MODELLING LUCERNE (*Medicago sativa* L.) CROP RESPONSE TO LIGHT REGIMES IN AN AGROFORESTRY SYSTEM

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By
Alexandre Costa Varella

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The general goal of this research was to understand the agronomic and physiological changes of a lucerne crop in distinct physical radiation environments and to verify the potential of lucerne to grow under shaded conditions. To achieve this, the research was conducted in four main steps: (i) firstly, experimental data collection in the field using two artificial shade materials (shade cloth and wooden slats) under irrigated and non-irrigated conditions; (ii) a second experiment with data collection in a typical temperate dryland agroforestry area under non-irrigated conditions; (iii) generation of a light interception sub-model suitable for shaded crops and (iv) a linkage between the light interception sub-model and a canopy photosynthesis model for agroforestry use.

In experiments 1 and 2, lucerne crop was exposed to 6 different light regimes: full sunlight (FS), shade cloth (FS+CL), wooden slats (FS+SL), trees (T), trees+cloth (T+CL) and trees+slats (T+SL). The FS+SL structure produced a physical radiation environment (radiation transmission, radiation periodicity and spectral composition) that was similar to that observed in the agroforestry site (T). The mean annual photosynthetic photon flux density (PPFD) was 41% under the FS+CL, 44% under FS+SL and 48% under T compared with FS in clear sky conditions. Plants were exposed to an intermittent (sun/shade) regime under both FS+SL and T, whereas under FS+CL the shaded light regime was continuous. The red to far-red (R/FR) ratio measured during the shade period under the slats was 0.74 and under the trees was 0.64. However, R/FR ratio increased to 1.26 and 1.23 during the illuminated period under FS+SL and T, respectively, and these were equivalent to the ratio of 1.28 observed under the FS+CL and 1.31 in FS.

The radiation use efficiency (RUE) of shoots increased under the 5 shaded treatments compared with full sunlight. The pattern of radiation interception was unchanged by radiation flux, periodicity and spectral composition and all treatments had a mean extinction coefficient of 0.82. However, the magnitude of the decrease in canopy growth was less than those in PPFD transmissivity. The mean lucerne annual dry matter (DM) yield was 17.5 t ha^{-1} in FS and 10 t ha^{-1} under the FS+CL, FS+SL and T regimes. This declined to 3.4 t DM ha^{-1} under T+CL (22% PPFD transmissvity) and 4.1 t DM ha^{-1} under T+SL (23% transmissivity). A similar pattern of response was observed for leaf net photosynthesis (Pn) rates under the shade treatments compared with full sun. In addition, spectral changes observed under the trees and slats affected plant morphology by increasing the number of long stems, stem height and internode length compared with full sunlight. Thus, there were two main explanations for the increase in RUE under shade compared with full sun: (i) preferential partition of assimilates to shoot rather than root growth and/or (ii) leaves under shade were still operating at an efficient part of the photosynthetic light curve.

The changes proposed for the canopy Pn model were appropriate to simulate the radiation environment of an agroforestry system. However, the model underestimated DM yields under the continuous and intermittent shade regimes. These were considered to be mainly associated with plant factors, such as overestimation in maintenance respiration and partitioning between shoots and roots in shade and the intermittency light effect on leaf Pn rates. Further investigation in these topics must be addressed to accurately predict crop yield in agroforestry areas. Overall, the lucerne crop responded typically as a sun-adapted plant under shade. It was concluded that lucerne yield potential to grow under intermediate shade was superior to most of C_3 pastures previously promoted in the literature.

Key words: alfalfa, fluctuating light, light intensity, light quality, *Pinus radiata*, shade and silvopastoral system.

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CHAPTER 1

General introduction

The process of crop growth in any environment is driven by energy transformation through photosynthesis, in which incident solar radiation is converted to more useful forms of chemical potential energy. To achieve this transformation, three processes are essential: (i) interception of incident solar radiation by the leaf canopy; (ii) conversion of the intercepted radiant energy to chemical potential energy; (iii) partitioning of the photosynthates to different parts of the plant.

Classic research published by Monsi & Saeki (1953), Monteith (1965), Loomis *et al.* (1967), for example, have stated that radiation and its distribution within the canopy are the most important elements of microclimate affecting crop growth. Diurnal changes of solar radiation dictate the course of photosynthesis and transpiration, and the vertical gradient of radiant flux within a canopy is a measure of the absorption of energy by foliage at different heights. This work stimulated the development of a number of canopy photosynthesis models for full sunlight conditions. The general assumption was that a critical study of radiation in relation to canopy architecture gives the truest description of light distribution within the canopy and hence the best estimate of photosynthesis. However, there is little information available to know if such a photosynthesis canopy model can be used to predict plant responses under shaded environments.

To date most studies have focused on fully illuminated crops under steady-state conditions of radiation density. However, in some circumstances, plants in crop communities are submitted to changes in the periodicity of illumination. For example, in multi-strata cultivation, such as agroforestry or inter-cropping systems, the understorey species is exposed to alternating periods of sun and shade as the sun passes through the upper canopy foliage. The effect of such temporal variation of radiation on understorey plants has rarely been investigated in agroforestry research. Indeed, plastic shade cloth, that produces a continuous and uniform pattern of shade, is the most frequently used artificial material to simulate the shade of trees (Wilson, 1996; Healey & Rickert, 1998). The use of alternative methodology, that could artificially closely resemble the actual radiation environment of an agroforestry system in its three aspects (flux, periodicity and spectral composition), is still unknown. Therefore, in this study, an alternative shade structure is compared with the traditional shade cloth for its ability to artificially mimic the radiation patterns and understorey plant responses observed in an agroforestry system. In addition, adjustments to a classic canopy photosynthesis model (Loomis *et al.*, 1967) are proposed to allow it to predict the ideal canopy architecture to maximize yield under different shade regimes.

The null hypothesis of this thesis is that the understorey plants grown under an intermittent light regime respond in the same way as those in a continuous light regime. To test this hypothesis, research was conducted in four main steps:

(i) Experimental data collection in the field using different artificial shade materials under irrigated and non-irrigated conditions. This was to test distinct shading methodologies and determine crop responses beneath them.
(ii) Experimental data collection in a typical temperate dryland agroforestry area under non-irrigated conditions. This was to compare artificial shading methodologies directly with a field site.
(iii) Generation of a light interception sub-model suitable for shaded crops and plant communities. This was to determine theoretically how plants could optimize canopy radiation interception under different light regimes.
(iv) Linkage between the light interception sub-model and a canopy photosynthesis model for agroforestry use. This was to verify the theoretical canopy responses with field data and identify areas for improvement.

The general goal is to understand the agronomic and physiological changes of a temperate legume in the physical radiation environment of an agroforestry system and to verify its potential to grow under shade conditions. In this research, lucerne (*Medicago sativa* L.) is used as the indicator crop because of its high ability to uptake soil water and nutrients and fix nitrogen from the air into plant protein, which decreases the chances of interactions between light, water and nitrogen stresses. To simulate the physical radiation environment in an agroforestry system, an alternative shade material constructed from wooden slats is proposed. The aim of the slatted structure was to recreate the alternating sun/shade pattern, observed through a day, of a typical agroforestry system. Plant responses were measured, predicted and compared with field data collected in full sunlight, under the artificial shade structures and in the agroforestry area.

The thesis consists of 7 chapters (Figure 1.01). Chapter 2 is a review of the literature related to a description of the physical environment of agroforestry systems, light and water relations involved between trees and understorey pastures and current methodology used to artificially simulate tree shade. It also briefly describes the main agronomic and physiological features of a lucerne crop that may enable it to persist under trees. Finally, current 'state of art' of agroforestry modelling, including its main constraints and challenges to accurately predict understorey pasture yield are reviewed. Chapter 3 outlines a field experiment conducted to compare different artificial shade structures, and the crop responses observed beneath them, created to simulate the radiation environment of an agroforestry area. Chapter 4 describes a second field experiment to assess how close one or both artificial shade structures resemble the physical radiation environment and plant responses observed in an agroforestry site. In Chapter 5, adjustments to a classic canopy photosynthesis model to predict crop yield under continuous and intermittent light regimes are proposed. A theoretical analysis is performed to investigate the canopy architecture strategy to optimise canopy photosynthesis under 3 different light regimes. Chapter 6 uses field data to test the theoretical assumptions from Chapter 5 and verify the accuracy of the canopy photosynthesis model to predict yield under the 3 light regimes. Finally, in Chapter 7, the overall results are discussed and compared with those previously reported in the literature. This includes an agronomic analysis of the potential of lucerne to grow in agroforestry areas. The most appropriate shade structure to resemble under tree radiation is also discussed in relation to agroforestry research. In addition, a critical analysis is performed about the adjustments proposed for the canopy photosynthesis model and its use to predict understorey yield in shaded regimes. Finally, future research recommendations are outlined to improve modelling in agroforestry and to confirm the potential use of lucerne as an understorey crop for agroforestry systems in dryland temperate environments.

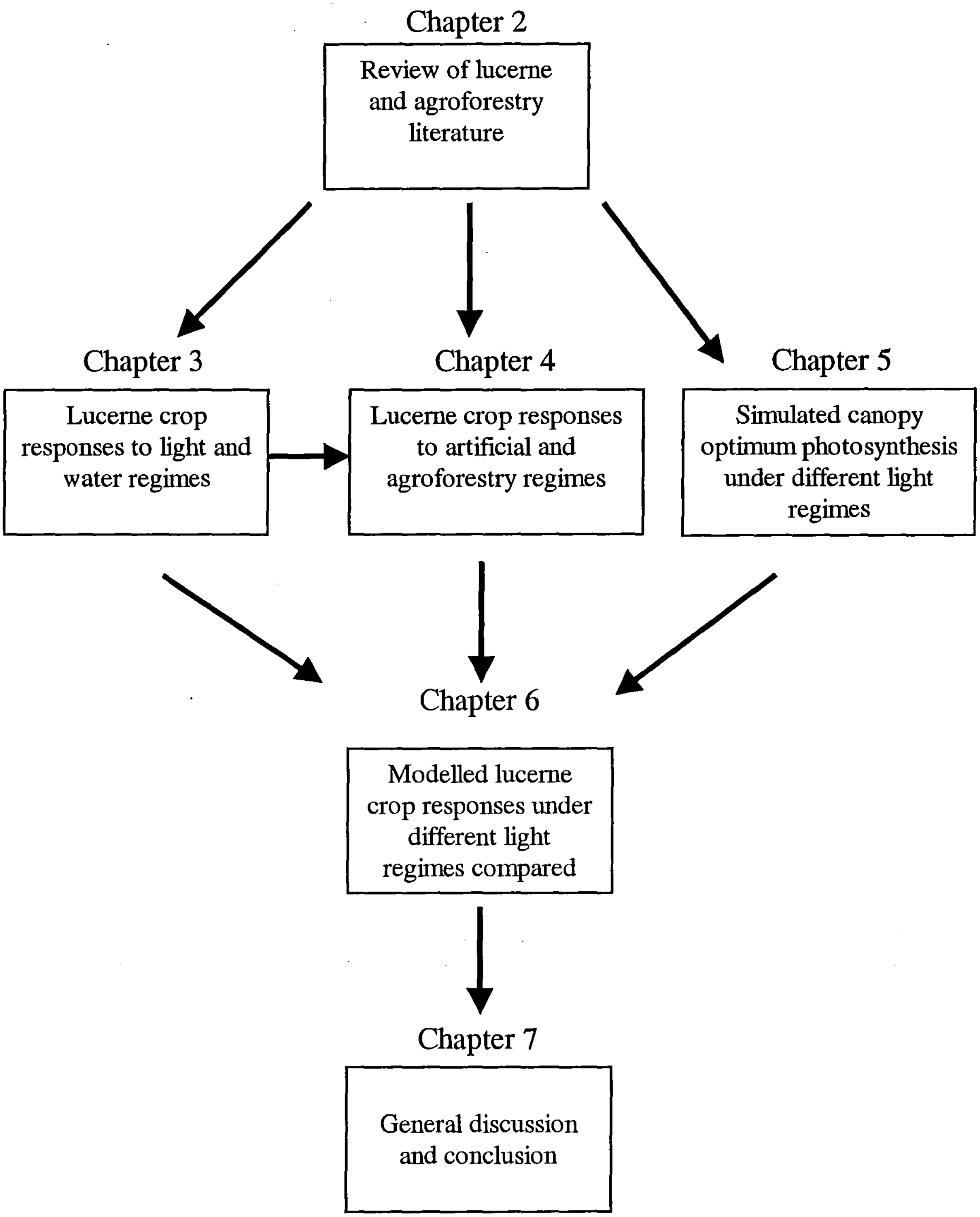

Figure 1.01- Diagrammatic representation of the relationship between chapters of the PhD thesis.

CHAPTER 2

Literature review

2.1- Definition and types of agroforestry systems

Agroforestry is defined as a land-use system where woody perennials are deliberately used on the same land-management units as agricultural crops and/or animals, in some form of spatial arrangement or temporal sequence (Nair, 1993). There are various types of agroforestry combinations in different ecological and geographical regions of the world, including silvopastoral (pasture/animals and trees), agrosilvopastoral (crops and pasture/animals and trees), agro-silvicultural (crops and trees) and multi-purpose tree systems (trees cultivated for multi-purpose objectives). In temperate areas like New Zealand, the most common systems are the agri-silvicultural use of windbreaks and shelterbelts, woodlots and silvopastoral systems (Hawke *et al.*, 1997; Mead *et al.*, 1999). The main motives for agroforestry in New Zealand farms are: (i) prevention and control of soil degradation, (ii) diversification and increase of land productivity, (iii) aesthetics and (iv) environmental awareness (Mead, 1995).

2.2- Most used temperate species in agroforestry

In New Zealand, the most frequently used tree species for agroforestry purposes were listed by Mead *et al.* (1999) as radiata pine (*Pinus radiata*), alder (*Alnus cordata*), poplar (*Populus deltoides*), eucalypts (*Eucalyptus fastigata and E. nitens*), Douglas fir (*Pseudotsuga menziessi*) and cupressus tree (*Cupressus macrocarpa*). From this group, radiata pine is the main species planted, especially the improved varieties, for woodlots, silvopastoral systems and shelter. The great virtue of radiata pine trees is the rapid growth, ease of establishment, wide tolerance of sites, amenability to silviculture and the ready acceptance in the timber, chipwood and round wood markets (Mead *et al.*, 1999). This tree species is usually planted in woodlots at between 666 (5m x 3m) and 1250 (4m x 2m) stems ha^{-1}. These trees are normally pruned to 6m and eventually thinned to between 250 and 500 stems ha^{-1} to produce high-quality and high-value logs. Radiata pine trees are generally felled between 25-30 years old. In silvopastoral systems, initial stockings are often at 600 (6m x 2.8m) stems ha^{-1} and final stocking at 200 stems ha^{-1}. Research and farm models (Knowles, 1991) suggest that a final stocking less than 200 stems ha^{-1} tends to produce low grade logs due to excessive branch sizes and may not be the best financial alternative.

There is a wide range of pasture species for agroforestry purposes in New Zealand. The main understorey grasses used are perennial rygrass (*Lolium perenne*) and cocksfoot (*Dactylis glomerata*). Among legumes, the main species used are white clover (*Trifolium repens*), sub-clover (*Trifolium subterraneum*) and lotus (*Lotus pedunculatus* cv. Maku). Results from agroforestry experiments in the South Island of New Zealand showed that lucerne and cocksfoot have been the most productive and persistent species under radiata pine trees after 9 years (Chang *et al.*, unpublished data). In another experiment, Mead & Chang (2002) found that sub-clover was a better pasture species than white clover and lucerne to form a silvopastoral system with alder, poplar, eucalypt and radiata pine trees, because it was the least competitive with trees for soil water. In the North Island of New Zealand, cocksfoot was also successfull under an 11 year-old stand of alder trees (Devkota *et al.*, 1998).

The use of lucerne as an understorey species for agroforestry systems is uncommon. One of the few examples found in the literature was the integration between lucerne and walnut trees (*Juglans regia*) to study soil physical properties and soil water competition in the central area of Italy (Pini *et al.*, 1999). The authors found that lucerne improved soil porosity to a depth of 0.35 m and facilitated soil water movement in the agroforestry area. Dupraz *et al.* (1998) intercropped walnut trees and lucerne in France and observed that the perennial legume was more competitive for soil water than tall fescue (*Festuca arundinacea*) and other plants, but enhanced the nitrogen content of the tree leaves. In New Zealand, a long-term agroforestry experiment showed that radiata pine trees grown for 7 years with a lucerne understorey were

8.6 m high, whereas plots with cocksfoot and ryegrass were approximately 9.2 m (Chang *et al.*, unpublished data). Diameter at the breast height (DBH) of trees was also greater in the cocksfoot and ryegrass than in the lucerne plots. However, these same authors reported an averaged annual understorey dry matter yield of 8.2 t ha^{-1} for lucerne, 7.1 t ha^{-1} for cocksfoot and 5.4 t ha^{-1} for ryegrass under trees. In this same experiment at age 10, Peri *et al.* (2002a) observed that trees in the lucerne treatments grew to 12.2 m high, whereas trees were 13.2 m high in cocksfoot and ryegrass treatments. Likewise, trees at age 10 showed a DBH of 0.26 m in cocksfoot, 0.27 m in ryegrass and 0.26 in lucerne. These authors explained that understorey water competition affected tree growth particularly during summer and early autumn when large soil water deficits occur in the Canterbury plains of New Zealand.

2.3- Physical environment in agroforestry systems

The vegetative components of agroforestry systems often differ greatly in size and other morphological characteristics. The presence of such distinct canopy profiles means that the radiation environment in agroforestry areas may change substantially. Skylight conditions (diffuse or direct) above the trees have also been shown to influence the pattern and magnitude of the radiation changes in a particular environment (Healey & Rickert, 1998; Bell *et al.*, 2000). Besides that, different root systems between the agroforestry components sometimes promote competition for soil water uptake, particularly in semi-arid regions or during water deficit periods in sub-tropical and temperate areas. Water use by crops in agroforestry systems is complex and it is typically regulated by the quantity of soil water capture and the conversion efficiency (Ong *et al.*, 1996). Competition for light is the primary limitation for understorey plants when water and nutrients are freely available. However, in many situations water availability rather than light can become the major limiting factor in an agroforestry environment.

2.3.1- Radiation above trees

There are 3 features of solar radiation relevant to crop ecology (Monteith, 1969): (i) solar angle elevation, (ii) the spectral composition of the radiation and (iii) the relative intensity of diffuse and direct radiation. Solar angle elevations (β) are typically lower in temperate areas (high latitudes) than in tropical areas (low latitudes). New Zealand is located between latitudes 34° S and 47° S. For instance, at 43.5° S is Canterbury, New Zealand, where a maximum solar angle elevation of 69° is measured on 22 December and a minimum of 23° on 22 June both at about 1.00 PM (Building Research Bureau of New Zealand Inc., 1966). The mean total daily radiation (long term data) for these days are 22.3 MJ m^{-2} and 6.5 MJ m^{-2} on 22 December and June, respectively (Wallace, 1994). While total short wave radiation (400-3000 nm) is commonly measured in meteorological stations, it is the photosynthetically active radiation (PAR), from blue to red wave lengths or 400-700 nm approximately, that is actually used by plants for photosynthetic processes (Salisbury & Ross, 1991). In photosynthesis, it is the number of photons per unit of area per unit of time (PPFD) absorbed by plants rather than the total light energy that is important. Additionally, fractions of diffuse sky and direct solar radiation transmitted by a forest each day can be greatly affected by the present sky weather conditions (Saeki, 1973). According to Robinson (1966) working in a temperate area, the fraction of PAR in diffuse radiation decreases from about 80% with low sun angles ($\beta<10^{\circ}$) to 60% with high solar elevations ($\beta>60^{\circ}$) and increases in direct beam from 40% with $\beta<10^{\circ}$ to 48% when $\beta>30^{\circ}$. On cloudless days, diffuse radiation is predominant at sunrise and sunset, but on overcast days all radiation is diffuse and the intensity of radiant flux increases towards the zenith

2.3.2- Radiation below trees:

Trees are exposed to full skylight conditions, but when solar radiation passes through the tree canopy, understorey species experience changes in the radiation environment. At ground level, these modifications are strongly affected by solar angle elevation and relative intensity of diffuse and direct radiation (Monteith, 1969) and by tree canopy characteristics, such as foliage arrangement, orientation, size and shape (Ong *et al.*, 1996). Therefore, the physical radiation environment under the trees is the major factor influencing understorey production, provided adequate soil water and nutrients are available (Nair, 1993).

Radiation transmission:

There are 3 main changes in radiation environment below trees: (i) quantity, (ii) quality and (iii) periodicity. Light transmission through a canopy varies with the proportion of direct to diffuse light. Diffuse light penetrates better than direct light because it emanates from the whole hemisphere of the sky rather than from the point source of the sun (Wilson & Ludlow, 1991). Due to the greater penetration of diffuse light and the progressive absorption of direct radiation, the proportion of diffuse to direct radiation increases towards the bottom of the canopy (Ludlow, 1978). Therefore, light transmission and distribution under trees may change slightly with different sky conditions.

The amount of radiation intercepted by trees in an agroforestry system depends on the quantity of solar energy received, solar angle elevation, canopy characteristics (leaf area index, leaf angle and distribution), canopy duration and fractional interception of light (Monteith, 1981). Because of the extensive horizontal and vertical variation in canopy structures, there is great spatial variation in light transmissivity in agroforestry systems. The differences in canopy structure are due to distinct species combinations, planting dates, plant establishment arrangements, leaf size, shape and orientation and finally plant height (Ong *et al.*, 1996). Even in a particular agroforestry area, light transmission varies as trees develop. Yunusa *et al.* (1995a), in an agroforestry area with radiata pine (800 trees ha^{-1}) and several pasture understoreys in New Zealand, observed that the fraction of PAR intercepted by trees in winter increased from about 25% in year 2 to about 50% in year 3. In this same experimental area, Joshi (2000) reported that 200 trees ha^{-1} intercepted about 30% of the mean incoming PPFD after pruning in year 7. This same author also found that mean radiation interception in late spring was approximately 33% at 8.00 AM, but 45% at 12.00 PM.

Spectral composition:

In addition to the changes in radiation quantity, as sunlight passes through the tree canopy, spectral composition is altered because tree crowns preferentially absorb blue (480 nm) and red (660 nm) wavelengths over far-red (>700 nm) light (Holmes, 1981; Wilson & Ludlow, 1991; Sanderson *et al.*, 1997). In particular, the red to far-red ratio (R/FR) of incident light can be dramatically reduced under a closed canopy compared with values in full sunlight (Schmitt & Wulff, 1993). The R/FR is an important clue by which plants may detect changes in radiation environment and promote morphogenetic adjustments (Smith, 1982; Ballare *et al.*, 1995; Wong, 1991). There are few reports in the literature about changes in light spectral composition under tree canopies. For instance, Wilson & Ludlow (1991) reported that R/FR ratio measured in tropical full sun conditions was 1.20, whereas under an immature rubber plantation it was 1.07 and under mature rubber trees the ratio decreased to 0.62. These authors also cited R/FR values of 1.03 under old coconut and 0.43 under rainforest plantations. Devkota *et al.* (1998), working in an agroforestry area with alder trees and temperate grasses in the North Island of New Zealand, found that R/FR decreased from 1.24 under high pruned trees (77% PPFD transmission compared with full sunlight) to 0.96 under low pruned trees (17% transmissivity).

