavy shade					
Ryegrass+wc					
Grass	33	40	47	70	45
Legumes	34	29	17	20	33
Other	33	31	36	10	22
Y.fog+wc					
Grass	37	41	59	63	55
Legumes	34	26	16	23	16
Other	29	33	25	14	29
C.foot+wc					
Grass	47	55	62	68	67
Legumes	33	24	18	25	15
Other	20	21	20	7	18
C.foot+lotus					
Grass	51	54	66	65	63
Legumes	33	27	15	24	18
Other	16	19	19	11	19
Medium shade					
Ryegrass+wc					
Grass	35	37	54	63	43
Legumes	28	30	15	26	36
Other	37	33	31	11	21
Y.fog+wc					
Grass	38	43	48	56	60
Legumes	32	26	18	29	18
Other	30	31	34	15	22
C.foot+wc					
Grass	49	47	60	64	64
Legumes	29	27	16	29	18
Other	22	26	24	7	18
C.foot+lotus					
Grass	55	52	59	70	61
Legumes	28	27	19	22	18
Other	17	21	22	8	21
Light shade					
Ryegrass+wc					
Grass	36	42	52	62	41
Legumes	32	30	16	27	35
Other	32	28	32	1	24
Y.fog+wc					
Grass	53	46	56	61	50
Legumes	26	32	19	24	23
Other	21	22	25	15	27
C.foot+wc					
Grass	44	59	68	68	62
Legumes	27	21	14	23	12
Other	29	20	18	9	26
C.foot+lotus					
Grass	54	53	60	69	54
Legumes	23	28	15	24	22
Other	23	19	25	7	24

wc= whie clover, Y.fog=Yorkshire fog, C. foot= cocksfoot

Appendix 7.1b Percent mean botanical composition under different levels of shade at Aokautere, 23 December 1997 to 28 May 1998.

Treatments/ % mean composition	23 December 1997	23 January 1998	27 February 1998	27 March 1998	23 April 1998	28 May 1998
Heavy shade						
Ryegrass+wc						
Grass	41	35	55	32	40	45
Legumes	24	13	9	19	22	29
Weed	19	23	10	12	3	12
Dead materials	16	29	26	37	35	14
Y.fog+wc						
Grass	49	53	46	28	32	59
Legumes	15	9	9	9	12	13
Weed	12	7	3	4	6	4
Dead materials	24	31	42	59	50	24
C.foot+wc						
Grass	73	62	68	5	51	65
Legumes	8	7	2	3	4	3
Weed	2	8	2	2	2	3
Dead materials	17	23	28	44	43	29
C.foot+lotus						
Grass	67	65	65	56	57	71
Legumes	9	6	2	1	3	4
Weed	6	4	2	2	2	2
Dead materials	18	25	31	41	38	23
Medium shade						
Ryegrass+wc						
Grass	42	48	60	32	44	50
Legumes	23	19	6	15	18	20
Weed	18	8	12	5	4	8
Dead materials	17	25	22	48	34	22
Y.fog+wc						
Grass	54	47	47	8	40	57
Legumes	24	18	7	33	10	9
Weed	2	7	6	4	3	4
Dead materials	20	28	42	55	47	30
C.foot+wc						
Grass	62	61	63	47	53	63
Legumes	16	13	3	4	4	4
Weed	2	3	2	2	1	1
Dead materials	20	23	32	47	42	32
C.foot+lotus						
Grass	64	61	60	47	52	58
Legumes	17	7	3	2	5	4
Weed	7	7	4	4	3	2
Dead materials	15	25	33	47	40	36
Light shade						
Ryegrass+wc						
Grass	38	44	49	34	54	57
Legumes	37	23	17	13	20	20
Weed	7	4	4	16	2	3
Dead materials	18	29	30	37	24	20
Y.fog+wc						
Grass	62	42	38	24	42	65
Legumes	16	20	8	17	15	12
Weed	4	8	2	2	2	2
Dead materials	18	30	52	57	41	21
C.foot+wc						
Grass	59	60	59	46	54	62
Legumes	15	11	5	4	6	8
Weed	3	3	2	1	2	2
Dead materials	23	26	34	49	38	28
C.foot+lotus						
Grass	59	52	50	40	49	65
Legumes	17	12	8	3	8	7
Weed	7	7	4	6	2	2
Dead materials	17	29	38	51	41	26

wc= whie clover, Y.fog=Yorkshire fog, C. foot= cocksfoot

2.5m pruning height

Replication I	Replication II	Replication III	Replication IV
YW 4m	CW	RW	YW
CW 2m	CL	YW	RW
CL	RW	CW	CL
RW	YW	CL	CW

5.0m pruning height

Replication I	Replication II	Replication III	Replication IV
RW	CW	CL	RW
YW	CL	RW	YW
CL	YW	CW	CL
CW	RW	YW	CW

7.0m pruning height

Replication I	Replication II	Replication III	Replication IV
CW	RW	CW	CL
RW	YW	RW	CW
CL	CW	CL	YW
YW	CL	YW	RW

Appendix Figure 7.1 Lay out of the field experiment. RW= perennial ryegrass with white clover, YW=Yorkshire fog with white clover, CW= cocksfoot with white clover, and CL= cocksfoot with lotus.

BIOGRAPHY

I, Naba Raj Devkota was born in 19th August 1961 in Gorkha, Nepal. I studied I. Sc, and B. Sc. Agriculture at Institute of Agriculture and Animal Sciences (IAAS), Tribhuvan University (TU), Nepal from 1981 to 1986. I joined TU/IAAS in December 1986 as an Assistant Lecturer and were involved in teaching undergraduate courses on animal husbandry and fodder production and pasture management besides being involved in related research. From 1991 to 1993 I studied M. Sc. Agriculture (Agricultural Systems) in Chiang Mai University, Thailand, for which I got a scholarship from the Ford Foundation. I resumed my teaching and researching job at TU/IAAS, department of Animal Nutrition and Pasture Production, Rampur, Nepal in 1993 to the capacity of Lecturer and have been continuously associated with IAAS to date. I worked as a Farm Superintendent at the IAAS Livestock Farm in 1995. From 1996 to 1999/2000, I undertook a Ph.D program in Pastoral Science at Massey University, with the support of a scholarship provided by the New Zealand Official Development Assistance (NZODA). After completing my Ph.D studies, I will return to Nepal and continue my teaching and researching job at TU/IAAS, Rampur.