Both the shade source and shade density influence the changes in spectral composition. This is particularly important in agroforestry research, when artificial shade materials are used to simulate tree shade. According to Bell *et al.* (2000) the proportion of blue light and far-red relative to total short wave radiation increase, whereas the red light portion decreases under deciduous and coniferous tree shade compared with full sun. It was also interesting in this study that a decline was observed for red light, but not for far-red light, in the shade of a building compared with an open field. The increase of the blue portion was explained by the authors as a result of the diffusion property of blue light by atmospheric aerosols, which allowed this spectra to strike the earth's surface at any angle originating from the sky hemisphere and to penetrate any shade source. On the other hand, Bell *et al.* (2000) explained that red spectra was only from direct radiation (not from the diffuse portion) and it was mostly absorbed by tree canopy leaves or blocked by the building. In addition, the direct far-red light mostly penetrated the gaps within the tree canopies, but did not penetrate a building. This work was important to show that both shade source and shade density affects the proportion of red light, whereas far-red light is only influenced by shade source. These findings explain most of the changes in R/FR ratio reported in the literature in agroforestry areas and under artificial shade materials.

The most commonly used artificial shade material to simulate tree shade in agroforestry research is plastic shade cloth (Wong & Wilson, 1980; Samarakoon *et al.*, 1990; Devkota *et al.*, 1997). However, light quality has been reported to remain similar under shade cloths to full light conditions. This was shown initially by Gaskin (1965), who observed that green shade cloth did not change the proportion of blue wavelength as observed under tree shade at light transmissivity between 25 and 75% compared with full sun. Then, Yates (1989) showed that both tree canopies and green shade cloth enhanced the green region of the spectrum, but light transmitted through vegetation contained a much higher proportion in the near infra-red range than under shade cloth. Devkota *et al.* (1997) never found differences in R/FR between shade cloth with distinct light transmissivities of 43, 27, 18 and 14% compared with full light. Finally, Healey & Rickert (1998) investigated the radiation under a different shade structure made from a wooden lattice, besides shade cloth of different colours and under a *Leucaena leucocephala* canopy. These authors reported a dramatic increase in the proportion of diffuse radiation under white shade cloth, a wooden lattice structure and the leucaena canopy. In addition, Healey & Rickert (1998) concluded that shade cloth materials worked as an artificial filter of radiation compared with full sun, because it uniformly reduced light in the 300-1100 nm waveband. From these publications, it is concluded that mimicry of the radiation environment beneath a tree canopy may be possible quantitatively, but the filtering of radiation by a plant community is qualitatively different from that by most common artificial shade materials.

Radiation periodicity:

Direct light penetrates a discontinuous forest canopy by (i) passing through the gaps in the tree foliage and (ii) passing between individual trees (Reid & Ferguson, 1992). Beneath the discontinuous canopy of an agroforestry system, there are shadow patches originated when sun is located behind the tree crown and trunks. As sun angle elevation changes, the position of the tree shadow moves. Therefore, understorey plants in forest environments are typically submitted to a fluctuating sun and shade regime, which may vary from long periods of light to rapidly alternating periods of sun and shade (Rabinowitch, 1956; Pearcy, 1988; Yates *et al.*, 1988). In agroforestry systems, Wilson & Ludlow (1991) were one of the first to show the spatial variation of radiation under different trees canopies, but these authors did not address a discussion of its effects on understorey physiology and morphology.

This physical phenomena, observed in agroforestry areas, promotes an intermittent light regime distinct from that observed under artificial shade cloth. Periodicity of radiation is an important aspect of the radiation environment in agroforestry systems, but unfortunately its effect on understorey plant responses has rarely been investigated. Transmission and periodicity of light under forest canopies is largely dependent on tree crown variables, such as total green crown length and mean green crown length per area (Percival *et al.*, 1984), tree rows alignment and spacing. Reports from Rabinowitch (1956) in laboratory conditions to Pearcy (1990) in natural environments indicated that physiological plant responses under fluctuating light could be somewhat different from the continuous regime. In addition, most light interception models used for agrofrestry systems (Satterlund, 1983; Quesada *et al.*, 1989; Reid & Ferguson, 1992; Friday & Fownes, 2001) underestimate the intermittence effect of radiation underneath trees. The consequence is that predictions of understorey growth by mathematical models currently used for full sunlight conditions may not be appropriate to simulate canopy production in agroforestry systems.

2.3.3- Water relations under trees

Besides sharing the light resource, trees and understorey crops can compete for soil water extraction in agroforestry systems (Nair, 1993). This can be particularly important in dryland areas, such as those in the South Island of New Zealand where soil water deficits are frequent in summer and autumn seasons (Hoglund & White, 1985), and can limit the growth of one or both agroforestry vegetative components (Ong *et al.*, 1996).

Competition for soil water in agroforestry is dependent on the plants water requirements and root systems. The root systems of over and understorey species often differ in size and growth patterns. According to Noordwijk *et al.* (1996), the association between trees with deep fine root systems and crops/pastures with shallow root distribution is likely to be successful during short drought periods. This observation anticipates, for example, that most grasses would integrate better than lucerne with radiata pine trees for agroforestry purposes in non-irrigated areas. Lucerne has a deep root system, which has been reported to reach up to 2.4 m depth in unrestrictive soil under irrigation in New Zealand, whereas most of the other temperate pastures showed root depths between 0.3-0.8 m (Evans, 1978; McLaren & Cameron, 1990). Likewise, taproots of radiata pine trees can penetrate to 1.1m soil depth in soils of Canterbury, New Zealand (Balneaves & De La Mare, 1989; Gautum *et al.*, 1999).

Understorey lucerne has consistently been considered a competitor with radiata pine trees for soil water, especially during droughts and early in the agroforestry establishment, because of its deep root system and high water requirement (Yunusa *et al.*, 1995a; Mead & Chang, 2002). Despite this finding, lucerne had a water use efficiency (total DM biomass produced per unit of soil water used) of 41 kg mm^{-1} ha^{-1} in a 3 year-old agroforestry trial, compared with 24 kg mm^{-1} ha^{-1} for radiata pine trees (Yunusa *et al.*, 1995b). In this same study, lucerne was shown to decrease the storage of soil moisture in the 0.9 m profile more intensively than the ryegrass/clover understorey and bare ground treatment in summer. Cumulative evapotranspiration was also greater for lucerne than ryegrass/clover understorey. In the same work, it was reported that lucerne water competition decreased the tree crown volume by 46% compared with 24% for the grass/legume understorey relative to the bare ground treatment. This was likely to be due to faster root growth for the perennial legume than for the radiata pine trees at early stages. Nevertheless, lucerne soil water competition with trees appeared to decline as the pine root system developed in this trial. By tree age 10, Peri *et al.* (2002a) reported a decrease of 20% in tree diameter at breast height (DBH) with a lucerne understorey, 18% with cocksfoot/clover and 16% with ryegrass/clover compared with the bare ground treatment. Neither of these references reported the extra liveweight gain input promoted by this legume compared with the other understorey temperate pastures.

On the other hand, shade has been shown to indirectly improve the performance of understorey grasses in subtropical areas (Wilson & Wild, 1991). Working with 4 subtropical pastures under artificial shade cloth, Wilson (1996) observed that the proportion of water-stress days for plant growth were substantially reduced for irrigated and non-irrigated conditions. This author explained that the indirect effect of shade on slowing soil moisture loss is important to maintain microbial activity in litter and soil surface and the mineralisation of nitrogen. However, Wilson (1996) highlighted that an increase of yield in subtropical grasses may not always occur in agroforestry because of soil water competition between trees and understorey vegetation.

The general wisdom is that complementarity in root distribution is the key to success of simultaneous agroforestry systems (Noordwijk *et al.*, 1996). However, long-term data from the Lincoln University agroforestry trial (Yunusa *et al.*, 1995a; Yunusa *et al.*, 1995b; Mead & Chang, 2002; Peri *et al.*, 2002a) have indicated that soil water competition between trees and some understorey pastures can be critical at early stages during droughts, but it tends to decrease over time. In the long-term (10 years), understorey pastures with shallow root systems were not persistent or productive under the radiata pine trees. Thus, the long term output from trees, pasture and animals will actually determine the most advantageous agroforestry system for the temperate non-irrigated areas rather than concentration on one factor in isolation.

2.4- Lucernes important features for agroforestry

2.4.1- General description and use

Lucerne is an herbaceous perennial legume widely used as a forage crop. In the South Island of New Zealand, lucerne is typically used for hay and silage production or grazing in sheep and dairy farms (White *et al.*, 1999). In the summer non-irrigated areas of Canterbury, lucerne is used to provide forage of high yield and quality. This is because of its tap-rooted systems, which penetrates the soils and allows the plant to extract water from deeper layers than any other temperate pasture species (Douglas, 1986) and its ability to fix high amounts of nitrogen from air and convert these into plant protein (Barnes & Sheaffer, 1995).

Poor management has been one of the main constraints to successfully growing lucerne in New Zealand (Douglas, 1986). A practical guide to properly understand lucerne management and obtain high forage yield, quality and persistence was presented by Keoghan (1991). The growth pattern of lucerne requires that it is rotationally grazed rather than set-stocked. Plants require approximately 35 days between defoliations for root reserves to be replenished (White *et al.*, 1999). Otherwise, regrowth is decreased and disease and pest attacks are more stressful. A period of fully flowering in summer each year encourages a build-up of root reserves for the following growing season and improves persistence. Results for height of cut in lucerne have been conflicting in the literature, but for practical management it is unimportant as long as the crown is preserved or unless frequent cutting is conducted (Keoghan, 1967). Stem regrowth after defoliation occurs from a crown, located just below ground level, and new tissue grows from the apical tip of the shoots with a trifoliate leaf at each node (Langer, 1994). Growth of new basal shoots begins at an advanced stage of maturity or following defoliation. If the duration of grazing is too prolonged, then yield is decreased owing to damage to the crown shoots. Well-managed lucerne, in high fertility and well-drained soils, can result in more than 20 t DM ha^{-1} yr^{-1} in New Zealand areas (Kemp *et al.*, 1999) with a maximum yield of over 28 t DM ha^{-1} reported under irrigated condition in Canterbury (Brown *et al.*, 2000). In this same area of New Zealand, growth rates of irrigated lucerne vary from about 150 kg ha^{-1} d^{-1} in summer to 30 kg ha^{-1} d^{-1} in autumn and spring seasons (Douglas, 1986).

2.4.2- Light relations

DM yield usually declines under shade conditions, except for in some grasses when soil nitrogen is limiting (Wilson, 1996). Studying photosynthetic and morphological responses to shade can be used to explain most of plant adaptation strategies for growth under different irradiance levels (Givinish, 1988). The lucerne crop is considered an efficient solar energy converter into plant biomass in full sunlight conditions (Loomis & Connor, 1992). However, there is limited information in the literature concerning the ability of lucerne to acclimate at low radiation levels as experienced in agroforestry conditions.

Radiation use efficiency (RUE):

Lucerne has been reported to have high RUE in full sunlight conditions, similar to crops such as wheat, maize and sunflower (Loomis & Connor, 1992). This is because of its favourable canopy architecture, high photosynthetic efficiency and ability to fix nitrogen from air and convert it into plant protein. For instance, a lucerne crop was reported to have a RUE of approximately 2.8 g of total DM MJ PAR^{-1} (data adapted from Loomis & Connor, 1992). Likewise, Khaiti & Lemaire (1992) estimated a mean RUE of 2.4 g total DM MJ PAR^{-1} for 2 lucerne cultivars grown in summer field conditions. In their study, RUE for total DM (shoot +roots) was constant over seasons, however when estimated from shoot DM only, it was 1.8 g DM MJ PAR^{-1} in summer and decreased to 1.1 g DM MJ PAR^{-1} in autumn. This indicated that lucerne RUE based on total DM was insensitive to environmental (temperature and photoperiod) factors, but influenced by partitioning of assimilates between shoots and roots when based on harvestable biomass.

There are limited data in the literature about RUE of crops and pastures under low radiation levels. In general, RUE has been shown to increase under low levels of light in grasses compared with full sun condition (Sophanodora, 1989; Cruz, 1995). For lucerne, Loomis & Connor (1992) cited that RUE increased from 2.8 to 3.2 g total DM MJ PAR^{-1} when radiation was reduced from about 1800 μmol photons m^{-2} s^{-1} to 700 μmol photons m^{-2} s^{-1}. The reasons involved with increasing RUE under shade could be associated with more DM partitioned to shoot than roots, increase in leaf to stem ratios, increase of leaf nitrogen concentration and morphological changes that enhance light interception by canopy. Finally, Healey *et al.* (1998) observed that a decrease of incident radiation is usually followed by an increase in the proportion of diffuse radiation under artificial shade materials (solarweave and birdguard) and this would enhance light penetration within the canopy compared with full sunlight. Overall, the mechanisms involved with greater RUE under light stress conditions are still not well clarified.

This can become more complex when analysed for lucerne, because of shading effects on root reserves and nitrogen fixation.

Dry matter yield:

In full sunlight, lucerne has been proved to be a highly productive crop. Nevertheless, under shading conditions the DM biomass was shown to decrease. Pritchett & Nelson (1951) were one of the first to observe a non-proportional decline of lucerne total dry weight with reducing light. For example, these authors observed a decrease of 38% in total dry weight when lucerne was exposed to 73% light reduction compared with full light (~ 610 μmol photons $.m^{-2}$ s^{-1}) inside a glasshouse. More recently, Lin *et al.* (2001) also reported a decrease of 19% in above ground DM for lucerne growing under 50% shade cloth compared with full sun in glasshouse conditions, whereas plants under 80% shade declined shoot DM by 47%. According to Pritchett & Nelson (1951), shading depressed the weight of roots more than shoots as shown by declining root to shoot ratios. In contrast, Philippot *et al.* (1991) found that by decreasing the total daily amount of radiation (from 4.6 MJ PAR m^{-2} d^{-1} to 2.6 MJ PAR m^{-2} d^{-1}) received by lucerne plants in controlled conditions, no changes in biomass partitioning between shoots and roots were observed. The authors implied that leaf area expansion occurred independently of daily radiation, but shoot DM was strictly proportional to daily radiation. Indeed, the amount of radiation intercepted by the lucerne canopy has a major effect on plant photosynthesis, which then regulates the process of biomass accumulation.

Photosynthetic responses:

The carbon pathway characteristic of lucerne is typical of C_3 (reductive pentose phosphate cycle) plants. However, lucerne has an intermediate photosynthetic response between C_3 and C_4 species, which allows this crop to be photosynthetically more efficient than most C_3 crops at intermediate to high radiation intensities (Nelson & Moser, 1994). The net photosynthesis (Pn) rates of young lucerne leaves appear to saturate at approximately 1/3 to 1/2 of full sunlight radiation (Pearce & Lee, 1969; Wolf & Blaser, 1972, Macdowall, 1983, Brown & Radcliffe, 1986). However, Asseng & Hsiao (2000) more recently reported a maximum Pn canopy rate of

40 μmol CO_2 m^{-2} s^{-1} and no sign of light saturation up to 1700 μmol photons m^{-2} s^{-1} in full sun conditions in California. USA.

Studies of lucerne photosynthetic activity under shade reported in the literature were mostly performed in laboratory or greenhouse conditions. Overall, results have shown the non-linearity response of leaf photosynthesis with decreasing irradiance as observed for plant DM. For example, Pearce & Lee (1969) reported a decrease in top leaf Pn from about 24 μmol CO_2 m^{-2} s^{-1} under 860 μmol photons m^{-2} s^{-1} artificial light to 13 μmol CO_2 m^{-2} s^{-1} under 280 μmol photons m^{-2} s^{-1}, followed by similar reductions in specific leaf weight. This represented a decrease of approximately 46% in Pn rates compared with a decline of 67% in radiation flux. Likewise, Wolf & Blaser (1972) reported that the leaf photosynthetic saturation point decreased from 1500 μmol photons m^{-2} s^{-1} for a field grown lucerne crop in full sun to 1300 μmol photons m^{-2} s^{-1} (13% reduction) under 30% shade cloth regime and to 970 μmol photons m^{-2} s^{-1} (35% reduction) under 55% shade. A similar indication was shown by Walgenbach & Marten (1981), who found that field lucerne reduced total non-structural carbohydrates (TNC) of the upper 0.10-0.15 m canopy strata from 16% in full sun to 15% and 13% after being exposed to 20 days under 50% and 70% shade cloth, respectively. These authors suggested that a similar decrease would be found in roots TNC and thus explain the decrease in DM under shade observed in subsequent growth periods. The extent to which light influences growth of lucerne in the field depends on the level of radiation received, but it is the radiation distribution throughout the canopy that determines the final potential yield at a particular environment.

Canopy architecture:

The distribution of leaf area within a canopy and leaf orientation have been used by crop physiologists to explain the high photosynthetic activity and efficiency observed in lucerne compared with other crops grown in fully sun conditions. In these conditions, Woodward & Sheehy (1979) observed that a field grown lucerne canopy reached a leaf area index (LAI) of 6 after 56 days regrowth in late spring (bud stage) and that approximately 50% of this leaf area was concentrated in the top canopy strata between 0.5 and 0.6 m height. Critical LAI occurred between 0.3 and 0.4 m canopy height or approximately at LAI 4. The indication was that the canopy expanded leaf area in the most efficient position for the interception of PAR. Another important strategy of lucerne is to maintain top leaves at intermediate to vertical angle dispersals, reducing light saturation at the top canopy strata and allowing radiation to reach deep foliage layers (Heitchel *et al.*, 1988). Warren & Wilson (1965) observed that mean foliage angle dispersal of lucerne was 50° and varied little with depth in canopy. However, Keoghan (1970) showed for lucerne grown in chamber condition that plants had an increasing extinction coefficient (K) from top (K= 0.35) to bottom (K=1.72) canopy strata. The author reported a mean K of 0.77 for the second regrowth and a critical LAI of 3.9. Those results approximate to K estimations of about 0.61-0.77 reported by Wilfong *et al.* (1967) and 0.88 by Gosse *et al.* (1982) for field grown lucerne in full sun. A similar result was observed by Travis & Reed (1983) for field grown lucerne (LAI 4-5) at noontime, when leaflet angles were between 40 and 80°.

Changes in canopy architecture under shade were previously reported for other species such as for woody deciduous dicots (McMillen & McClendon, 1979) and for cocksfoot (Peri, 2002), but results for lucerne are unknown. According to Charles-Edwards (1981), there is an optimal canopy K for maximum canopy photosynthesis which changes with the incident light flux density: the lower the light, the more productive pasture will have planophile leaves. In fact, most of the changes in canopy architecture found under shade are likely to be an indirect effect of the plant morphological changes, such as stem density, leaf size and elongation, soil nutrient and water supply (Trenbath & Angus, 1975). Therefore, the morphological characteristics may become particularly important in low radiation environments where the efficiency of light capture is mandatory for maintaining the crop yield potential.

Morphological responses:

One of the first studies performed to investigate lucerne morphological changes in shade was undertaken by Cooper (1966), who observed that plant height was reduced by 10% under a 50% shade cloth regime compared with full sun. An increase of leaf area ratio (leaf area to plant DW ratio) with decreasing light intensities was observed. In contrast, Wolf & Blaser

(1972) found an increase in stem height and a decrease in stem weight for field grown lucerne exposed to 30 to 70% shade cloth compared with full sunlight condition. These results were consistent with Lin *et al.* (2001), who reported a significant decrease in the leaf to stem ratio and an increase in the internodal length of two lucerne cultivars under 50 and 80% shade cloth compared with those grown in full sunlight. In this same study, the authors never found changes in the proportions of leaf and stems for tropical legumes under shade. Despite some contradictions, lucerne appeared to respond as a typical sun-adapted plant when exposed to shade. That is, increasing plant height to have more access to incident light as has been observed in the dynamics of stem competition for light (Gosse *et al.*, 1988; Lemaire, 2001).

Partitioning of assimilates between shoots and roots:

Partitioning of assimilates between shoots and roots for lucerne is still a topic to be investigated and clarified by research. At the present, it is understood that nitrogen and carbohydrate reserves are mobilized from roots to shoots after defoliation until photosynthesis by the new leaf area canopy is sufficient to exceed the needs of new shoot and root growth and maintenance requirements (Mitchell & Denne, 1967; Keoghan, 1991). Typically, plants are about 15-20 cm (Keoghan, 1991) or LAI<2 (Woodward & Sheehy, 1979) or take between 7-14 days after defoliation (Pearce *et al.*, 1969), when root reserves reach their minimum levels and begin to increase again. Then, root reserves increase with increasing plant maturity until full flowering (Heitchel *et al.*, 1988). There is also a seasonal effect on the partitioning of assimilates between shoots and roots. For example, Khaiti & Lemaire (1992) estimated that a field grown lucerne mobilised about 22% of its assimilates from shoot parts to roots by the end of the first regrowth period in summer, but this increased to 55% partitioning for the subsequent rotation in autumn. These authors highlighted that accumulation of reserves in tap roots was a consequence of the reduction in stem elongation rate because of low temperatures and shorter photoperiod.

At present, there are no data published for lucerne partitioning rates under shade conditions. However, it is generally expected that plants under shade would be short of carbon production, thus they would tend to prioritise more shoot than root growth and transfer less photosynthates to roots compared with full sun plants (Loomis *et al.*, 1971). Under full sunlight, recovery of growth after defoliation may be more dependent on residual leaf area than on stored reserves, but under shade this situation may be reversed because other morphological responses to low light may result in little leaf area and few axillaries growing points remaining after grazing (Wilson & Ludlow, 1991). The complexity of this issue was reported by Luo (1991), using the ALFALFA 1.4 model (Denison & Loomis, 1989). This author observed an unexpected increase of fine-root to leaf ratios of simulations performed with 33 and 67% of full sunlight over a 40 day rotation in spring. The carbohydrate translocations between the tap-crown and fine root pools were complex and underestimated by this model under low light intensity.

2.4.3- Water relations

Periods of soil water deficits usually occur in summer and autumn in the non-irrigated areas of New Zealand. In agroforestry, shade and low soil water content effects on canopy yield are confounded. Therefore, caution should be taken when analysing experimental data during these drought periods in agroforestry. Because competition between lucerne and trees have been previously reported (Section 2.1.3.3), it is important to review some important water relations that can affect yield of this crop under trees.

Lucerne is considered an efficient water use crop in full sunlight conditions if the cost in assimilates associated with symbiosis and partitioning between roots and shoots are accounted for (Asseng & Hsiao, 2000). This is because morphological and physiological features allow lucerne to adapt to a wide range of soil moisture conditions. However, the magnitude of these changes is highly dependent on the level of soil water deficit, soil characteristics, management and cultivar. When a drying period begins with the soil at field capacity, water is extracted mainly from the upper soil layers where root density is greatest and the flow path is shortest. As the upper soil dries, the zone of active extraction moves down, although it continues from the upper layers as long as the potential in the root xylem is lower than that of the soil water (Sheaffer *et al.*, 1988). Lucerne has the ability to extract water from deep soil layers because of its deep root system. Lucerne was reported to reach between 180 and 240 mm depth in unrestrictive soils of Canterbury (Evans, 1978; McLaren & Cameron, 1990). For instance, Brown (1998) found that lucerne extracted water from at least 2.3 m soil depth in non-irrigated conditions and 1.9 m in irrigated conditions in Canterbury.

Among the morphological changes induced by water stress in lucerne, Hall (1993) observed, in both greenhouse and field conditions, that mean stem length of previously water-stressed plants (plant water potential < -1.5 MPa) reduced 12% and leaf area per stem increased only 8% compared with previously non-stressed plants. The authors never observed changes in the number of stems per square meter in the field or per plant in the greenhouse. Canopy architecture was also observed to change with water stressed plants. Moran *et al.* (1989) observed in a field lucerne stand that leaf zenith angle was more horizontally arranged (40°) in irrigated than non-irrigated (27°) plots over a late spring day. These authors also concluded that well-watered lucerne leaves tended to track the sun throughout the day in both azimuthal and zenithal directions, whereas stressed plants reduced the tracking ability and produced mostly a leaf cupping action.

Among the physiological responses induced by water stress, the depletion of stomatal conductance and leaf photosynthesis are the most frequent effects reported in the literature (Sanderson *et al.*, 1997). Antolin & Sanchez-Diaz (1993) showed a decrease of 33% and 77% in the leaf photosynthesis saturation point for lucerne seedlings under moderate (pre-dawn leaf water potential of –1.8 MPa) and severe (pre-dawn leaf water potential of –2.6 MPa) water stress, respectively, compared with well-watered conditions (pre-dawn leaf water potential of –1.3 MPa). The authors also observed a decline in stomatal conductance, electron transport and apparent quantum yield. However, after isolating the stomatal effect, these authors concluded that the decline of leaf photosynthesis in lucerne under the two temporal droughts was mainly affected by non-stomatal factors, such as the inhibition of carboxylase activity (RuBP). Although the decrease of stomatal conductance is a plant mechanism to reduce leaf transpiration and save plant water content, a well-established lucerne crop requires severe soil water deficits before canopy photosynthesis declines to minimal rates. For example, Brown

(1998) reported that lucerne DM yield decreased, relative to irrigated conditions, when soil moisture deficits reached about 215 mm for 2.3 m soil depth profile.

Below the maximum potential yield in well-watered conditions, lucerne DM yield decreases proportionally to the decrease in transpiration. Daily and seasonal ET are influenced by climatic factors, such as daily air temperature, advection and length of growing season. Sheaffer *et al.* (1988) summarized research for lucerne from diverse climates and reported that about 56 to 83 mm of water are required to produce 1 t DM ha^{-1}. In Canterbury, irrigated lucerne required about 36 mm of water to produce 1 t DM ha^{-1} in full sunlight (McKenzie *et al.*, 1990). In contrast, for a 3 year-old agroforestry area in Canterbury, Yunusa *et al.* (1995a) reported that evapotranspiration of lucerne under radiata pine trees ranged between 2.3-3.8 mm d^{-1} in summer.

Finally, the presence of intercropped trees can change lucerne water relations. Firstly, because the tree root system is likely to compete with that of lucerne (and vice-versa) during drought periods, and second because the presence of trees can change the micro-climatic environment for plants nearby trees. How a lucerne crop responds when exposed to both low radiation and low soil moisture content simultaneously is unknown and forms one of the objectives of the present study.

2.5- Crop yield modelling in agroforestry

The complex relations between the over and understorey species make yield predictions a challenge in agroforestry systems. Although water relations may change dynamically in agroforestry areas over years as both trees and understorey crops grow, current crop yield models would easily simulate these modifications by assessing the plant water status. Indeed, light relations are the most complex factor to be considered in crop yield modelling under trees. Having an accurate model to predict understorey crop yield in shaded environments, would assist researchers and farmers to plan the most adequate arrangement and combination of trees and pastures.

2.5.1- Current models in agroforestry and constraints

In agricultural ecosystems, production models have been developed for most of the major exchange processes between the plant community and the environment. These models are not only valuable research tools, but they can also become powerful tools to improve the management of crop production systems when integrated into sophisticated crop simulation models. Scientists have been remarkably successful in predicting plant behaviour at the molecular, physiological and agronomic levels by creating models in full sunlight conditions. However, they are still trying to accurately simulate understorey production in the complex agroforestry environment.

Many models were developed to predict the amount of radiation below trees based on site, trees and stand variables (Satterlund, 1983; Quesada *et al.*, 1989; Reid & Ferguson, 1992). These models are useful tools to assist with forestry practices (e.g. tree thinning and pruning) in agroforestry areas, but they are usually not linked with predictions of understorey crop yield. In New Zealand, Knowles *et al.* (1999) developed a simple linear function to predict pasture yield under trees based on the overstorey canopy closure. This function was developed with data from ryegrass (*Lolium perenne*), yorkshire fog (*Holcus lanatus*) and browntop (*Agrostis capillaris*) with white clover (*Trifolium repens*) pasture grown under radiata pine (Percival & Knowles, 1988). However, this model only predicts pasture yield under trees relative to an open pasture, and it appears to predict seasonal pasture growth conservatively. In addition, it seems necessary to estimate other coefficients for different pasture species or combinations and to exercisecaution in extrapolating to different growth environment conditions.

Wilson & Ludlow (1991) suggested a simple model to simulate pasture growth under trees based on the radiation use efficiency and average amount of photon irradiance intercepted daily.

In fact, this model originated from previous physiological models, which included a partitioning coefficient between shoots and roots, photosynthetic efficiency, radiation interception and loss of biomass as variables (Charles-Edwards, 1982). The authors minimized the importance of the partitioning coefficient for tropical grasses, because of their physiological characteristics. A seasonal variation in partitioning of assimilates between roots and shoots would modify RUE of above ground biomass as discussed in Section 2.1.4.2. Nevertheless, this seems inappropriate for species with large root reserves, such as lucerne, after defoliation (Avice *et al.*, 1997). Another concern was discussed by Healey *et al.* (1998), who observed that RUE usually increases with the proportion of diffuse conditions and this effect should be taken into account to avoid underestimation of predicted yield under trees. Additionally, Cruz (1995) showed a critical point for using estimates of RUE in shaded environments. The author observed that for those species that partition carbon in favour of shoot growth, RUE would be mostly overestimated. To eliminate the effect of carbon partitioning on plants under shade, it would be necessary to estimate RUE based on total herbage biomass (Khaiti & Lemaire, 1992). So far, studies concerning canopy RUE under shade using this methodology are unknown. Finally, the model presented by Wilson & Ludlow (1991) neglected the intermittency effect of radiation in agroforestry areas when accounting for daily intercepted PAR from understorey plants. The model developed originally by Charles-Edwards (1982) used relationships observed in a steady-state light regime. This would be perhaps appropriate for predicting understorey growth under shade cloth materials, for example, but might not be under trees where fluctuations of sun/shade are frequently observed. The hypothesis of a greater photosynthetic efficiency under intermittent light compared with continuous regime was firstly discussed by Rabinowitch (1956). In conclusion, it seems adequate to avoid models with variables of such complexity, such as RUE, whose crop responses are not completely clarified by research. To improve that, it is necessary to firstly return to classical canopy photosynthesis models successfully used in full sun crops and make the necessary adjustments to accurately simulate the fluctuations of radiation observed under trees.

2.5.2- Successful models in full sunlight and potential use in agroforestry

Many scientists have used the canopy photosynthesis model integration to predict crop yield. For example, de Wit *et al.* (1970) with the Elementary Crop Growth Simulator (ELCROS) in corn provided one of the first applications of those sub-models integrated with others. Afterwards, Brennan *et al.* (1970) also applied the same concepts to a dynamic model for sugar beet. More recently Weir *et al.* (1984) used those sub-models to create part of a whole-crop model (ARCWHEAT). The basic approach of the sub-models is used for full sunlight crops in a number of environmental conditions. However, there are some plant physiological situations that may require adjustments. One example was given by Thornley & Johnson (2000) when leaves in the upper region of a canopy are suffering from some degree of water stress owing to high radiation levels, whereas the leaves lower down may be relatively unstressed. In this situation, leaves within the canopy may have quite different photosynthetic responses. Another example comes from shaded environments where leaves may show different morphological and biochemical responses within the same canopy, depending on the intensity and periodicity of illumination.

To derive the net canopy photosynthesis, scientists have developed three basic sub-models: (i) radiation interception, (ii) light utilisation in gross photosynthesis and (iii) partitioning of photosynthates to respiration. These sub-models when integrated are considered essential parts of a number of canopy growth models (Thornley, 1976; Marshal & Biscoe, 1980; Weir *et al.*, 1984).

Radiation interception by the community:

The actual flux of light received by each individual leaf within the canopy must be known to estimate photosynthesis (Loomis & Williams, 1969). Foliage angle affects the relative illumination of a fully exposed leaf and the projected shadow area of the leaf and thus the flux of light available to lower leaves. Besides, the morphological organization of individual leaves in the foliage canopy is critical, since the interception of light is a function of leaf area (Loomis *et al.*, 1971). So, it is evident that simply averaging the light flux densities over a stratum overestimates the rate of total photosynthesis, since the photosynthetic rate of single leaves is a curvilinear function of the light flux density (Saeki, 1973). The key problem is to relate the distribution of direct and diffuse radiation to the morphology within the plant community. In this way, the light environment of each photosynthetic organ can be characterized. These considerations led to the development of mathematical models to predict light distribution within canopies.

i) Canopy architecture:

The vertical distribution of LAI in each of a series of horizontal strata was first described by Monsi & Saeki (1953) and Monsi (1968). It was found that light attenuation at any depth can be related to interposed LAI by the Bourguer-Lambert law:

$I = Io \exp(-K*LAI)$ (Equation 2.1)

Where I and Io are light fluxes to horizontal receivers at points within and above the canopy and K is the extinction coefficient. K varies with cloudiness and strongly with solar angle (Loomis *et al.*, 1971). Important differences occur among species in terms of K values and these are closely related to the structure of the canopy, particularly to foliage angle (Hay & Walker. 1989).

ii) Light distributions:

Monsi & Saeki (1953) developed the mathematical model (Equation 2.1) for homogeneously arranged leaves and uniform foliage angle, where the K was a variable computed from geometrical considerations of leaf angle (ϕ), solar elevation angle (β) and LAI. Warren Wilson (1960) developed a geometrical theory based on the probability of a point quadrat contacting leaves of a given angle. The assumption was that with increasing angle between foliage and horizontal, the area projected vertically became progressively smaller and was minimal when the foliage was vertical. These authors suggested a method of calculation that revealed mean values of (i) the angle between the foliage and the horizontal and (ii) the denseness of the foliage. This method was useful, since no accurate method of studying the vertical distribution of a foliage area *in situ* had been developed.

Saeki (1963) and Anderson (1966) showed the correspondence between Equation 2.1 and the Warren Wilson (1960) theory. The point quadrat probabilities could be taken to represent the average shadow area (F') cast in the direction β of a large number of leaves of area F. Equation 2.1 was then derived by Duncan *et al.* (1967) to estimate the probability of penetration of rays of direct visible light as follows:

$I(z) = I_0 \exp(-LAI*[F'/F]_{\phi,\beta} / \sin\beta) = I_0 \exp(-LAI*K)$ (Equation 2.2)

Where I, Io [W $(m^2 \text{ ground})^{-1}$] and LAI are defined as above, [F'/F] is the ratio between the area of a leaf and the shadow it casts for a particular leaf angle ϕ and elevation of the sun β. This form of the Bouguer-Lambert law gives the area of direct light from a point source penetrating each foliage layer.

$[F'/F]_{\phi,\beta} = \cos\alpha * \sin\beta$ **if** $\phi \leq \beta$ or

$[F'/F]_{\phi,\beta} = \sin\beta * \cos\alpha * [1+2/\pi (\tan\theta_0 - \theta_0)]$ **if** $\phi > \beta$

where $\theta_0 = \text{acos}(\cot\phi * \tan\beta)$, expressed in radians, is the angle whose cos= $\cot\phi * \tan\beta$.

To compute the area of sunlit leaves (A) within each layer, the flux of sunlight entering each layer (Iz at the top of the layer) is subtracted from the flux of radiation leaving (Iz at the bottom of the layer). Equation 2.2 can also be used to calculate the penetration of diffuse sky light. The difference between the total LAI per layer and the area in direct sunlight (A), gives the area of leaves illuminated only by diffuse light (Duncan *et al.*, 1967). The flux of diffuse skylight can also be computed in the same manner as for direct light by adding the light received from zones of the sky, each considered as a point source (Duncan *et al.*, 1967).

Equation 2.2 is an essential step to predict canopy photosynthesis as it simulates the distribution of direct and diffuse radiation within the foliage canopy. Validating measurements in real plant communities confirmed the marked influence of canopy architecture on the absorption profile (Warren Wilson, 1967; Anderson, 1966).

Gross photosynthesis in a single leaf:

The response of gross photosynthetic rate (Pg) to irradiance has often been described as a rectangular hyperbola curve (Blackman, 1905; Rabinowitch, 1956). The rectangular hyperbola of the photosynthetic light response curve provided a good fit to data obtained under controlled environments. However, Thornley (1976) and Marshall & Biscoe (1980) showed that plants growing in the field could produce a somewhat different photosynthetic light response curve. This derived a model to combine a simplified description of the biochemical reactions occurring within the chloroplast with the physical diffusion of CO_2 from the atmosphere and other parameters. This basic model has been widely used by many scientists to develop dynamic models of plant growth (Weir *et al.*, 1984; Thornley & Johnson, 2000). The equation is described as follows:

$$Pg = \frac{[Pmax + \alpha I(z)] - ([Pmax + \alpha I(z)]^2 - 4\theta\alpha I(z)Pmax])^{1/2}}{2\theta} \qquad \text{(Equation 2.3)}$$

[mg CO_2 m^{-2}ground s^{-1}]

Where Pmax is the photosynthetic rate at saturating point, α is the photosynthetic efficiency, Iz is obtained from Equation 2.2 and θ is the ratio of physical (includes boundary layer, mesophyll and stomatal resistances) to total resistance to CO_2.

Total resistance is considered to be the sum of physical and biochemical (carboxylation) resistance to CO_2 transfer. When θ is zero, implying that the biochemical resistance is much greater than physical resistances, Equation 2.3 reduces to a rectangular hyperbola. By contrast, when θ is unity, physical resistances are dominant and Equation 2.3 reduces to a non-rectangular asymptotic curve (Marshall & Biscoe, 1980). Ludlow & Wilson (1971) reported θ values about 0.98 and 0.81 for Siratro (*Phaseolus atropurpureus*) and Green-Panic (*Panicum* *maximum*), respectively, in 100% growth irradiance conditions. More recently, Peri (2002) reported that θ in cocksfoot leaves was unaffected by a range of temperature, leaf nitrogen, regrowth duration and shade and had a mean value of 0.96. Other experimental evidence indicates that θ is largely independent of temperature (Thornley & Johnson, 2000).

The photosynthetic efficiency (α) can be calculated as the slope of the linear part of the photosynthetic light curve and it has been shown to vary little with percentage of growth irradiance (Thornley & Johnson, 2000). However, Norman & Arkebauer (1991) found differences in α values between crops. The authors cited a mean daily α of 0.007 mg CO_2 J^{-1} PAR (photosynthetic active radiation, 400-700 nm) intercepted on corn whereas Ludlow and Wilson (1971) reported α values about 0.009 and 0.02 mg CO_2 J^{-1} PAR for Siratro (*Phaseolus atropurpureus*) and Green-Panic (*Panicum maximum*), respectively. Ehrlinger & Björkman (1977) stated that α was independent of temperature for C_4 plants, whereas for C_3 plants over the range between 14 and 24° C, α decreased by about 14 %.

Thornley & Johnson (2000) stated that α and θ are much less affected by growth irradiance than Pmax. The authors suggested that once the leaves saturate at intermediate to low levels of irradiances, the fitted values for α and θ are less reliable. Therefore, it is reasonable to assume that the only significant effect of the growth irradiance is on Pmax, and that α and θ are constants throughout the depth of the canopy. Johnson & Thornley (1984), supporting Acock *et al.* (1978) results, suggested a definition for Pmax appropriate to those leaves at the top of the canopy, while recognizing that Pmax does vary within the canopy. The basis for this assumption was that leaves developed under low irradiance have virtually the same rate of photosynthesis at that irradiance as do leaves developed at a much higher light level, indicating that leaves grown under shade maintain sufficient photosynthetic machinery to function efficiently in their growth environment. A more realistic expression for the relationship between maximum photosynthesis rate and the growth irradiance was suggested by Thornley & Johnson (2000):

$$Pmax' = Pm^{o} * [1-\lambda/2 * (1-Iz/Io)] \qquad [mg\ CO_2\ m^{-2}\ leaf\ s^{-1}] \qquad (Equation\ 2.4)$$

where Pm^o is the asymptotic value of photosynthesis at saturating irradiance and λ is a constant set as 0.70. Iz and Io were defined previously in Equations 2.1 and 2.2.

The main limitation of Equation 2.4 is that other natural environmental factors are not considered to affect maximum leaf photosynthetic rate. Peri (2002) pointed out that the light flux, leaf temperature, soil moisture content and leaf nitrogen level may directly affect the Pmax values for temperate grasses. In his calculation, Pmax showed a maximum value of 1 mg $CO_2.m^{-2}.s^{-1}$ when light intensity was highest at noon time. Thornley & Johnson (2000) also stated that plant water status would affect stomatal resistance and possible biochemical resistance throughout enzymatic activities. Therefore, the same authors suggested a complementary calculation for Pmax as described in Equation 2.4:

$$Pm= Pmax' * [1-c *(1-PLWC)] \quad [mg\ CO_2\ m^{-2}\ leaf\ s^{-1}] \quad \text{(Equation 2.5)}$$

Where c is a dimensionless constant which reduces Pmax below its maximum value of Pm (Equation 2.4) as plant water content (PLWC) falls below unity. When the plant is free from water stress, WC approaches to unity and vice-versa.

Additionally, Johnson & Thornley (1984) observed that Pmax depends strongly on temperature. In experiments on leaves of white clover and perennial ryegrass, Woledge & Dennis (1982) also found considerable variation with temperature in the rate of photosynthesis at saturating irradiance. These authors observed increases from $0.4x10^{-6}$ to $1.2x10^{-6}$ kg CO_2 m^{-2} s^{-1} as the temperature was increased from 5 to 25°C. Johnson & Thornley (1984) assign a simple linear relationship, which was different from that published by Woledge & Dennis (1982), to explain Pmax variation with air temperature:

$$Pmax= Pm (Tr) * (T-T'/Tr-T') \quad \text{(Equation 2.6)}$$

Where Tr is some reference temperature and T' is the temperature at which photosynthetic activity ceases.

Total respiration in a single leaf:

It is well accepted that the plant respiration process is closely coupled to adenosine di-phosphate (ADP) supply and hence to biochemical activity (Beevers, 1961). Assuming that, Loomis *et al.* (1971) suggested, at least for the bulk of the respiration of a plant, two main components: (i) respiration associated with growth and (ii) respiration associated with maintenance activities. Growth respiration should be correlated with the amount and type of new materials formed in plant growth and maintenance respiration with the living biomass, its degree of differentiation and function.

Pirt (1965) first demonstrated that the respiration rate of some bacterial populations could be separated into two main components: one proportional to the growth rate and the second proportional to the dry mass. The same author derived a simple regression of the respiration rate on the growth rate and dry weight and obtained two constants (a and b), which were interpreted as being related to the underlying processes of growth and maintenance.

Afterwards, McCree (1970) showed that Pirt's relationship was also valid in the real vegetative world. In his work, McCree (1970) found the dependence of respiration rate on the gross photosynthetic activity, dry weight and time in white clover plants under a controlled environment. The author suggested the following equation to describe total respiration rate (R):

$$R = a*P + b*W \qquad \text{(Equation 2.7)}$$

Where a and b are constants, P is the gross photosynthesis during the light period and W is the plant dry weight in CO_2 equivalent units. For white clover, McCree (1970) found a=0.25 and b= 0.015 day^{-1}. The theoretical ideas behind Equation 2.7 are: (i) there is a loss in material when converting the immediate products of photosynthesis into plant material and (ii) some basal metabolism is required to maintain the current status of the plant. It was found that the coefficient *a* varies considerably with the type of plant tissue and that the coefficient *b* is also variable, depending on tissue organ and plant age (Thornley & Johson, 2000). Additionally, McCree (1970) concluded that over periods of more than one day, P, R and W were very dependent on the rates of death and regrowth of the various organs of the plants and those factors were often neglected in computer simulations. This means that models had failed when calculating respiration proportional to LAI and leaving out the rate of change of living material. In plant communities a large proportion of the synthesized material goes into leaf production. Thus the green leaf area continues to increase until the rate of death of old leaves equals the rate of production of new ones. This point is considered the optimum LAI (McCree & Troughton, 1966). After this point, it is reasonable to expect a slight decrease in canopy net photosynthesis as senescence develops.

Therefore, the final equation to calculate total respiration rate can be expressed as follows:

$$R = a \sum_{h=0}^{h=H} Pg_{(5min)} + b\,W\,2^{\,0.05(Tmax+Tmin)} \qquad \text{(Equation 2.8)}$$

$[mg\ CO_2\ m^{-2} ground\ s^{-1}]$

Where *a* is the growth respiration coefficient, H the number of daylight hours, *b* the maintenance respiration coefficient, Tmax and Tmin the daily maximum and minimum temperatures respectively, and W the crop weight expressed as grams of CO_2 equivalent. McCree (1974) defined each gram of crop dry weight to be equivalent to 1.43 g of CO_2. According to this Equation, growth respiration is a fixed fraction of gross photosynthesis, so it changes only with variables affecting photosynthesis rate. Maintenance respiration is dependent on the maintenance coefficient (*b*), daily mean temperatures and crop weight. By fixing all crop and micrometeorological variables, total respiration rate (R) would only vary with the growth and maintenance coefficients. Thornley & Johnson (2000) stated that many of the approaches to respiration can be regarded as attempts to gain some understanding of the *a* and *b* coefficients of McCree's equation. According to Hay & Walker (1989), most young plants use daily 25-35% of their assimilate to support growth (*a*= 0.25-0.35) and 1.5-3.0% of their dry weight (CO_2 equivalents) for maintenance processes (*b*= 1.75-3.47 x 10^{-7} s^{-1}). The same authors pointed out *a* and *b* coefficients of 0.34 and 0.012 day^{-1} for barley, respectively. In lucerne, Heichel *et al.* (1988), reviewing the literature, found that photorespiration can consume between 10 and 60% of net photosynthesis rate.

Net canopy photosynthesis:

Net canopy photosynthesis can be simulated with the integration of the three basic sub-models described above: (i) canopy light interception, (ii) canopy gross photosynthesis rate and (iii) canopy total respiration rate. The rate of gross photosynthesis is calculated for each layer of the canopy and for each daylight hour by solving Equation 2.3 and using appropriate values of Iz from Equation 2.2. This gives gross photosynthesis in units of g CO_2 m^{-2} leaf s^{-1}. From this is obtained the hourly value, which is multiplied by the leaf area index of the layer. The values of each layer are then summed to give the hourly canopy gross photosynthesis, which can be converted to carbohydrate equivalents by multiplying by 0.65. Daily total respiration is a function of daily canopy gross photosynthesis and can also be converted to a carbohydrate base. Finally, daily canopy net photosynthesis rate is calculated as the difference between daily gross production and total respiration.

2.1.5.3- Potential use of the canopy net photosynthesis model in agroforestry:

The reasons for fluctuating light in natural communities include changes in solar position, movements of clouds across the sun and movement of leaves. Additionally, in multiple agricultural systems, individual components may often have different height profiles and this would promote an alternating sun/shade regime for the understory vegetation. Physiological responses under an intermittent light regime are sometimes expected to be different from those in continuous radiation (Rabinowitch, 1956; Barden, 1977, Sager *et al.*, 1980). Useful integrated models should be able to simulate all possible environments that occur in agricultural ecosystems. In this study, it is necessary to review the canopy agronomic and physiological responses under two main light regimes: (i) continuous radiation and (ii) intermittent illumination.

A considerable part of the classic work published by Rabinowitch (1956) reviewed the photosynthesis and related processes in intermittent light. Firstly, the author stated that intermittent light could be classified in the ways: (i) *alternating light* which was defined as an intermittent regime with equal periods of sun and shade and (ii) *flashing light* in which the period of light is much shorter than the period of shade. Rabinowitch (1956) pointed out that the true momentary light intensity during the flashes seemed to become unimportant. In agroforestry, both situations can occur depending on tree canopy closure, but usually flashing light is more characteristic of understorey environment in commercial or native forests (Yates *et al.*, 1988).

Rabinowitch (1956) hypothesis was that photosynthesis production could be expected to be larger in alternating light compared with continuous illumination if the periods of shade and sun are very long or very short. Long intervals of the order of several hours can improve the utilization of light energy because during the shade "rest period" the plant can recuperate from the injury or exhaustion that often follows a period of intense photosynthesis. Very short periods (< 1 second) may also cause an improvement of the energy conversion yield, because it allows the dark catalytic reactions of photosynthesis to run to completion, restoring the photosynthetic apparatus to its full efficiency at the beginning of each new light period. Conversely, in the intermediate range of frequencies (> 1 minute and < 1 hour) alternating light can be expected to cause a depression of the photosynthesis production because shade intervals of this length permit the development of induction phenomena, which occupy most of the subsequent light periods. Additionally, Rabinowitch (1956) suggested that the inertia of the stomata (both the opening of stomata in light and their closure in the shade are not instantaneous) could be only a contributing cause of the inhibition of plant growth by alternating light with an intermediate frequency. The main cause was said to be induction, which is almost fully developed after 1 minute of shade and permits little photosynthesis in the first minute of subsequent illumination.

Therefore, the question that arises is: are plants under trees using radiation more efficiently than plants in a continuous shade of equivalent light transmission? If the answer is positive, then the use of artificial shade cloth materials (Section 2.1.3.2) to simulate the agroforestry radiation environment will be underestimating potential growth under trees. If the answer is negative, then what are the main effects of light intermittency on plants that would reduce growth compared with a continuous shade regime? Although there is evidence that photosynthetic efficiency between continuous and intermittent light is different, much of the research on shade effects has focused on artificial environments (glasshouse or growth chamber). Further studies with crops under agroforestry light regimes, or at least under intermittent light close to that observed in agroforestry, are necessary. In addition, studies about light interception within the plant community may be of particular interest in limited radiation conditions as a canopy normally adjusts its plant architecture to optimise light interception. Most of the studies of canopy photosynthetic efficiency in continuous and intermittent light reported previously were performed with horizontally orientated leaves. The net photosynthesis model may be a useful tool to investigate plant physiological responses and strategies to tolerate shade. To do that, environmental functions in shade must be provided as input data. Nevertheless, it is unusual to find in the literature the use of models to simulate canopy photosynthesis in shaded environments and under different light regimes. The complexity of plant responses under shade may bring an extra challenge for scientific investigation in this area, particularly in agroforestry where there is a number of 'scenarios', involving light intensity, spectral composition and radiation periodicity, to which understorey plants are exposed.

In the next chapter, an alternative artificial shading material to the commonly used shade cloth is created for agrofrorestry research. Both methodologies are tested and compared in a field experiment for their radiation physical environments and crop responses under irrigated and non-irrigated conditions.

CHAPTER 3

Lucerne responses under different artificial shade and soil moisture conditions

3.1- Introduction

In agroforestry research, artificial shading is an important tool used to simulate tree shade on understorey vegetation. The light environment in an agroforestry area changes slowly as tree crown develops (Section 2.1.3.2). For example, in a New Zealand agroforestry area (Knowles *et al.*, 1999) radiata pine trees were dominant over underneath pasture species after 20 years. This makes research on understorey species difficult to undertake. Artificial shade structures provide a practical way to examine morphological and physiological changes in plants and to screen for shade tolerant species for agroforestry systems.

In temperate areas, such as the East Coast of New Zealand, agroforestry systems may experience periods of full water supply, after soil moisture recharge in winter, followed by temporal drought in summer. In these conditions, it is necessary to isolate the effects of light and soil water content when using artificial shade materials to study plant responses for agroforestry purposes. Correspondingly, the interaction effects between variable soil water conditions and low light in plants are of interest in many agroforestry systems.

Plastic cloth is the most common artificial shade material used in agroforestry research and it is abundant in the market in several colours. The cloth produces a continuous pattern of radiation over the day, but does not change spectral composition. However, understorey plants in agroforestry areas are usually submitted to fluctuating light regimes and changes in radiation spectral composition (Section 2.1.3.2). Therefore, shade cloth may not by the best methodology to resemble the radiation environment of an agroforestry area. Modifications in the pattern of light intensity, quality and regime may be particularly important when plant morphology and production are concerned (Yates *et al.*, 1988; Buxton & Fales, 1994).

The experiment described in this chapter was a 'pilot project' used to examine the effects of two artificial shade regimes on lucerne growth and development in irrigated and non-irrigated conditions. In addition to cloth, a slatted structure was built to mimic the intermittent light regime observed in an agroforestry trial near to this experimental area. Thus, the aims of this study were: (i) to create artificial regimes of continuous and intermittent light and (ii) to determine if the crop responses of lucerne to both shade regimes were different and how they changed from those in an full sun in irrigated and non-irrigated conditions. If there were no differences in the crop response to the different shade patterns, then either shade structures could be used as an experimental methodology to mimic the agroforestry system.

3.2- Materials and methods

3.2.1- Site description

The experiment was located at the Lincoln University Field Service Centre (FSC), Canterbury, New Zealand (43°39'S and 172°28'E) The soil was a Wakanui deep silt loam (Eutrochrept) with 180-350 mm silt loam top soil overlaying variable textural layers, ranging from a clay loam to a sandy loam. In this soil, there is typically 2 m of fine material overlying gravel and stones (Watt & Burgham, 1992). The total water holding capacity for this experimental site ranges from 613 to 801 mm over 2.3 m soil depth (Brown, 1998; Inch 1998). Irrigation requires careful monitoring to prevent water build-up and should be applied on a high frequency/short duration basis (Watt & Burgham, 1992).

The climate is characterised by an annual rainfall of about 670 mm, which is slightly higher in winter than other seasons (Table 3.01). The annual mean temperature is 11.4 °C varying from a monthly average of 6.0° C in July to 17.4° C in January. The meteorological data used for this experiment were measured at the Broadfields Meteorological Station (Crop & Food Research Ltd., New Zealand), which is located 1 km north of the Lincoln University campus.

Table 3.01- Actual (1998-1999) and long term monthly means (*LTM* from 1960 to 2001) for total global short wave solar radiation (SR), maximum (Tmax), minimum (Tmin) and mean (Tmean) air temperatures, total rainfall (R), Penmann evapotranspiration (ET) and sum of thermal time (TT) and measured in an full sun at the Broadfields Meteorological Station (Crop & Food Research Ltd., Lincoln, New Zealand), which is located 1 km north of the experimental site.

Month	SR	*LTM*	Tmax	*LTM*	Tmin	*LTM*	Tmean	*LTM*	R	*LTM*	ET	*LTM*	TT*	*LTM*
	--MJ m^{-2} d^{-1}--		--------------------------°C--------------------------						------mm-----		-----mm d^{-1}----		----°C days----	
Dec' 98	23.9	*23.3*	21.2	*21.2*	10.4	*10.1*	15.5	*15.6*	24.1	*52.6*	4.8	*4.7*	461.4	*442.1*
Jan' 99	22.3	*23.0*	22.1	*23.2*	13.3	*11.8*	17	*17.4*	36.2	*56.8*	4.2	*5.0*	512.1	*540.3*
Feb' 99	22.3	*20.2*	22.2	*23.4*	12.4	*11.9*	17.1	*17.6*	38.3	*46.1*	4.8	*4.4*	467.6	*435.0*
Mar' 99	15.4	*14.4*	21.6	*20.5*	12.2	*10.0*	16.5	*15.2*	56.1	*56.8*	3.5	*3.1*	498.5	*416.8*
Apr' 99	9.8	*9.8*	16.5	*17.7*	8.1	*6.9*	11.9	*12.2*	36.3	*54.8*	2.0	*2.1*	343.0	*325.6*
May' 99	6.9	*6.0*	16.8	*14.3*	5.2	*4.1*	11.2	*9.2*	23.6	*54.9*	1.8	*1.4*	334.5	*234.1*
Jun' 99	5.4	*4.6*	12.1	*11.5*	1.8	*1.6*	6.6	*6.5*	69.1	*62.6*	1.0	*1.1*	183.8	*189.7*
Jul' 99	4.8	*5.2*	10.5	*10.9*	2.4	*1.4*	6.7	*6.1*	135.1	*67.1*	0.9	*1.1*	200.6	*183.7*
Aug' 99	8.5	*7.9*	12.0	*12.3*	2.4	*2.5*	6.9	*7.3*	58.0	*63.7*	1.4	*1.6*	210.1	*211.2*
Sep' 99	13.9	*12.2*	14.8	*14.6*	4.4	*4.3*	9.4	*9.4*	26.6	*42.2*	2.5	*2.3*	274.9	*250.3*
Oct' 99	16.8	*17.4*	17.3	*17.3*	8.1	*6.3*	12.2	*11.7*	50.9	*47.9*	3.1	*3.4*	365.0	*326.8*
Nov' 99	20.6	*21.4*	17.3	*19.0*	9.0	*7.9*	12.9	*13.4*	60.5	*53.9*	3.4	*4.2*	367.4	*386.3*

* Sum of thermal time was calculated above a base temperature (Tb) =0 °C.

3.2.2- Site history

The experiment was contained within a 1.5 hectare paddock that had 'Kaituna' lucerne as one of the three pasture species in a split-plot experiment previously established on 1st November 1996. One month prior to sowing, lime was applied at 4 t ha^{-1}, sulphate of potassium at 150 kg ha^{-1} and super phosphate at 250 kg ha^{-1}. The area was sprayed with Triflur 40 (400 g l^{-1} Trifluralin) at a commercial rate of 2 l ha^{-1} diluted in 200 l ha^{-1} of water. Lucerne was sown at a rate of 7 kg ha^{-1} and plant populations of 200-250 plants m^{-2} had established by 28 October 1997 (Brown *et al.*, 2000).

3.2.3- Treatments and experimental design

The current experiment only used the six lucerne plots. These were 22 x 6.3m each with at least a 10m buffer between the edges of irrigated and non-irrigated plots. The experimental period was from 23rd December 1998 to 24th June 1999. The experimental design was a split-plot randomised block with the main plots as soil water status (irrigated and non-irrigated) and the sub-plots as light regimes (full sunlight, shade cloth or wooden slats) in three replicates. A view of the experimental site and details of the shade structures are shown in Plates 3.01 and 3.02, respectively.

Plate 3.01- A view of the artificial shade structures set on a lucerne plot at the Field Service Centre (FSC) experiment, Lincoln University.

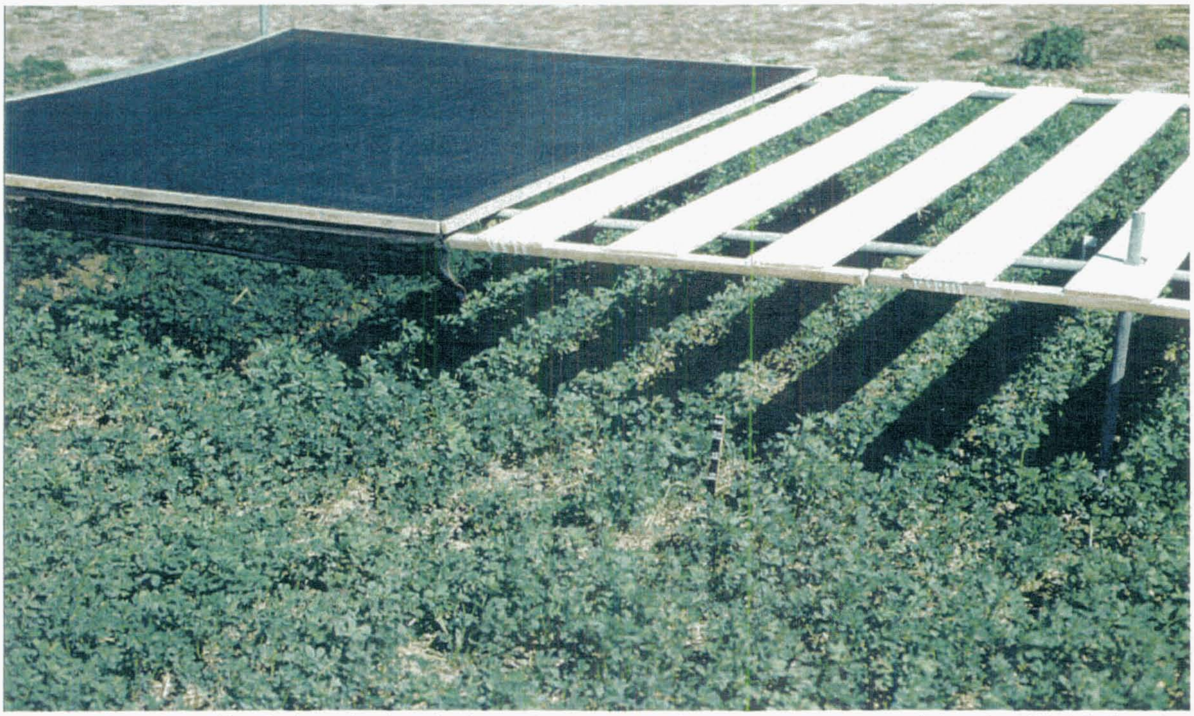

Plate 3.02- Detail of the shade cloth and wooden slats structures used in the Field Service Centre (FSC) experiment, Lincoln University.

3.2.3.1- Radiation regimes

The aim for one of the artificial shade structures was to mimic the radiation environment of a nearby radiata pine agroforestry area (Yunusa *et al.*, 1995). A previous analysis of this area showed that the mean light transmissivity under the trees was about 50% compared with full sun conditions (Pollock, unpublished data). In addition, the understorey vegetation was exposed to alternate periods of high and low radiation as the direct sunlight passed between and behind tree crowns over the day. A slatted structure was constructed to produce a similarly fluctuating light regime. To ensure that the duration of direct sunlight and shade under slats was similar to the agroforestry environment, the ratio of slat height above the lucerne canopy to slat width was kept the same as the ratio of the tree crown distance from its shadow to tree crown width (2:1). Owing to the fact that tree crowns are vertical and slats horizontal, the ratio of 2:1 was based on the diameter of the tree shadow. The ratio was calculated for the lowest solar zenith angle (about 30° at New Zealand standard noontime in summer) and used to define the height of the shade structure above canopy top. Figure 3.01 summarises the basis of the slatted structure construction for this experiment.

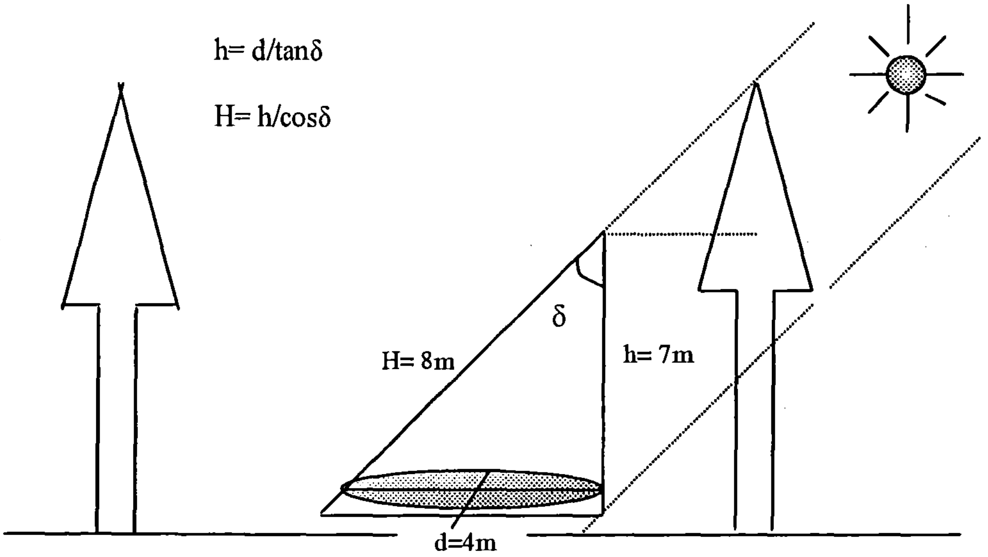

Figure 3.01- Diagram of the Lincoln University agroforestry area in October 1998, on which the slatted structure construction was based. H is the actual distance of shadow from tree crown; h is the distance from tree crown to top of canopy; d is the mean diameter of tree shadow and δ is the solar zenith angle (30°).

To achieve this, a slatted structure was created with 0.15m wide wooden slats (painted white on top) and 0.15m gaps between slats covering a total area of 2.4 x 5.2m. The same width for the slats and gaps was designed to produce a light transmissivity of about 50%. This structure was supported horizontally on a vertically adjustable metal pipe frame, which allowed the slats to be kept at 0.30m above the lucerne canopy. Thus, the ratio of distance from slats to lucerne top (h) to slat width (d) was maintained at 2:1 as previously observed in the agroforestry area.

For the shade cloth, the aim was to create a partial continuous light regime over the day that produced a similar level of light transmissivity to the slatted structure. Thus, black plastic shade cloth with 50% light transmissvity (commercial material description) was purchased from local horticultural supply stores and used to cover an adjacent 2.3 x 1.8m area. The shade cloth structure had an overhang material at both east and west sides to prevent direct radiation on plants at low solar inclination angles. The cloth structure was supported on the same metal pipe frame, adjusted weekly to approximately maintain 0.30m above lucerne top as the crop grew. Shade cloth and wooden slat structures were set in the field on 23rd December 1998.

Light measurement

The light environment was monitored with 2 quantum sensors (LI-190SB, Lincoln, USA), one installed above and one below the shade structures in Replicate 3. One quantum sensor was alternated from under shade cloth to under the wooden slat structure every 10 days and the other was set permanently in full sunlight conditions. Photosynthetic photon flux density (PPFD), within the range of 400-700nm, was recorded by a datataker (DT100, Roseville, Australia) every 30 seconds and the average was calculated at 8 minute intervals. The mean daily light flux transmissivity under both shaded structures was calculated for 10 different days in summer and autumn and on completely clear and overcast sky conditions. In Appendix 1, the daily course of the global solar radiation measured in full sun during the experimental period is shown.

Spectral radiation data were measured with a portable Spectroradiometer LI-1800 (LI-COR Inc., Lincoln, USA). Measurements were performed under the three light regimes prior to the experiment on 10th October 1998 at noontime. Readings were performed in both clear and overcast sky conditions. The red (660 nm) to far-red (730 nm) ratio (R/FR) was calculated in full sunlight, under the shade cloth, under the slats during the sun phase and during the shade phase. Spectral data were measured in W m^{-2} nm^{-1} between wavelengths of 300 and 1100 nm with intervals of 5 nm.

3.2.3.2- Soil water status

Soil water measurements

Water content was measured in the top soil of each shade treatments from September 1998 to May 1999 in full sun plots and from January to May 1999 under the two shade structures, using the Time Domain Reflectometer (TDR) Trase system, Model 6050X1 (Soil moisture Equipment Corp., Santa Barbara, USA). To do this, metal rods measuring 0.50m and 0.20m long were permanently installed in the centre of each treatment. In addition, metal tubes measuring 2.25m long were permanently set in full sunlight treatments (irrigated and non-irrigated plots) for all replicates. From 0.25 to 2.3m depth, soil moisture was measured with a Neutron probe (NP), Troxler Model 3333 at 0.1m intervals. Such fragmentation of soil moisture measurement within the profile was necessary because of soil texture variability previously observed by Watt & Burgham (1992) and Brown (1998) in the same experimental site. Measurements using both TDR and NMM were taken at 7-10 day intervals during the experimental period.

Irrigation water

Irrigation was applied between November 1998 and February 1999 to irrigated treatments, using a travelling mini-boom irrigator. Table 3.02 shows a summary of the irrigation water applied. Previous research in the same plots (Inch, 1998; Brown, 1999) had shown the water extraction depth for lucerne in non-irrigated treatments was at least up to 2.3m and up to 1.9 m in irrigated treatments. The same authors reported that, for the non-irrigated lucerne, DM yield started to decrease below a soil moisture deficit (SMD) of 215mm for the 2.3m soil depth. Therefore, the target for the irrigated plots was to maintain a SMD below 100 mm within the top 1.0m soil depth or about half of the available water at field capacity. The soil field capacity (FC) of this area has been measured using nutreon probe readings for every 0.10m soil layer down to 2.3m depth from 1997 to 2000 (Brown, unpublished data). The values for FC varied within each soil profile because of changes in soil texture and water holding capacity. On average, it was found that FC for 0.10m layers ranged from 30-37% at the 2.3m soil profile, which is consistent with previous reports (Watt & Burgham, 1992).

The amount of irrigation water applied was measured with a flow meter (Neptune, type Sz, size 25.4 mm). The rate of water application was 15mm h^{-1}. Irrigation was applied immediately after trimming the residual material, post grazing, to replace the water lost in the previous rotation.

Table 3.02- Irrigation water applied to the plots in the FSC experiment at Canterbury, New Zealand for the 1998/1999 season.

Start date	**Finish date**	**Amount of irrigation water applied (mm)**
20/11/1998	25/11/1998	80
23/12/1998	27/12/1998	86
20/01/1999	25/01/1999	125
25/02/1999	01/03/1999	71
Total		362

Irrigated plots received a total amount of water (A) equal to the difference between estimated potential evapotranspiration (∑Ep) and rainfall (R) plus irrigation (Irr) in the previous rotation (Equation 3.1).

$$A = \sum Ep - (R + Irr) \qquad \text{Equation 3.1}$$

The actual amount of irrigation water applied (mm) was measured at the experimental site using a flow meter (Neptune, type Sz, size 25 mm). Total rainfall (mm) and Penmann Ep (mm) were collected at the Broadfields Meteorological Station. The potential SMD was calculated at 7-10 day intervals, using the following equation:

$$SMD = SMDi + (R + Irr) - E_A \qquad \text{Equation 3.2}$$

Where SMDi is the initial soil moisture deficit at the beginning of each measurement period and E_A is the estimated daily evapotranspiration for that period. The daily SMD values were accumulated over the lucerne growth period. Daily E_A was calculated from Equation 3.3:

$$\text{Daily } E_A = [(\Delta SWC + R + Irr) / \sum Ep] * Ep \qquad \text{Equation 3.3}$$

Where Ep is the daily Penmann evapotranspiration (mm day^{-1}) and ΔSWC is the change in soil water content between two successive measurements in the experimental plots.

Finally, six thermistor sensors (KTY/110, Cooltronics, Christchurch, New Zealand) were permanently set at 0.05m above the canopy for the three light regimes (full sunlight, shade cloth and wooden slat) in irrigated and non-irrigated plots in Replicate 3. The sensors were individually calibrated to a 0.1 °C mercury thermometer. The sensors were installed in a 0.10m long metal pipe shelter to remain protected from direct solar radiation. The pipe was painted black inside to avoid re-irradiation effects. Metal shelters along with the temperature sensors were set on an aluminium bar connected to the shaded structures. Thus, as the height of shaded structures was adjusted weekly (0.30m above canopy), temperature sensors were automatically lifted and maintained 50mm above the canopy. The aim was to measure air temperature differences at canopy height that might result from different canopy transpiration rates under the different light regimes. A data logger also recorded the temperatures every 30 seconds and the average was calculated at 15 minute intervals.

3.2.4- Site management

3.2.4.1- General

Thirty soil cores (300 mm diameter x 150 mm depth) were taken at random within each lucerne crop at the end of the experiment in May 1999 (Table 3.03). During the experimental period no fertilizers were applied based on results from 150 mm deep soil cores (Table 3.03). Results for soil nutrients indicated small differences between irrigated and non-irrigated plots.

Levels of soil nutrients were adequate (Morton & Roberts, 1999), except for Olsen phosphorus (P) and sulphate sulphur [S(SO_4)] in irrigated plots, which were slightly below the target for sedimentary soils in Canterbury.

Table 3.03- Soil test results for the Field Service Centre experimental site from samples taken in May 1999. Soil tests were performed using the Ministry of Agriculture and Fisheries Quick Test (MAF QT) procedures.

Treatment	Ca[1]	K[1]	Mg[2]	Na[1]	P[3]	S(SO_4)[4]	pH[5]
	---------------m.e. 100 g^{-1} soil-----------				Mg ml^{-1}	ppm	
Irrigated	8.0	1.1	1.1	0.2	17.0	6.0	7.0
Non-irrigated	7.5	1.2	1.1	0.2	20.0	9.0	6.8

1. Ammonium acetate extraction:AA determination test method; 2. Ammonium acetate extraction test method; 3. Olsen extraction:colorimetry test method; 4. Potassium phosphate extraction:IC test method; 5. 1:2.1 V/V water slurry test method (AgResearch, Lincoln, New Zealand).

3.2.4.2- Grazing

Shade structures were removed during the period of grazing and the whole area (including shaded plots) were grazed simultaneously with sheep of different classes. The timing of each grazing was a compromise between optimal development stage for lucerne persistence and nutritive value. The period of grazing never exceeded 6 days. The spelling period between successive grazing periods in summer also aimed to allow lucerne to reach early flowering (Stage 3, according to Fick & Mueller, 1989) in summer and store sufficient reserves for the following season (Brown *et al.*, 2000). Post-grazing, residual shoots were trimmed just above crown height in all plots, using a sickle bar mower to ensure only subsequent lucerne regrowth was measured. Table 3.04 shows the duration of each rotation and grazing period for the experimental period.

Table 3.04- Rotation length and sheep grazing period used in the present experiment at Canterbury, New Zealand.

Rotation	**Rotation period (from residual to final cut)**	**Rotation length (days)**	**Grazing duration (days)**
1	22 Dec – 13 Jan 99	23	4
2	19 Jan – 17 Feb 99	30	5
3	25 Feb – 12 Apr 99	47	6
4	22 Apr – 24 Jun 99	64	4

3.2.5- Measurements

3.2.5.1- Herbage dry matter samples

Herbage dry matter (DM) yield was calculated from samples collected at 7-10 day intervals. Samples were cut from a 0.2 m^2 quadrat about 50mm above ground level. From these samples, a randomised sub-sample of at least 50g fresh matter (FM) was separated and the total number of stems counted. Observations made during the first two rotations indicated variations in lucerne stem sizes between light regimes. Thus, the stem number sub-sample was also separated into three size classes: <10, 10-20, and >20 cm stem length for the final harvests in Rotations 3 (12th April 1999) and 4 (24 June 1999).

Once in each rotation, when lucerne was still at the vegetative stage (Stage 2, according to Fick & Mueller, 1989), a second 50g FM sub-sample was collected to estimate the proportion of leaf and stem (L/S ratio). This sub-sample was separated into leaf (leaflets) and stem (main stem + petioles). Main samples and sub-samples were dried in a forced air draft oven for at least 48 hours at 70 °C to constant weight. DM yield (kg ha^{-1}), number of stems (stems ha^{-1}) and L:S ratio were then calculated. Final harvests for each rotation were taken in the 24 hours before sheep were introduced to the paddock. Growth rates (kg ha^{-1} d^{-1}) were calculated for the linear portion of the growth curve in each rotation. For this calculation, it was assumed that the period between the day after grazing and first lucerne DM harvest (7-10 days) corresponded to the lag phase of the growth curve.

3.2.5.2-Green area index

Green area index (GAI) was measured using a LAI-2000 canopy analyser (LI-COR Inc., Lincoln, USA). Readings were taken in predominantly diffuse light conditions at 7-10 day intervals. The equipment was set to take two series of one reading above and 5 readings below the canopy (50mm above the ground level) in each plot. The same equipment automatically calculated the proportion of diffuse light transmission (DIFN) at ground level and the mean foliage angle (MTA). The final GAI, DIFN and MTA values result from the integration of 5 different zenith angles readings (7, 23, 38, 53 and 68°) measured by the canopy analyzer. The above and below canopy readings for the cloth treatment were taken immediately under the shade material when light conditions were uniform and predominantly diffuse. However, for the slatted structure, wooden slats were removed completely for the measurement period (2-5 minutes) to take the above and below canopy readings and to avoid overestimations due to the fluctuating light regime.

From these data, lucerne canopy architecture was described using the extinction coefficient (K) calculated from Beer's law (Equation 2.1, Section 2.1.5.2) and the MTA readings. To do this, a linear regression between Ln (I/Io) and GAI was plotted for each treatment during the experimental period and the slope of this line was considered K. Both light penetration (I/Io), assumed to be DIFN, and GAI were obtained from the canopy analyzer measurements. In addition, canopy radiation interception (%) in diffuse light condition was calculated by subtracting 1 from the DIFN value and multiplying for 100.

3.2.5.3- Radiation use efficiency (RUE)

Radiation use efficiency was calculated by the slope of the regression line obtained between mean shoot dry matter (g m^{-2}) against accumulated intercepted PAR (MJ m^{-2}) for each rotation period. Estimates of intercepted PAR (PAR_i) were calculated according to Gosse *et al.* (1982) and as applied by Khaiti & Lemaire (1992):

$$PAR_i / PAR_o = 0.97 * [1 - \exp(-LAI*K)] \qquad \text{Equation 3.4}$$

Where PAR_o is the incident PAR above canopy (in full sun and under the cloth and slat structures) and LAI is leaf area index. Light flux (μmol photons m^{-2} s^{-1}), measured by the quantum sensors in each treatment, was converted to PAR units (W m^{-2} = J m^{-2} s^{-1}) and used as daily accumulated PAR_o values (1 W m^{-2} = 4.61 μmol photons m^{-2} s^{-1} as reported in the LI-COR Radiation Measurement Manual). Specific K values for each treatment were used on this calculation and leaf area index was assumed as GAI. The daily value of GAI was estimated by linear interpolation between two successive GAI measurements.

3.2.5.4- Leaf net photosynthesis (Pn)

Leaf Pn rate was measured 6 times between Rotations 1 and 3 on three of the youngest fully expanded leaves per treatment and at an artificial light flux of 1000 μmol photons m^{-2} s^{-1}, using the portable infra-red gas analyser (LI-6400, LI-COR Inc., Nebraska). Air temperature in the leaf chamber was blocked at 21° C and CO_2 concentration set at 400 ppm. Readings were taken after stabilising at a coefficient of variance of 5% and results of Pn rate were expressed as the mean value of the three measurements in μmol CO_2 m^{-2} s^{-1}. When a lucerne leaf was smaller than the chamber, Pn rate was corrected according to leaf area. Samples were only collected in clear sky conditions between 1100 and 1400 h. Under the wooden slat regime, Pn rate was measured on fully illuminated leaves.

3.2.5.5- Phenological development

Five dominant stems from different plants were marked in the centre of each treatment to measure stem height (STH), number of fully expanded nodes (NOD), time to bud appearance and node number of the flowering bud (PFLOW). Measurements were taken at 10 day intervals until flower initiation (Stages 3-5 according to Fick & Mueller, 1989). New plants were marked at the beginning of each rotation. From these measurements, the phyllochron was calculated based on thermal time accumulation using Equation 3.5:

$$TT = \sum [(Tmax + Tmin) / 2] - Tb \qquad \text{Equation 3.5}$$

Where Tmax was the maximum daily air temperature, Tmin was the minimum daily temperature and Tb was the base temperature, below which no development takes place. Tb was 1 °C as calculated by Moot *et al.* (2000). Mean air temperatures were assumed to be equal between light regimes.

3.2.6- Statistical analysis

Results for all variables were analysed using a split-plot analysis of variance (ANOVA), where water status (irrigated and non-irrigated) was the main plot and light regimes (full sunlight, cloth and slats) the sub-plots, with 3 replicates. This analysis was performed on individual dates as measured in the field. A complementary ANOVA was performed for all variables using a split-split plot analysis, where the sub-sub-plot was the date of measurement (time), to identify seasonal differences. In both cases, means were compared whenever treatment effects in the ANOVA presented $p < 0.05$. Then, Fisher's protected least significant difference (LSD) was used for means separation at the 5% level ($\alpha = 0.05$). For the RUE, a regression analysis was performed between shoot DM against accumulated PARi and the plotted equations are reported with the regression coefficients, coefficient of determination (R^2) and standard errors (SE) for each treatment. Regression lines were performed with and without being forced through the origin. An ANOVA was then performed on the regression coefficients for the slope, using the split-plot design. The statistical package used was the GENSTAT 5, release 4.1 (Lawes Agricultural Trust, IACR, Rothamsted, UK).

3.3- Results

3.3.1- Environmental changes

3.3.1.1- Radiation environment

The use of both artificial shade materials produced distinct light flux transmissivity and periodicity (Figure 3.02 *abcd*). Specifically, on sunny days the light regime under the slatted structure was intermittent with equal alternating periods of near full sunlight and heavy shade (Figure 3.02*a*). For example, a maximum period of nearly 120 minutes of either heavy shade or high sunlight periods was measured in mid-summer at noontime. At this time, light flux transmissivity under slats was 94% during the sun and 6% during the shade period compared with the open. The mean daily light transmissivity under slats was 47%. In contrast, the shade cloth produced a continuous light regime similar to that observed in full sun on a clear and sunny day (Figure 3.02*c*). Light flux transmissivity under the cloth material reached a maximum of 45% (13.00h) and a minimum of 20% (18.00h) compared with the open. The mean daily transmissivity was 42% on a sunny day under the cloth regime.

In mid-summer on an overcast day, the difference in light periodicity between cloth and slats was minimal and both artificial shade structures followed the same pattern as the full sun. Mean daily light transmissivity in overcast sky conditions was 46% under the slatted structure (Figure 3.02*b*) and 38% under the shade cloth (Figure 3.02*d*) compared with the full sun. Additionally, measurements taken in mid-autumn showed that mean daily light transmissivity decreased to 46% under slats and 39% under cloth on either clear or overcast days. Spectral composition was analysed by calculating the red to far-red ratio (R:FR) and these are also indicated in Figure 3.02 (*abcd*). Under clear sunny sky conditions, the ratio was similar for full sunlight (1.32), shade cloth (1.30) and during the sun phase under slats (1.28). It decreased to 0.74 during the shade phase under wooden slats. The magnitude of differences was reduced in overcast sky conditions, with a uniform reading under slats of 1.20, with 1.29 in full sunlight and 1.26 under cloth.

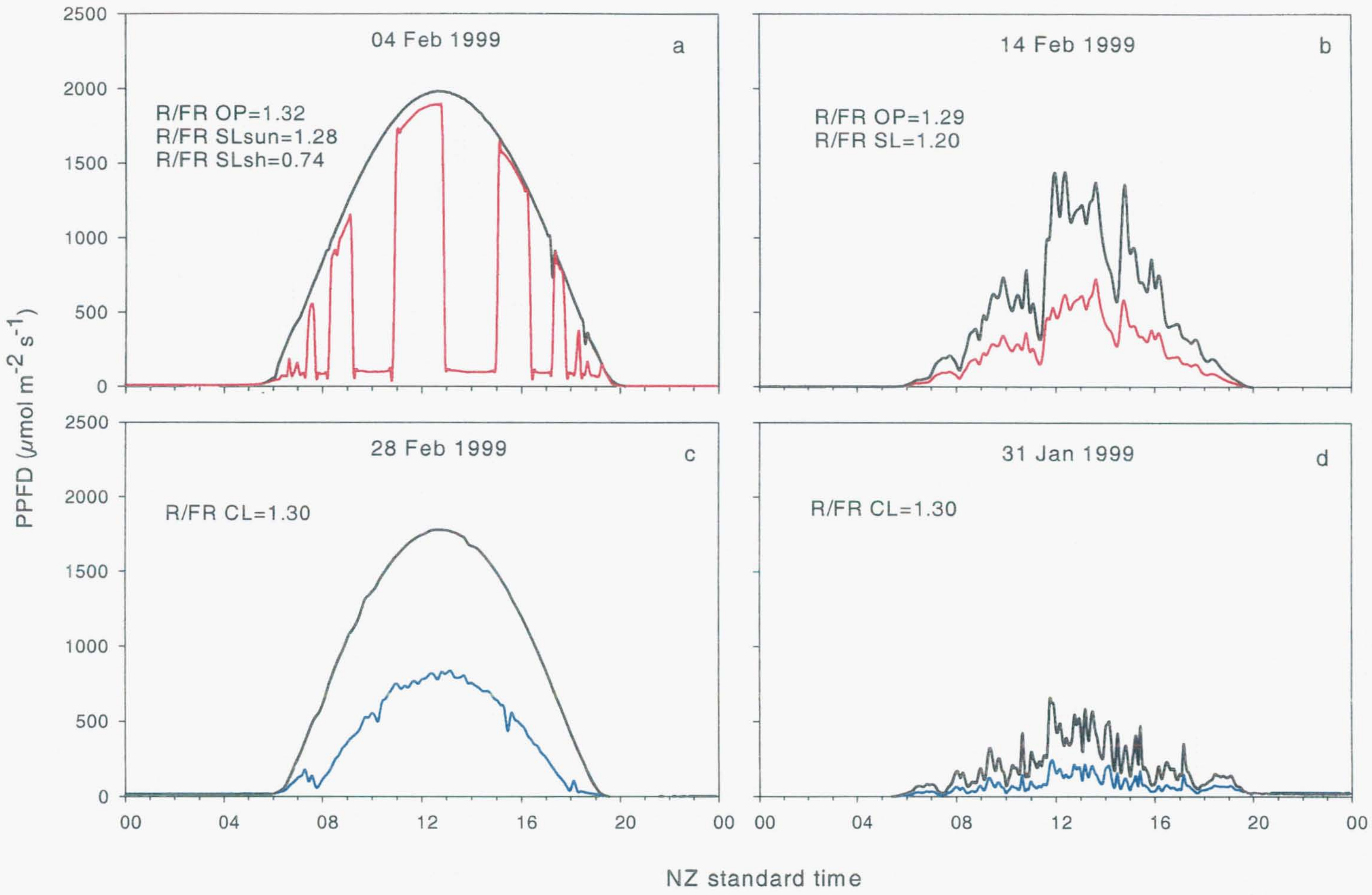

Figure 3.02- Photosynthetic photon flux density (PPFD) measured in full sunlight (▬), under shade cloth (▬) and wooden slat (▬) for typical clear sunny (*ac*) and overcast (*bd*) sky conditions in mid-summer in Canterbury, New Zealand. Red to far-red ratios (R/FR) are indicated for open field (OP), cloth (CL) and slats in the full sun (SLsun) and shade (SLsh).

3.3.1.2- Air temperature at canopy height (TCH)

There were only small changes in TCH between shaded and full sunlight regimes on a daily basis, but variation was found during the day (Figure 3.03 *abcd*). TCH under the two artificial shade structures was typically warmer than in full sunlight at night, but cooler during the day. For example, at night in the summer TCH was up to 19% warmer under the cloth and 16% warmer under the slat structures compared with the full sun in non-irrigated conditions (Figure 3.03*b*). In autumn, cloth was 11% and slats 12% warmer than full sunlight (Figure 3.03*d*). In contrast, daytime TCH in summer was cooler by up to 13% under cloth and 16% under slats and by autumn the difference was up to 19% under cloth and 14% under slats. The same trend continued for irrigated treatments, but cloth appeared to be even warmer at night than the non-irrigated treatment. Relative differences between the irrigated shaded regimes and full sunlight during the day were smaller than in non-irrigated conditions (Figure 3.03*bd*).

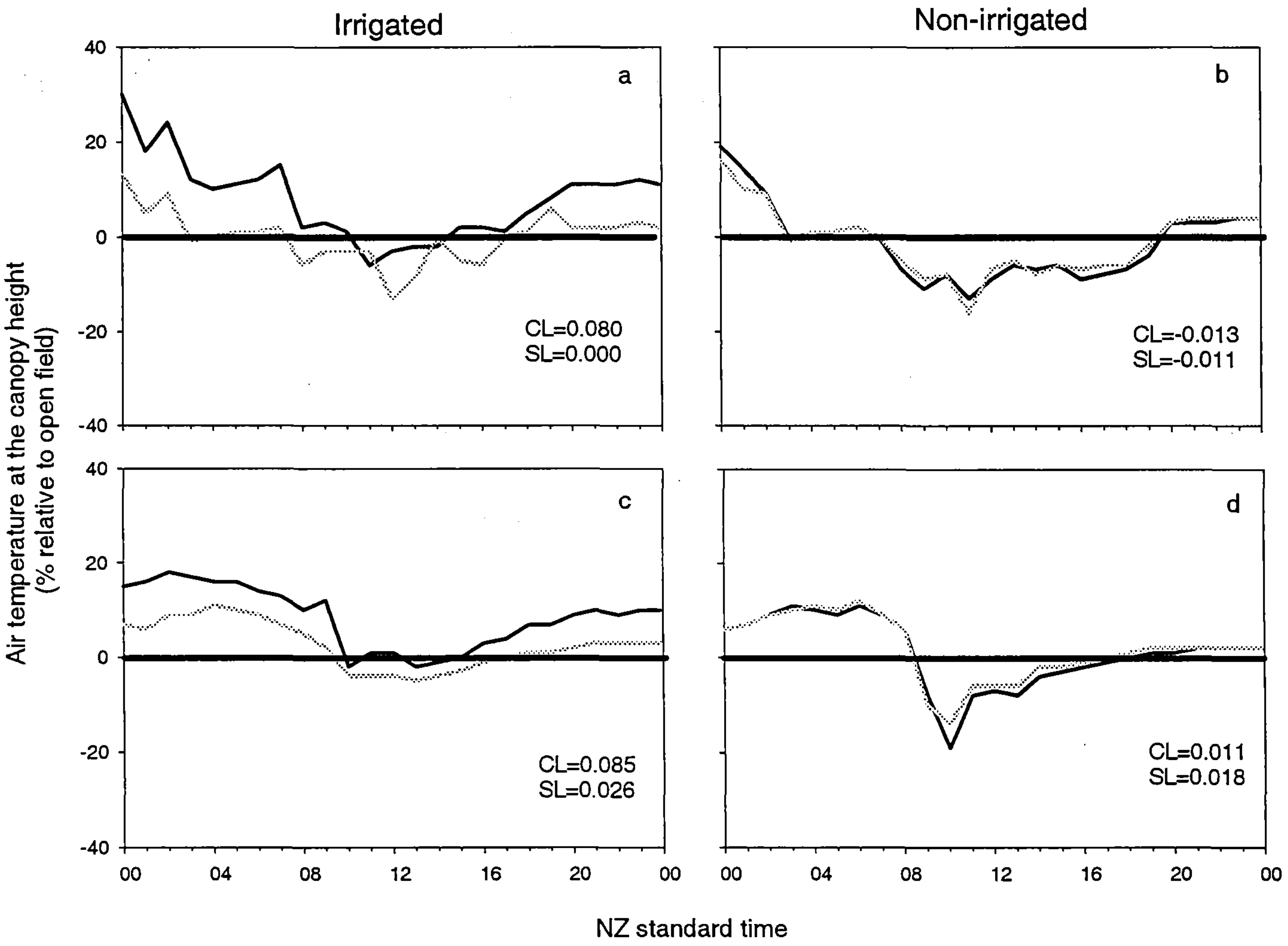

Figure 3.03- Relative air temperature (%) measured at the canopy height (TCH) under shade cloth (▬) and woodens slat (▨) structures compared with full sun in irrigated (*ac*) and non-irrigated plots (*bd*). Data are for a typical clear sunny day on 13 February (*ab*) and 10 May 1999 (*cd*). The thick line indicates the standardised TCH in the full sun. The mean daily relative values for cloth (CL) and slats (SL) are indicated in each graph.

3.3.1.3- Soil water content (SWC)

TDR measurements (Figure 3.04) showed that soil moisture in the top 0.5 m of the non-irrigated full sun treatment decreased from 30% on 16 September to 19% on 1 December 1998 and then remained constant until 17 February 1999, regardless of light regimes. Neutron probe measurements (Figure 3.05) showed a rapid decrease for SWC at 0-0.5 m from September to mid December in non-irrigated treatments and then SWC reduced at lower rates until 22 February 1999. For the layer 0.5-1.0 m, the SWC dropped from 34% on 16 September 1998 to about 9% on 22 February 1999. After this, there was no further water extraction until the end of June. Similarly, water extraction from 1.0-2.0 m was minimal from February to June. These data suggest moisture stress was likely to occur from the end of Rotation 1 until the beginning of Rotation 3.

Indeed, the SMD increased rapidly in non-irrigated full sun conditions from September 1998 to mid-February 1999 as total rainfall was minimal and evapotranspiration increased (Table 3.01 and Figure 3.06). The maximum SMD for the 2.3 m soil profile was 385 mm on the 25 February 1999 in the non-irrigated treatments. The subsequent recovery occurred after the beginning of rotation 2 with the 31 mm of rainfall on 26 February 1999 (Figure 3.06). Further rainfall in March continued to rewet the top 0.5 m soil layer and it then never returned to its minimal level (Figure 3.05), indicating crops did not experience any further water stress. For irrigated treatments the maximum SMD was 140 mm also on 25 February 1999, but the available water below 1.0 m indicated these crops were not moisture stressed at any time. The range in minimum SWC values (lower limit) for the different soil depths indicates the differences in soil texture, which are common in these soils (Watt & Burgham, 1992).

The imposition of light regimes after December 1998 did not affect the pattern of moisture extraction to 0.5 m soil (Figure 3.04). Small variations observed in SWC between light regimes were likely to be due to textural differences rather than a beneficial or detrimental effect of shading on soil moisture content.

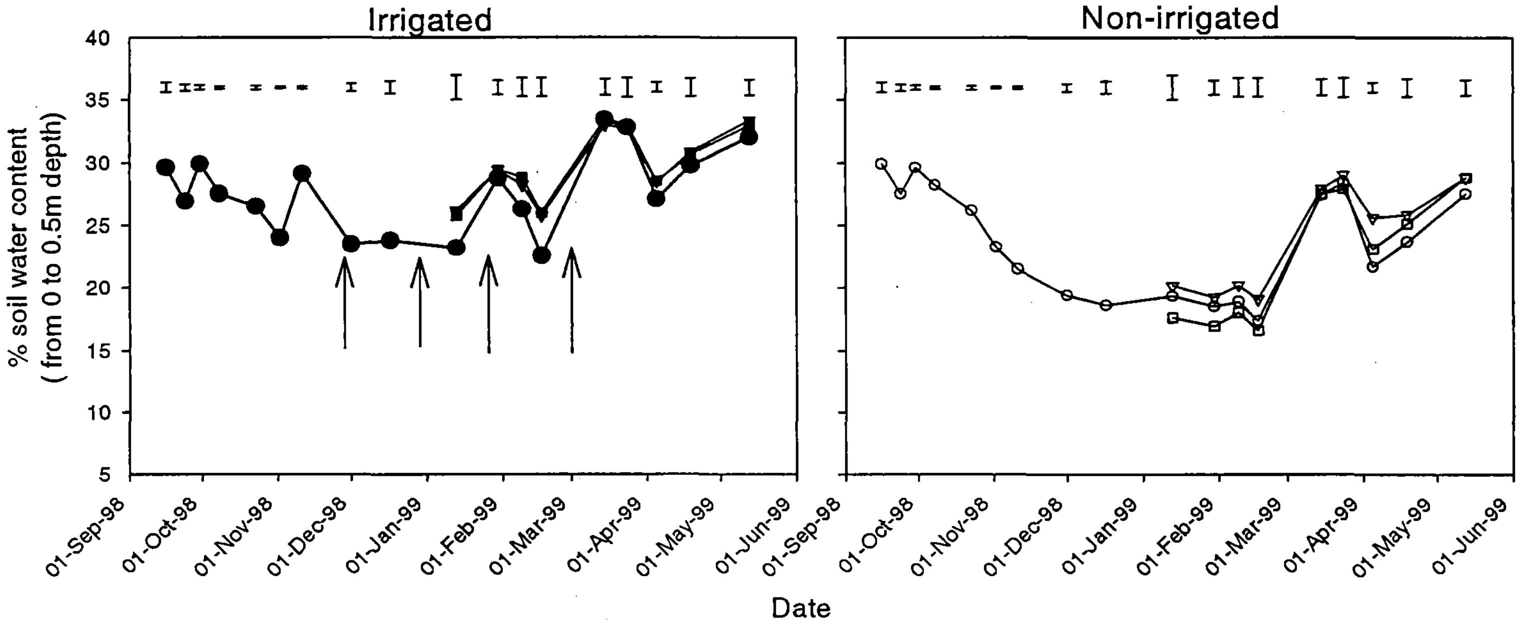

Figure 3.04- Mean soil water content (%) for the 0-0.5 m soil profile measured with TDR in irrigated (closed symbols) and non-irrigated (open symbols) conditions for lucerne crops grown under full sunlight (●,○), shade cloth (■,□) and wooden slats (▼,▽) during the experimental period at Canterbury, New Zealand. Arrows indicate when irrigation was applied. Data are the average of 3 replicates and bars show standard errors of means for each date of sampling.

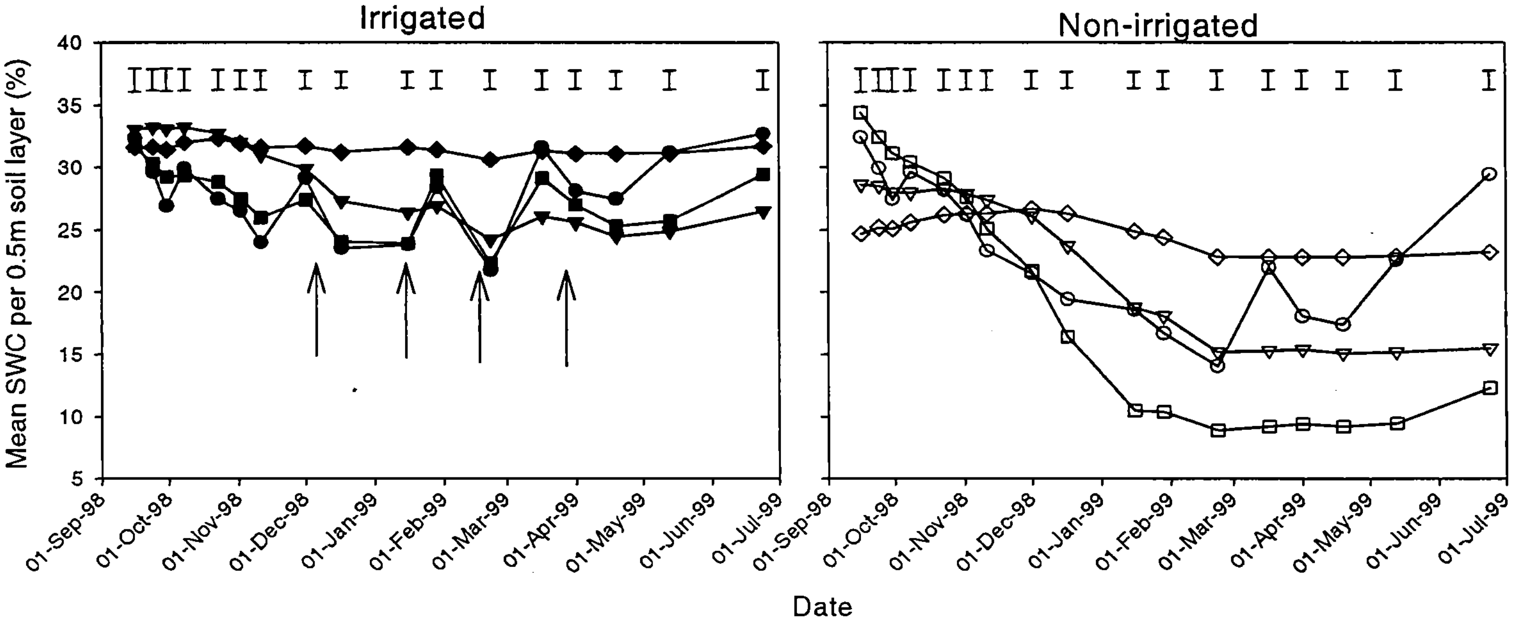

Figure 3.05- Mean soil water content (%) for irrigated (closed symbols) and non-irrigated (open symbols) treatments in full sunlight at various soil depth profiles: 0-0.5 m (●,○), 0.5-1.0 m (■,□), 1.0-1.5 m (▼,▽) and 1.5-2.0 m (◆,◇) for lucerne grown in 1998/1999 at FSC, Lincoln University. Arrows indicate when irrigation was applied. Data are averages of 3 replicates and bars show standard errors of means (soil depth) for each date of sampling. Measurements for the 0-0.5m were taken with TDR and for the layers below 0.5m with NP.

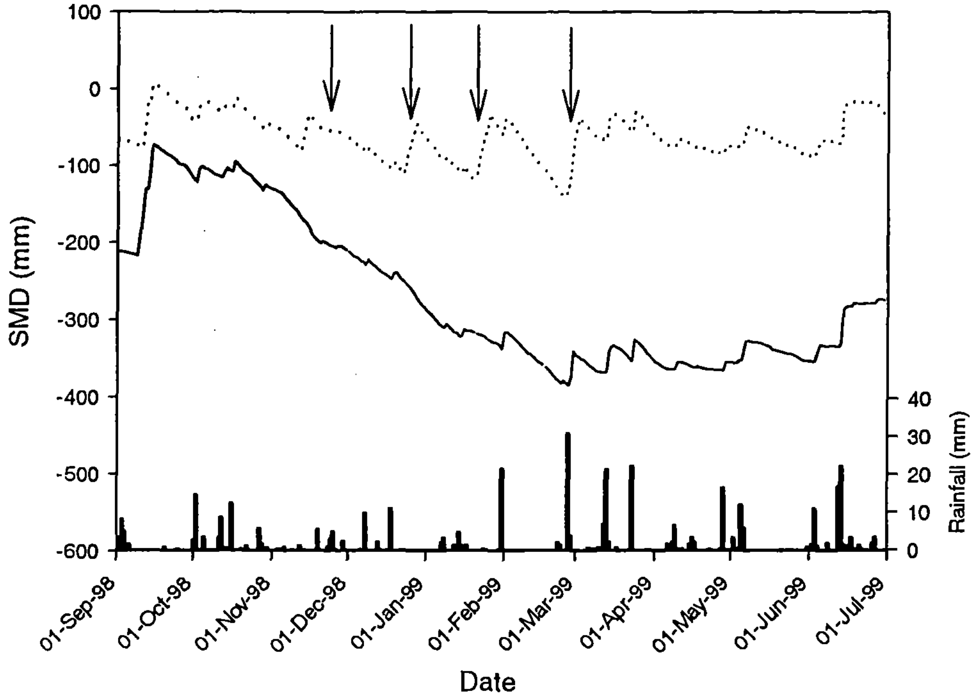

Figure 3.06- Soil moisture deficit (SMD) and rainfall for irrigated (⋯⋯) and non-irrigated (——) treatments measured in full sunlight conditions for the experiment. Data were means of 3 replicates from 1st December 1998 to 30th June 1999 at Canterbury, New Zealand. Arrows indicate when irrigation was applied (see Table 3.02 for details).

3.3.2- Biological changes

3.3.2.1- Herbage dry matter yield (DM)

An interaction ($P<0.05$) was observed between water status and light regimes for lucerne total DM yield over the experimental period. This was because irrigation increased DM yield more in fully illuminated crops, especially in Rotations 2 and 3, than under shaded treatments. Irrigation increased total DM yield by 19% (from 8.8 to 10.5 t ha^{-1}) in full sunlight, but only 10% under cloth (from 5.8 to 6.4 t ha^{-1}) and slat (5.5 to 6.0 t ha^{-1}) treatments over the experimental period. Total DM yield was reduced by about 40% under the two shaded treatments compared with full sunlight in irrigated and non-irrigated conditions. The associated growth rates calculated for the linear phase of the curves (Figure 3.07) decreased progressively from the first to the fourth rotation in almost all treatments ($P<0.05$), except for the non-irrigated full sunlight treatments, which were consistent between Rotations 1 and 2.

As expected, a difference in yield ($P<0.01$) between irrigated and non-irrigated treatments were observed for Rotations 2 and 3 (Figure 3.07). Irrigation showed no increase ($P>0.26$) in DM yield for the three light regimes in Rotation 1. However, irrigation increased DM yield ($P<0.05$) in Rotation 2 by 25% in full sun, 19% under cloth and 17% under slats and for Rotation 3 by 33%, 7% and 10%, respectively. The effects of irrigation were minimal for all light regimes in Rotation 4.

The two artificial shade structures resulted in a slower lucerne recovery (lag phase of the curve) than in full sunlight for almost all the rotations ($P<0.005$), except for non-irrigated conditions in Rotation 2. For example in Rotation 3, growth rate to the first harvest was 74 kg ha^{-1} d^{-1} in full sunlight, but only 40 kg ha^{-1} d^{-1} and 37 kg ha^{-1} d^{-1} under cloth and slats, respectively. In addition, the effect of shade cloth and slats on lucerne growth, after the first cut (linear phase of the curve), compared with full sunlight was small in Rotation 1, but progressively increased ($P<0.006$) over the experimental period.

For the Rotation 1, an interaction ($P<0.03$) between water status and light regimes was observed for mean growth rates. This was because the reduction in growth rates caused by shading was maximized in irrigated, but not in non-irrigated conditions. Growth rate was 119 kg ha^{-1} d^{-1} or 17% lower under shade cloth and 112 kg ha^{-1} d^{-1} or 22% lower under slats than the 144 kg ha^{-1} d^{-1} observed for full sunlight in irrigated treatments. However, growth rate was similar between the three light regimes in non-irrigated conditions with a mean value of 100 kg ha^{-1} d^{-1}. Differences between full sun and shaded growth rates were then observed in all subsequent rotations. The greatest reduction in DM growth occurred in Rotation 4, when plants under the shade showed a growth rate decrease of about 60% compared with full sunlight. Differences in growth rates were not observed between the shade cloth and the slatted treatments under irrigated or non-irrigated conditions.

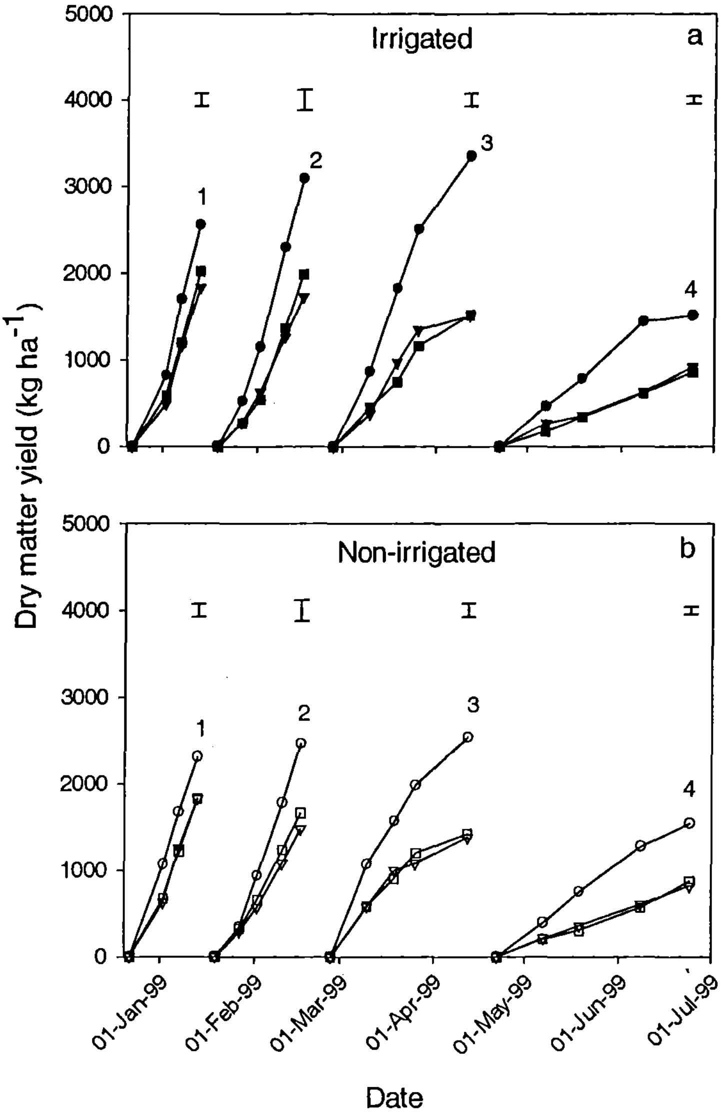

Figure 3.07- Mean dry matter yield of lucerne for 4 successive rotations in irrigated (*a*) and non-irrigated (*b*) treatments under full sunlight (●,○), shade cloth (■,□) and wooden slats (▼,▽) in Canterbury, New Zealand. Data are the average of 3 replicates and bars show standard errors for the final harvest in each rotation. Final harvests dates were given in Table 3.04.

3.3.2.2- Green area index (GAI)

Lucerne GAI expansion (Figure 3.08) followed a similar pattern to DM yield. Irrigation increased ($P<0.05$) total GAI over the experiment period by 15% in full sunlight (from 16.5 to 19.0), 14% under cloth (11.4 to 13.0) and 11% under slats (11.2 to 12.5). The accumulated GAI decreased ($P<0.001$) about 30% under the two shaded regimes compared with full sunlight in irrigated and non-irrigated conditions. The effect of irrigation on canopy GAI was observed ($P<0.02$) particularly in Rotations 2 and 3. In Rotation 2, irrigation increased GAI by 28% compared with the non-irrigated treatment in full sun, but only 20% under shade. For Rotation 3, irrigation increased GAI by 20% in full sun and under cloth, but only 11% under slats. Therefore, there was a lack of leaf expansion in non-irrigated treatments. For Rotations 1 and 4, irrigation did not affect ($P>0.32$) canopy GAI in any of the three light regimes.

The shade by cloth or slats decreased ($P<0.001$) lucerne GAI compared with full sun in all rotations and soil water conditions. The greatest reduction in final GAI under shade occurred in Rotation 3 ($P<0.001$), when the decrease was about 40% under the cloth (GAI=2.9) and slats (GAI=3.0) compared with full sunlight (GAI=5.0). Canopy GAI values were typically the same for the two artificial shade treatments in all rotations. Shading also delayed GAI expansion compared with full sunlight in all rotations ($0.04<P<0.001$). For example in Rotation 3, irrigated plants in full sunlight reached GAI=3 after 19 days regrowth, compared with 35 days in both shaded treatments. In non-irrigated treatments, plants needed 22, and 41 days to grow 3 units of GAI in full sun and under the two shaded regimes, respectively.

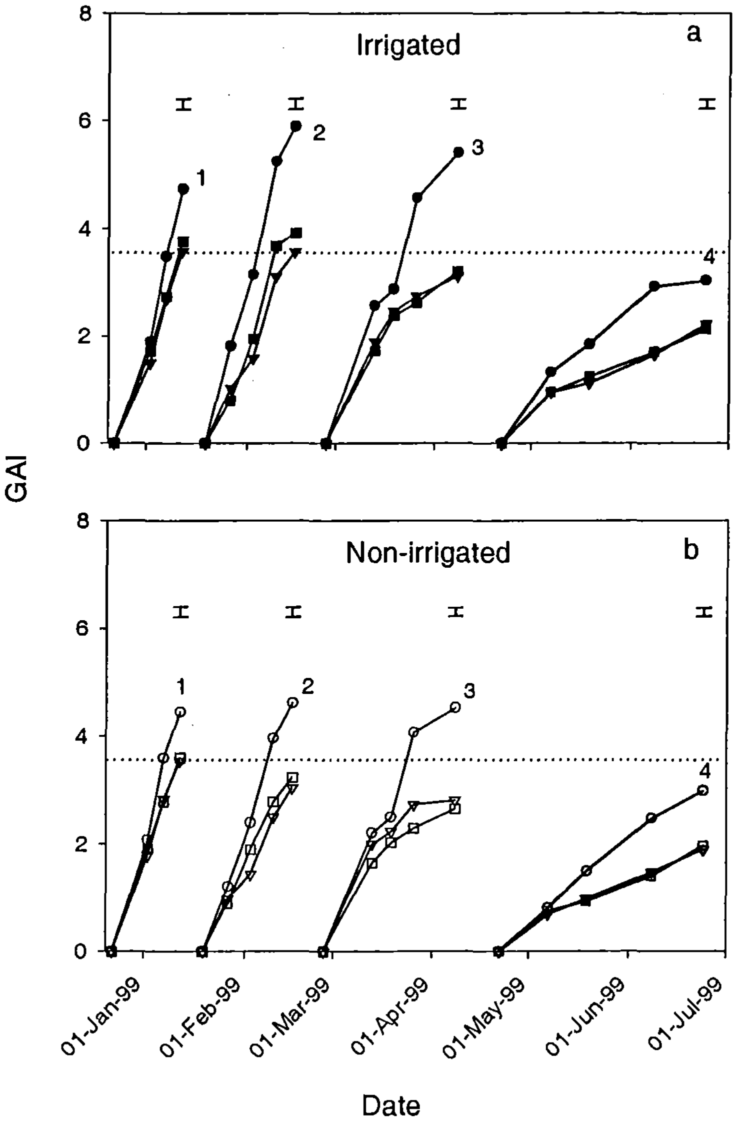

Figure 3.08- Mean green area index (GAI) for 4 successive lucerne rotations in irrigated (*a*) and non-irrigated (*b*) treatments under full sunlight (●,○), shade cloth (■,□) and wooden slats (▼,▽) at Canterbury, New Zealand. Data are the average of 3 replicates and bars show standard errors for the final harvest in each rotation. Dotted lines indicate the critical GAI for lucerne canopies. Final harvests dates were given in Table 3.04.

3.3.2.3- Canopy architecture

As expected, radiation interception increased exponentially against GAI for all treatments (Figure 3.09*ab*) with a common (P>0.83) mean critical GAI of 3.6. Calculations of the extinction coefficient (Section 3.2.5.2) showed a common (P>0.73) value of 0.82 was appropriate (Figure 3.09*cd*). Data for mean foliage angle (MFA) also indicated that foliage dispersal was similar (P>0.19) between water and light (P>0.12) treatments at the end of each rotation (Table 3.05). The exception was in Rotation 3 (P<0.05), when irrigated lucerne averaged 40°, non-irrigated 42° and plants under cloth showed a lower (P<0.05) MFA than under slats and in full sunlight. The overall lucerne MFA over the experimental period was 45 ° for all treatments.

Table 3.05- Mean foliage angle (MFA) of the lucerne canopy at the end of 4 rotations in Canterbury, New Zealand.

Water status	**Light regime**	**MFA (degrees)**			
		Rotation 1	Rotation 2	Rotation 3	Rotation 4
Irrigated	Full sunlight	45.7	43.3	42.0	45.3
	Shade cloth	44.7	42.0	38.3	46.7
	Wooden slats	47.0	48.0	41.0	47.0
Non-irrigated	Full sunlight	46.7	41.3	43.0	43.7
	Shade cloth	48.3	42.7	39.7	46.0
	Wooden slats	48.7	42.7	43.3	44.5
Mean		**46.9**	**43.3**	**41.2**	**45.5**
SEM†	Water status	3.12	0.80	0.21	0.98
	Light regime	1.75	1.03	0.92	0.68
F probability	*Water status*	*0.68*	*0.19*	*0.03*	*0.38*
(Pr > F)	*Light regime*	*0.78*	*0.12*	*0.05*	*0.23*
	*Water*Light*	*0.85*	*0.18*	*0.87*	*0.69*

† SEM is standard errors of means.

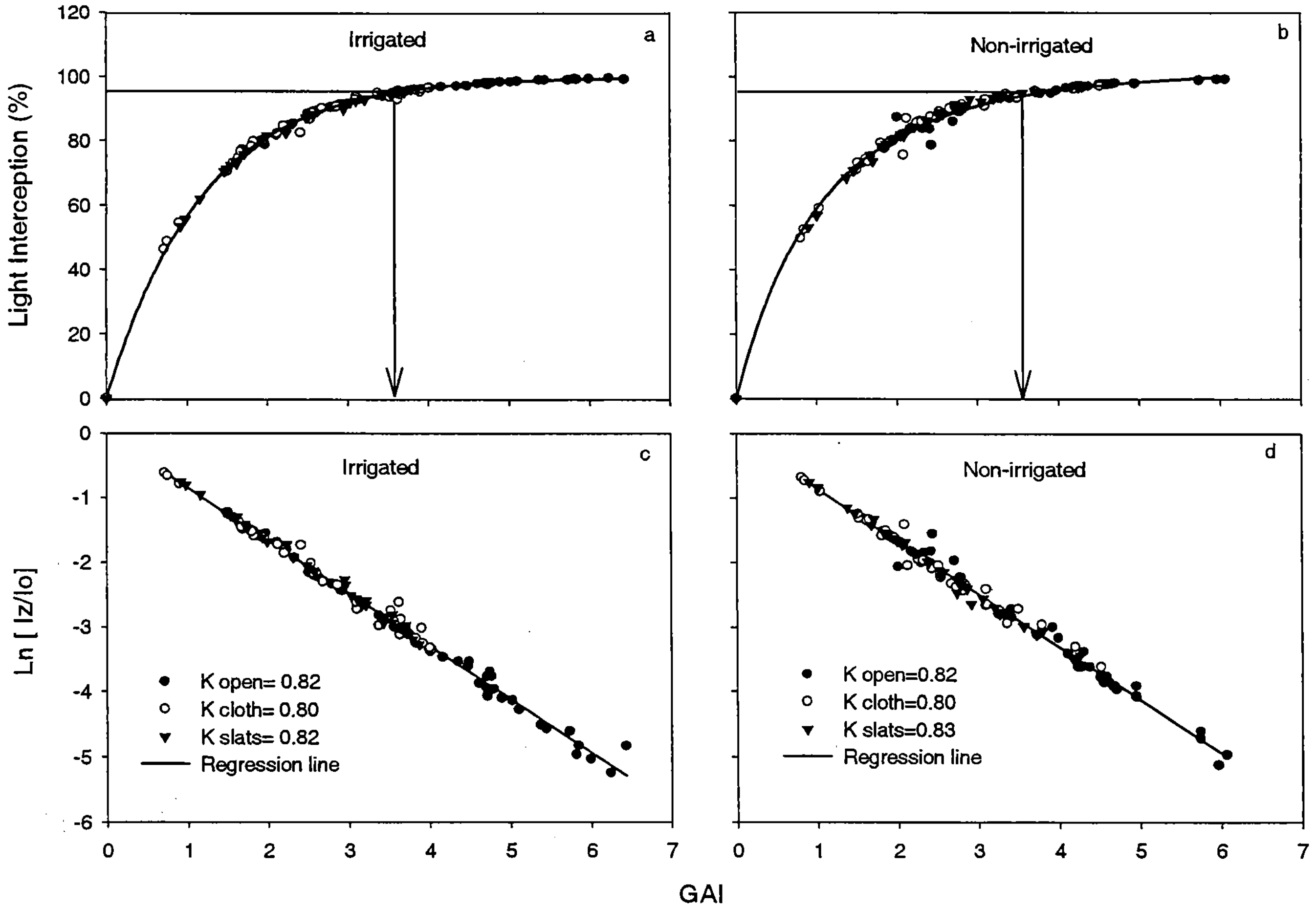

Figure 3.09- Radiation interception (*ab*) within lucerne canopy and natural log of radiation penetration (Ln Iz/Io) (*cd*) against green area index (GAI) in irrigated and non-irrigated conditions and under full sunlight (●), shade cloth (○) and wooden slats (▼) at Canterbury, New Zealand. The extinction coefficient (K) was calculated as the slope of lines in *c* and *d* (Section3.2.5.2). Arrows indicate the critical GAI when 95% of the radiation was intercepted by canopy. Plotted data includes all points from 3 replicates.

3.3.2.4- Stem height (STH)

Lucerne stem height (Figure 3.10) followed a similar pattern to the DM yield. The stem elongation rate decreased in all treatments across rotations ($P<0.001$). An interaction was observed between water and light regimes for elongation rate in Rotation 2 ($P<0.02$). This was because the reduction in stem elongation caused by shading was only observed in irrigated conditions (15.3 mm d^{-1}). Both shaded structures (18.7 mm d^{-1}) decreased stem elongation by 14% compared with full sunlight (21.7 mm d^{-1}) in irrigated conditions. The relative decrease in stem elongation under shade was also 14% for the subsequent Rotation 3 ($P<0.001$) in irrigated and non-irrigated conditions. No differences ($P>0.55$) in stem elongation rate were observed between the three light regimes in Rotations 1 (23.6 mm d^{-1}) and 4 (4.6 mm d^{-1}).

Despite the similarity in the numbers of dominant lucerne stems between plants grown under the cloth and slatted regimes, field observations indicated that canopy profiles were distinct for the 3 light treatments. Lucerne grown in full sun and under the cloth regime presented a more uniform appearance than under the slats. Data for stem classes measured in Rotation 3 showed the percentage of long stems (> 0.2m) was greater ($P<0.05$) in full sunlight (62%) than under cloth (56%) and slats (52%). The percentage of medium (32%) and short (18%) stems were similar between the two artificial shade regimes. A similar result ($P<0.02$) was found for stem classes in Rotation 4.

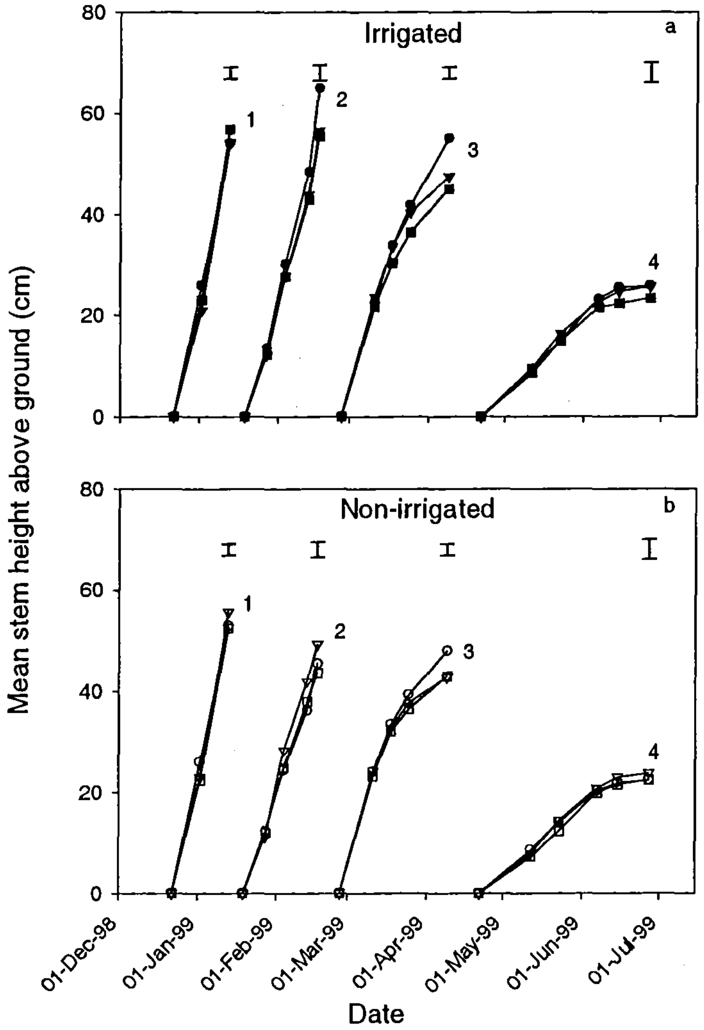

Figure 3.10- Mean height of dominant lucerne stem for 4 successive rotations in irrigated (*a*) and non-irrigated (*b*) treatments under full sunlight (●,○), shade cloth (■,□) and wooden slats (▼,▽) in Canterbury, New Zealand. Data are averages of 3 replicates and bars show standard errors for final harvests. Numbers on top indicate the rotation number.

3.3.2.5- Number of stems and leaf to stem ratio

In full sun, the mean number of stems over the 4 rotations was 671 m^{-2} in irrigated and 616 m^{-2} in non-irrigated treatments. Differences ($P<0.05$) between irrigated and non-irrigated lucerne under the two shaded regimes were observed in the full sun during Rotations 1 and 3 (Figure 3.11). The greatest differences ($P< 0.01$) was at the end of Rotation 1, with 637 stems per m^2 in irrigated and 540 per m^2 in the non-irrigated treatment. The mean number of stems over the experimental period was consistently reduced ($P<0.05$) by about 19% under cloth (522 m^{-2}) and 22% under slats (505 m^{-2}) compared with full sun (644 m^{-2}), but no difference was detected between the two shade regimes.

There was no difference (P>0.09) in leaf to stem ratio (vegetative stage 2, Fick & Mueller, 1989) between treatments for most of the rotations, although values were consistently greater for shaded than for sun plants. The exception was in Rotation 3, when non-irrigated (1.09) treatments showed a greater L/S ratio (P<0.05) than irrigated (0.91) and shaded regimes (1.1). The averaged L/S ratio over the 4 rotations was 1.14 in full sunlight and 1.22 under both shaded treatments.

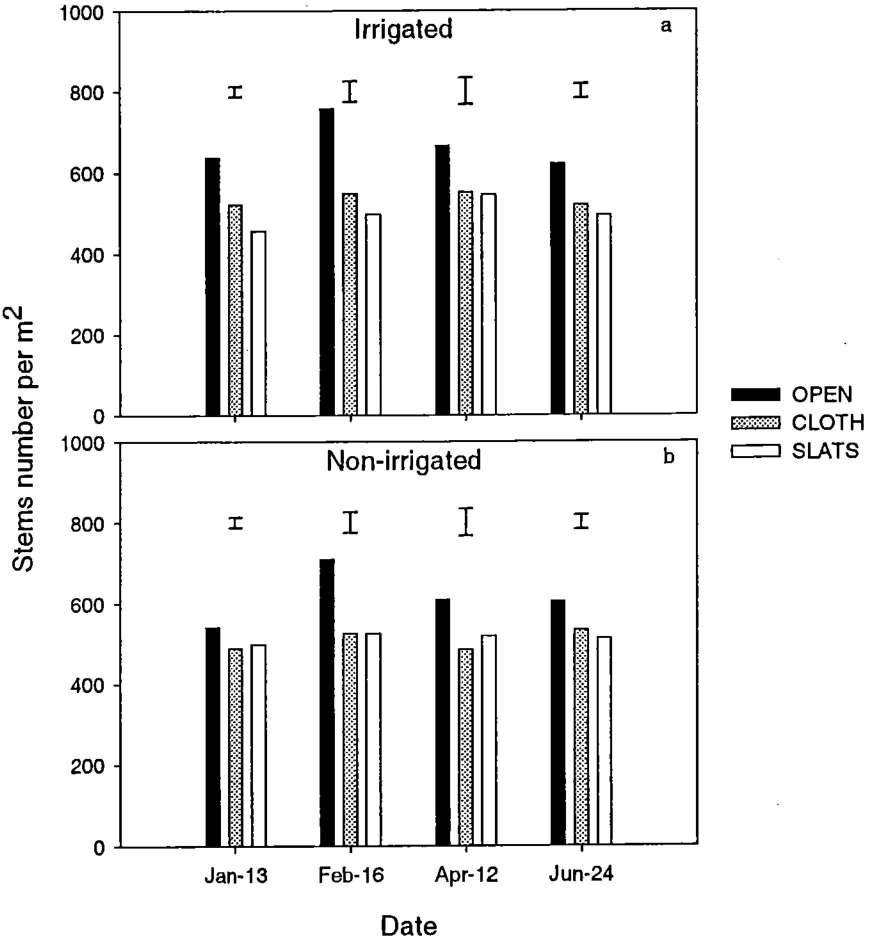

Figure 3.11- Number of lucerne stems per m^{-2} at the end of each rotation in irrigated (*a*) and non-irrigated (*b*) treatments in full sunlight, under shade cloth and wooden slats at Canterbury, New Zealand. Bars on top are standard errors calculated for each rotation.

3.3.2.6- Radiation use efficiency (RUE)

Linear regressions were fitted to lucerne shoot DM against accumulated PARi (Figure 3.12) to allow calculations of RUE in each rotation. Regressions were performed with (Appendix 2) and without (Table 3.06) being forced through the origin. Both methods showed similar statistical results, but in this section results based on the regression not forced through the origin are presented.

The effect of irrigation water on RUE was close (P>0.06) to the significant level used for the present study at Rotations 2 and 3. Irrigated treatments increased RUE by 27 and 51% compared with non-irrigated treatments in Rotations 2 and 3, respectively.

Full sunlight conditions gave lower RUE than shaded plants in all rotations (P<0.008). RUE under shade cloth was higher (P<0.001) than under slats from Rotation 1, 2 and 3, but similar in Rotation 4. The mean RUE over the experimental period was 1.06 g DM MJ^{-1} PARi in full sunlight compared with 1.73 under shade cloth and 1.49 g DM MJ^{-1} PARi under slats. There was a consistent trend of RUE to be lower (P<0.001) for all treatments in autumn.

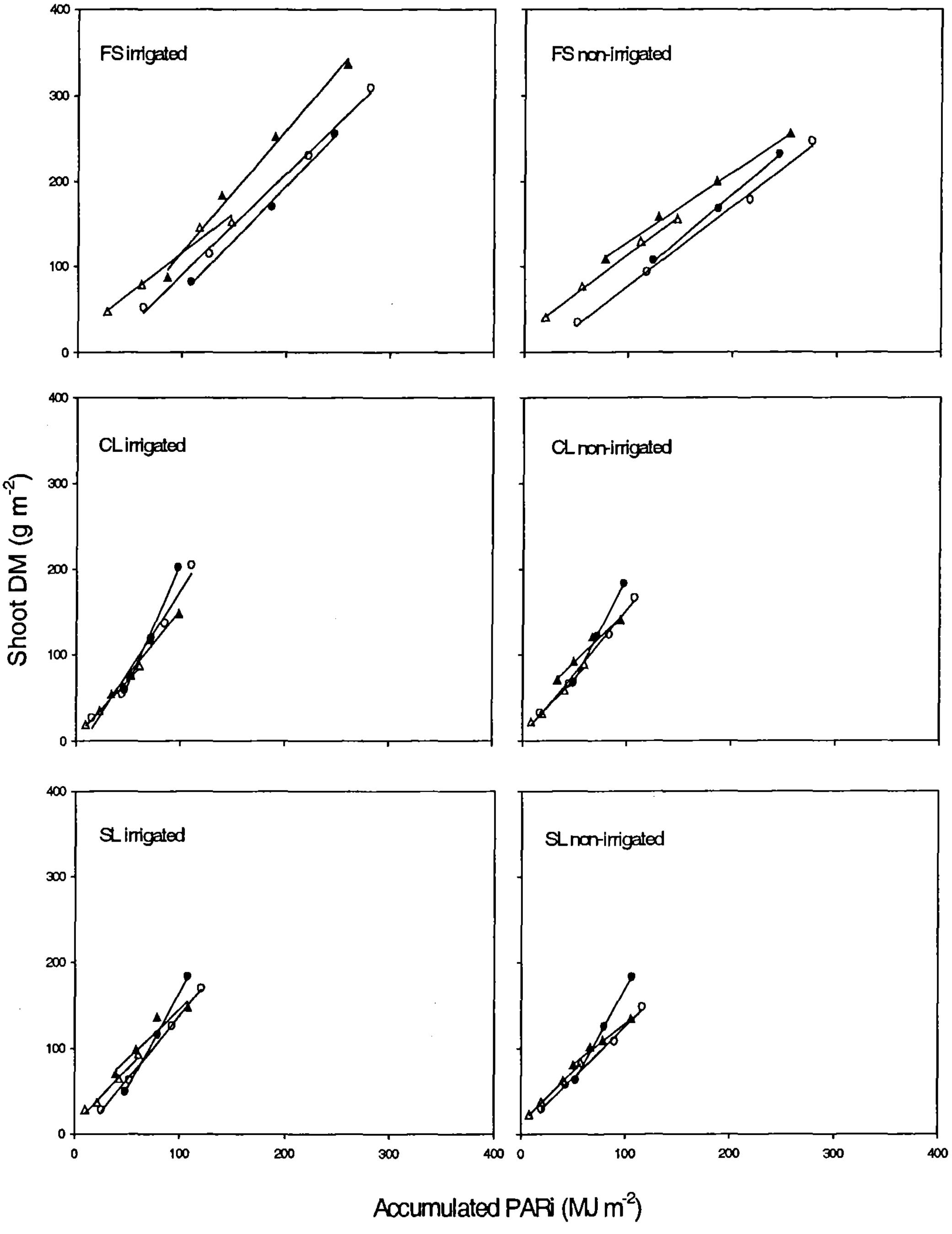

Figure 3.12- Lucerne shoot dry matter (DM) against accumulated photosynthetically active radiation intercepted by canopy (PARi) measured from Rotations 1 to 4 under irrigated and non-irrigated conditions in full sunlight (FS), shade cloth (CL) and wooden slat (SL) regimes for Rotations 1 (●), 2 (○), 3 (▲) and 4 (Δ) in Canterbury, New Zealand. Data are means of 3 replicates. The slope of each linear regression is the RUE for the treatment and is presented in Table 3.06.

Table 3.06- Mean coefficient of the slope (RUE) and intercept (I) calculated from the linear equation plotted in Figure 3.12 for irrigated and non-irrigated conditions. The slope of the linear regression is an estimation of the radiation use efficiency (RUE). The coefficient of determination (R^2) and standard errors (SE) for each coefficient is also indicated. Regression lines were not forced through the origin.

Treatment-	**R^2**	**Slope (RUE)**	**SE**	**Intercept (I)**	**SE (I)**
		-g shoot DM MJ $(PAR)^{-1}$-		g shoot DM m^{-2}	
Full sun irrigated- 1	0.99	1.26	0.075	-58.88	14.240
Full sun irrigated- 2	0.99	1.18	0.072	-28.27	13.876
Full sun irrigated- 3	0.96	1.43	0.194	-27.19	34.803
Full sun irrigated- 4	0.93	0.94	0.158	21.49	15.770
Cloth irrigated- 1	0.98	2.78	0.239	-73.96	18.045
Cloth irrigated- 2	0.96	1.88	0.261	-14.75	19.237
Cloth irrigated- 3	0.94	1.50	0.217	1.18	14.720
Cloth irrigated- 4	0.95	1.32	0.171	3.59	6.819
Slats irrigated- 1	0.99	2.26	0.047	-61.08	3.866
Slats irrigated- 2	0.99	1.51	0.130	-13.24	10.634
Slats irrigated- 3	0.97	1.23	0.115	23.04	8.680
Slats irrigated- 4	0.98	1.30	0.116	9.90	4.471
Full sun dry- 1	0.99	1.02	0.041	-21.28	7.847
Full sun dry- 2	0.98	0.92	0.071	-14.68	13.218
Full sun dry- 3	0.99	0.82	0.031	46.48	5.493
Full sun dry- 4	0.98	0.92	0.080	22.23	7.684
Cloth dry- 1	0.99	2.39	0.092	-49.68	6.881
Cloth dry- 2	0.99	1.48	0.075	3.86	5.388
Cloth dry- 3	0.94	1.17	0.213	33.40	13.843
Cloth dry- 4	0.98	1.30	0.102	7.21	3.781
Slats dry- 1	0.99	2.24	0.020	-54.56	1.615
Slats dry- 2	0.99	1.21	0.066	3.98	5.128
Slats dry- 3	0.92	0.96	0.069	32.66	5.399
Slats dry- 4	0.99	1.23	0.033	11.08	1.186
	Rot. 1	**Rot. 2**	**Rot. 3**	**Rot. 4**	
*SEM**	0.057	0.099	0.055	0.040	
F probability					
Water	0.223	0.059	0.059	0.777	
Light	< 0.001	0.007	0.008	< 0.001	
*Water*light*	0.102	0.863	0.276	0.862	

† Rotation lengths (1-4) are indicated in Table 3.04. * SEM= standard error of means for light effect

3.3.2.7- Leaf net photosynthesis (Pn)

The Pn rate was unaffected by irrigation over the first 3 rotations ($0.14<P<0.62$), but in most cases shading decreased ($0.001<P<0.016$) the photosynthetic activity of individual top leaves compared with full sunlight (Table 3.07). The mean Pn rate measured in irrigated conditions was 31.4 µmol CO_2 m^{-2} s^{-1} in full sunlight compared with 28.8 under shade cloth and 27.0 under slats. In non-irrigated conditions, the Pn rate was 31.1 µmol CO_2 m^{-2} s^{-1} in full sun, 27.6 under cloth and 26.1 under slatted treatment. Top leaf photosynthesis measured under cloth was 18% greater ($P<0.005$) than under slats only on 16 February 1999, but similar for the other rotations.

Table 3.07- Instantaneous net photosynthesis rate at 1000 photons m^{-2} s^{-1} of the youngest fully expanded lucerne leaf of crops grown in full sunlight (FS), under shade cloth (CL) and wooden slats (SL) in irrigated (irr) and non-irrigated (dry) conditions in season 1999.

Treatments	FS irr	CL irr	SL irr	FS dry	CL dry	SL dry
	---------------------------µmol CO_2 m^{-2} s^{-1}-------------------------					
12 Jan	25.75	23.52	22.84	25.36	22.71	20.79
03 Feb	38.32	38.89	36.77	36.94	37.58	35.06
16 Feb	30.77	29.67	23.08	31.72	26.07	22.90
22 Mar	31.25	25.62	24.53	30.07	26.54	27.72
30 Mar	33.44	26.57	27.73	34.18	26.81	24.83
12 Apr	29.08	28.81	27.04	28.30	25.60	25.40
	12 Jan	***03 Feb***	***16 Feb***	***22 Mar***	***30 Mar***	***12 Apr***
F probability						
Water(W)	0.617	0.561	0.807	0.144	0.569	0.161
Light(L)	0.016	0.533	0.005	0.007	0.001	0.293
W*L	0.697	0.990	0.436	0.236	0.303	0.713
SEM*	0.704	1.457	1.233	0.829	0.836	1.037

* SEM= standard error of means.

3.3.2.8- Node appearance and flowering time

Calculations for the phyllochron were performed with the assumption that light regimes presented equivalent mean air temperatures over the experimental period (Table 3.08, Figure 3.13). The phyllochron increased ($P<0.001$) from Rotation 1 to 4 for all treatments with mean values of 34, 39, 56 and 57 °C day for Rotations 1 to 4, respectively. Irrigation only affected node appearance in Rotation 3 ($P<0.01$) with values of 55 °C day and 57 °C day in irrigated and non-irrigated treatments, respectively. Light regimes never affected ($0.07<P<0.71$) lucerne development.

The presence of flowering buds was observed in Rotations 1, 2 and 3 in full sunlight conditions and only in Rotation 2 for the shaded treatments. In the Rotations 1 and 2, irrigated plants accumulated about 374 °C day to reach early bud in the full sun, but this increased to about 603 °C day in Rotation 3. For Rotation 2, the thermal time required to flower was 490 °C day under both shaded treatments, regardless of water status regimes. During Rotation 3, irrigated plants showed buds from node 10 upwards, compared with from node 7 in non-irrigated conditions. This required 603 °C day to flower in irrigated and 437 °C day in non-irrigated treatments.

Table 3.08- The mean phyllochron (°C day) of lucerne in irrigated and non-irrigated conditions submitted to full sunlight, shade cloth and slatted regimes for the 4 rotation periods in Canterbury, New Zealand. Mean air temperature for each rotation is indicated in parenthesis.

	Rotation 1† (17.3 °C)	**Rotation 2 (16.9 °C)**	**Rotation 3 (14.9 °C)**	**Rotation 4 (9.8 °C)**
	----------------------------- °Cd -----------------------------			
FS irrigated	33.17	35.52	51.71	57.11
CL irrigated	33.50	37.38	55.95	55.70
SL irrigated	33.53	39.98	57.84	57.83
FS non-irrigated	36.90	40.93	55.96	56.17
CL non-irrigated	34.80	40.16	57.75	60.51
SL non-irrigated	34.61	42.04	57.75	54.60

	F probability				
	Water(W)	*Light(L)*	*W*L*	*Mean*	*SEM**
Rotation 1	0.341	0.712	0.542	34.42	1.275
Rotation 2	0.187	0.122	0.412	39.33	1.255
Rotation 3	0.008	0.069	0.393	56.16	1.498
Rotation 4	0.735	0.439	0.101	57.15	1.887

† Calculations were performed for the whole rotation length. Final readings were performed on 12 January, 17 February, 09 April and 15 June 1999.

* SEM= standard error of means.

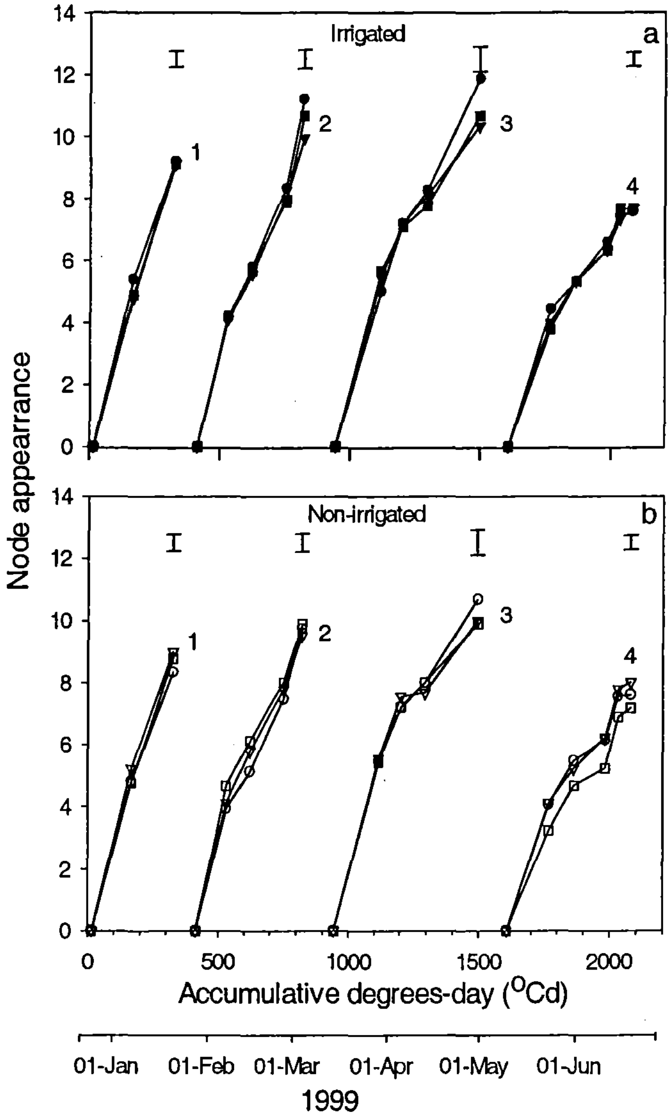

Figure 3.13- Node appearance of lucerne stems against cumulative thermal time for 4 successive rotations in irrigated (*a*) and non-irrigated (*b*) treatments in full sunlight (●,○), under shade cloth (■,□) and wooden slats (▼,▽) at Canterbury, New Zealand. Thermal time calculation starts on 23 December 1998. Bars indicate the standard errors for final reading. Numbers on top indicate the rotation number. The phyllochron is calculated as the slope of the curves.

3.4-Discussion

3.4.1- Environmental changes

3.4.1.1- Light regimes

The two artificial shade structures produced distinct temporal and spectral light regimes for the lucerne crop. The level of radiation intensity was similar between structures (at about 46% PPFD transmittance) compared with full sunlight, but only the slatted structure produced the alternating periods of sun and shade typically observed in agroforestry systems on clear and sunny days. The longest single period of full sun received by the lucerne crop under the slats was 120 minutes near midday in February (Figure 3.02).

In addition, the spectral changes in R/FR ratio found under the slats during the shade phase (0.74) were consistent with values found in coniferous (0.8) and deciduous (0.9) shade by Bell *et al.* (2000). Because of the high proportion of diffuse light during shading and since red light is only observed in the direct radiation, it is speculated that the reduction in R/FR ratio under slats was primarily caused by a blocking effect from the slats. Healey & Rickert (1998) found a dramatic increase in the proportion of diffuse light under a dense wooden lattice structure on a sunny day. In contrast to the slatted structure, shade cloth produced a uniform light regime similar to that observed in full sun. The R/FR ratio under the cloth (1.30) was equivalent to full sunlight conditions (1.32) and the sun phase under slats (1.28). The indication was that the black shade cloth did not absorb or block any of the PAR wave bands and therefore it approximated a 'neutral filter', which uniformly reduces transmission of light in the 300-1100 nm wave band (Yates, 1989). This is inconsistent with tree canopies where the radiation transmitted contains a lower proportion of red (Ludlow, 1978) and a greater proportion of near infra-red (Healey & Rickert, 1998) light than found under shade cloth (Yates, 1989).

3.4.1.2- Temperature

The two artificial shade structures altered the temperature at the canopy height, particularly in summer time (Figure 3.03). Shade cloth and slats decreased the TCH relative to full sun during daytime and increased it at night. These results require careful analysis because temperature sensors could be influenced by changes from the components of the energy balance, by differential transpiration rates from the lucerne canopy or by disrupted air flow under the shade structures.

According to Brenner (1996), in clear full sunlight conditions, temperatures above the canopy usually increase during the day and cool at night in full sun conditions. This was consistent with full sun data measured in this experiment and occurs because the amount of emitted long wave radiation is usually greater than the amount absorbed by soil and vegetation during the daytime (Monteith & Unsworth, 1990). However, under shaded environments, downward long wave radiation fluxes tend to be similar to upward long wave fluxes from soil and vegetation. Thus, the rate of atmosphere cooling at night is considerably slower than in full sunlight (Brenner, 1996). As a consequence, night temperatures above the shaded canopy can be warmer and daytime temperatures cooler compared with the full sunlight. This pattern was measured for both shade structures in this experiment on typical clear days of summer and autumn. In addition, it was noted that TCH under shade cloth was warmer than under slats at noon and this was probably because of a greater daily amount of long wave radiation emitted downwards by the black plastic material compared with the wooden slats.

Changes in temperature above the canopy between light treatments could be also caused by differential transpiration rates. Stomata are expected to be more closed under shaded than full sunlight regime, because of the low radiation effect on stomatal conductance. According to Salisbury & Ross (1993), light acts on mesophyll cells, which then send a message to the guard cells. As a consequence, rates of transpiration would be greater in the full sun than under the shaded regimes especially when water stress was not severe. However, temperatures were warmer in full sun than under cloth during the day. Under the slatted treatment, a bi-model pattern similar to the light regime was observed for TCH. Temperatures above the canopy under slats ranged from nearly the same as in full sun to well below that observed under cloth. This explains the slower rate of temperature cooling observed under slats compared with under cloth during the night (Figure 3.03). In a subtropical environment, Wong & Wilson (1980) also found a decrease of 1-2 °C in mean air temperatures above canopy and leaf temperatures measured below shade cloth (60 and 40% light transmissivity) compared with full sunlight at noontime. These authors associated such results simply with lower radiation load under shade compared with full sun. Wilson (1996) never observed the effects of 50% shade cloth on maximum or minimum above-canopy temperatures for tropical grasses, but shade lowered temperature extremes of surface soil up to 10-12 °C compared with full sunlight. Soil temperatures were not measured in the present study, but are perhaps far more critical for plant performance under shade than small differences in air temperatures, specialy because of large potential differences in surface soil temperatures (Wilson, 1998). The study suggested that the lower temperatures under shade than in full sun had a beneficial effect on microbial activity and in holding soil water content in the warm subtropical area.

3.4.1.3- Soil Moisture

As expected, changes in SWC (Figure 3.04) observed in this experiment were a result of the amount of rainfall, irrigation and evapotranspiration at the experimental site. The lowest soil moisture readings measured in non-irrigated treatments were at the end of summer in late February (Figures 3.04 and 3.05). This was consistent with the total rainfall being below and evapotranspiration above the long-term means in February (Table 3.01). There was an indication that plant water extraction was restricted in non-irrigated treatments from Rotations 1 to 3 (Figure 3.04). The SWC at 0.5-2.0 m (Figure 3.05) declined from September 1998 to January 1999 and remained nearly constant until the end of the season, indicating that water had been extracted from these layers and was not recharged again during the experimental period.

The small differences observed between the three light regimes were assumed to be from soil textural variation. The rates of SWC decrease under artificial shading were similar to those in full sun for non-irrigated conditions. In contrast, Wilson & Wild (1991) suggested that the combined-effects of low radiation load and decreased evapotranspiration resulted in greater SWC from 0-0.2 m soil depth under a shade cloth compared with an open treatment in a subtropical environment. This anomaly was probably because of the high humidity, which would decrease the evaporative demand in subtropical areas compared with the temperate area used in this study.

3.4.2- Biological changes

3.4.2.1- Effects of irrigation

Lower DM yield, GAI and STH indicate that lucerne was water stressed in the open non-irrigated treatments for Rotations 2 and 3. The increase of SWC in the top 0.5 m due to irrigation was 20, 30 and 25% compared with non-irrigated in full sun at the end of Rotations 1, 2 and 3, respectively, and was accompanied by an increase in DM yield of 11, 25 and 32% in Rotations 1, 2 and 3, respectively. The progressive reduction of DM yield under shade from rotation 1 to 4 was probably a cumulative effect of reduced carbohydrate storage in roots in non-irrigated treatments since the beginning of the water stress period. Likewise, the increase due to irrigation in canopy GAI (Figure 3.08) was about 5, 28 and 20% compared with non-irrigated treatments in Rotations 1, 2 and 3, respectively. The greatest decrease in yield and GAI observed in non-irrigated conditions occurred during Rotations 2 and 3, when SMD (Figure 3.06) reached averages of about 340. In Rotation 1, the mean SMD in non-irrigated treatments was 297 ± 21 mm and only a small benefit on lucerne yield from irrigation was observed. Two years before this experiment and at the same site, Inch (1998) and Brown (1999) reported that the DM yield of the lucerne crop in the non-irrigated decreased relative to the irrigated treatment with a SMD of 215 mm. Any difference in the critical SMD between years probably resulted from a change in root structure leading to greater water extraction in the later seasons. The differences between irrigated and non-irrigated treatments for DM yield and GAI were smaller in Rotation 4 due to the recovery of SMD starting from 26 February 1999 when 31 mm of rain fell on the experimental site (Figure 3.06).

Evidence of water stress in Rotations 2 and 3 agreed with lower RUE in the non-irrigated than irrigated treatments (Table 3.06) for all of the light regimes, although plant architecture (Table 3.05) and leaf photosynthesis (Table 3.07), two important determinants of radiation interception and utilization by canopy (McKenzie *et al.*, 1999), were not affected by irrigation during this study. The primary effect of water stress on plants is a progressive loss of cell turgor pressure, which results in a decline of cell and leaf area expansion (Hay & Walker, 1989). As a secondary effect, foliage angle can change and radiation interception by the canopy decreases with consequences on photosynthetic activity (Trenbath & Angus, 1975). Contrary to the reports by Moran *et al.* (1989), who worked with lucerne under a larger soil water deficit than observed in this study, the level of water stress experienced by lucerne crops did not affect either foliage angle or top leaf photosynthesis. It is speculated that the main effect of water stress on lucerne yield in this study resulted from a decrease in the total amount of carbohydrates partitioned to shoots after defoliation. One indication was the slower lucerne GAI recovery, after grazing to the first measurement, in non-irrigated compared with irrigated treatments.

In Rotations 2 and 3, the increase in DM yield and GAI caused by irrigation was typically lower under the shaded treatments than in full sunlight. This suggests that the crop growth under cloth and slats was primary limited by the low PPFD, which probably never offered sufficient energy (activated electrons) for photosynthesis activity and efficient use of the available soil water for biomass production. Therefore, the apparent ‘benefit’ of shading in holding soil water content in non-irrigated areas, as discussed by Wilson & Wild (1991) and Wilson (1996) for subtropical environment, would depend on the level of radiation, the evaporative demand and the water stress to which crops are exposed.

Such benefits for C_3 and C_4 crops are likely to be observed under conditions of greater water stress than those experienced during this experiment and under light levels close to the photosynthetic saturation point (Nelson, 1995). For the level of shading (about 50% transmission) and water stress experienced by lucerne plants in this study, irrigation was advantageous particularly in Rotation 2. Irrigation is not an ordinary practice in agroforestry systems, but it was used in this study to isolate the effects of radiation and soil water content during drought periods, which are occasionally observed in tree-crop/pasture associations in both subtropical and temperate regions.

3.4.2.2- Effects of light regimes

DM and growth rates

Lucerne decreased yield under shade compared with full sunlight conditions and only slight differences could be noted between shade cloth and wooden slat regimes. The DM yield (Figure 3.07) under shade relative to the full sunlight decreased progressively over the experimental period. This started at about 25% of the DM yield in full sun for irrigated and 21% for non-irrigated conditions in Rotation 1, but increased to a maximum of 55 and 45% for irrigated and non-irrigated treatments, respectively, in Rotation 3. This progressive decrease of DM yield was probably caused by a progressive decline in root reserves from the beginning of the experiment. The consequences of that would only become apparent in later rotations as plants adjust to the new source and sink relationships experienced previously under shade conditions.

Growth rates during the linear phase also indicated a progressive reduction under the two artificial shade regimes compared with full sun treatments. The reduction was 49% for irrigated and 39% for non-irrigated treatments in Rotation 3. These results agree with Walgenbach & Marten (1981), who submitted field lucerne to 47 and 73% shade cloth in summer. The authors observed decreases of shoot total carbohydrates content from 8-16% in the first rotation to 28-44% in the second rotation under the two shaded regimes compared with full sunlight conditions. This caused a progressive reduction in the rate of subsequent regrowth periods.

The relative reductions of DM yield or growth rates observed under shade in Rotation 3 were less than the decrease of radiation caused by cloth (58%) and slats (53%) compared with full sun. This apparent anomaly could occur because, in a lucerne canopy, photosynthesis decreases progressively, but not proportionally to the reduction in available light (King & Evans, 1967; Cooper, 1969; Pearcy & Lee, 1969; Wolf & Blaser, 1972). Although top leaf Pn rates (Table 3.07) consistently showed lower values under the two shaded structures than in full sunlight, the magnitude of these differences was much lower than the differences found for DM yield. The greatest reduction in leaf photosynthesis was only 18% for cloth and 25% under slats in irrigated conditions in Rotation 3. It is important to note that photosynthesis was measured only on the youngest fully expanded leaf and only at a constant artificial light flux of 1000 μmol m^{-2} s^{-1} for all three light regimes. This indicates that shaded leaves in the top part of canopy were still operating close to saturation levels and maintaining sufficient photosynthetic machinery to operate efficiently in their growth environment. Although photosynthesis was not measured in different canopy layers in this study, it is reasonable to estimate that there would be a faster decline for lower canopy strata under shade treatments than in full sun and this would agree with observations by Acock *et al.* (1978). Therefore, in the whole canopy basis, the net photosynthesis decrease under the two shaded treatments could be expected to be proportional to those observed for DM yield.

GAI expansion

The shading effects on lucerne DM yield appeared to be largely due to change in GAI (Figure 3.08). That is, the canopy GAI decline was progressive under the shaded regimes compared with full sun, starting from 23% for irrigated and 20% for non-irrigated conditions in the first rotation to a maximum of 42 and 40% for irrigated and non-irrigated treatments, respectively, in Rotation 3. The magnitude of the differences between light regimes was slightly lower for GAI than those measured for DM yield; This result might be expected because changes in lucerne stem parts would have a greater influence on dry weight than they would have on GAI. From the DM (Figure 3.07) and GAI curves (Figure 3.08), it was noted that plants under cloth and slats had a slower initial regrowth (longer lag phase) than in full sunlight. This is consistent with a lower level of root reserves, which reflects primarily in early leaf area growth (Avice *et al.*, 1997). In other words, the canopy under cloth and slats took longer to reach the critical GAI than in full sunlight. The greatest delay was observed in Rotation 3, when irrigated plants grew 3 units of GAI in 19 days in full sun, whereas under the two shaded treatments this occurred in 35 days.

The reductions in DM yield, and presumably root reserves, were also reflected in the number of stems per unit area (Figure 3.11), which decreased under shade compared with full sunlight. This decrease was consistent with the changes observed in canopy GAI, whereby fewer stems would lead to fewer leaves for canopy expansion. However, the maximum reduction of stem number caused by shading was only 31% in irrigated and 26% in non-irrigated compared with full sun plants. This suggests that canopy GAI under shade was affected by other changes, besides the number of stems. One indication was the decline in STH (Figure 3.10), particularly for Rotations 2 and 3. But decline in STH is an unusual response to shade. In most species shade increases STH because of reduction in R/FR ratio (Ballare et al.,,1995). It is possible that this experiment was not long enough for lucerne crop to show all its morphological plasticity in shade. Another assumption is that specific leaf area growth was greater under the two artificial shade regimes than in full sunlight and this was supported by a consistently greater L/S ratio (Section 3.3.2.5) for shaded than full sun plants in all rotations, but particularly in Rotation 3. Woodward & Sheehy (1979) observed a similar L/S response for heavily shaded lucerne stems and concluded that some of the reserves were remobilised to grow extra leaf area and optimise light interception under low radiation conditions. A reduction in the number of stems in lucerne has also been reported as a consequence of low levels of root reserves (Lemaire, 2001).

Canopy architecture

Canopy architecture was unaffected by light regimes. The mean foliage angle (Table 3.05) was 45° for all treatments over the experimental period, which was similar to the range (40 and 50°) reported for lucerne by Heichel *et al.* (1988) and Moran *et al.* (1989). The results indicate that plants intercepted a similar relative amount of radiation per unit of GAI (Figure 3.09*ab*), regardless of light regimes. This was confirmed by the constant extinction coefficient (K=0.82) between treatments (Figure 3.09*cd*). The mean K value was greater than those (0.61-0.77) found by Wilfong *et al.* (1967) and Sheehy *et al.* (1979) both in full light, but consistent with the value of 0.88 reported by Gosse *et al.* (1982) and Gosse *et al.* (1988).

The common canopy architecture meant that the critical GAI of 3.6 was equal for all three light regimes (Figure 3.09*ab*). However, there were occasions when the canopy never reached this critical value (Figure 3.08). For example, non-irrigated plants under cloth only reached a maximum of GAI=3.2 and slats GAI=3.0 in Rotation 3. For the two shaded treatments, the critical GAI was only reached for irrigated conditions in Rotations 1 and 2. Even full sun plants did not grow to critical GAI in Rotation 4. In full sunlight, the reason that canopy GAI growth rates decreased was the low temperatures in the last autumn rotation, reaching only GAI=3 after 60 days of regrowth. For shaded conditions, it seems likely that plants tried to maximise net canopy photosynthesis by adding leaf layers until the net return from the bottom (most heavily shaded leaves) was zero (Horn, 1971). That is, canopy GAI was adjusted under cloth and slats until the irradiance penetrating to the most shaded leaves equalled their compensation point (Givinish, 1988).

RUE

There was an indication that more shoot growth per unit of intercepted PAR was obtained under cloth and slats than in full sunlight (Figure 3.12 and Table 3.06). Radiation decreased by about 55% under cloth and slats, but potential leaf Pn was about 90 and 85% of that observed in irrigated and non-irrigated full sunlight crops, respectively. Thus, lucerne leaves developed under cloth and slats seemed to still have the capacity to photosynthesise effectively compared with the saturated leaves developed in full sun. For the whole canopy, this difference is expected to be lower than for the top leaves, but still the overall rates under shade were estimated to decrease less than the reduction in the amount of radiation.

The values reported for RUE (Table 3.06) in full sunlight were lower than those reported by Khaiti & Lemaire (1992) for field lucerne seedlings in the summer (1.80g DM MJ^{-1} PAR) and in the autumn (1.13g DM MJ^{-1} PAR). The reason for such differences was possibly the greater remobilisation to roots for the 3 years old lucerne stand used in this study compared with that calculated for a seedling crop. A greater RUE for shaded than sun plants has been reported previously for other crops, especially in intercropping and agroforestry systems (Wilson & Ludlow, 1991; Cruz, 1995; Sophanodora, 1989). For example, Healey *et al.* (1998), working with subtropical grasses under 25% black shade cloth observed that increased shoot to root ratio and decreased respiration rate contributed to the 16% enhancement in RUE under the shade compared with full sunlight. However, the authors stated that it was actually the increase in diffuse radiation under the cloth, allowing more radiation to be spread over sunlit and shaded leaves, that enhanced RUE compared with the full sun environment. There are other factors, which have been indicated to explain increased RUE under low levels of incident radiation (Wilson & Ludlow, 1991): more DM is partitioned to above-ground herbage; increased L/S ratio, thereby reducing light interception by less efficient stem tissue; increased leaf nitrogen content and less CO_2 limitation for leaf photosynthesis. In this study, no changes were observed for L/S ratio (Section 3.3.2.5). Although lucerne root aspects were not measured, the present study suggests a substantial decrease in roots and root reserves under shade (eg. progressive decrease in herbage DM yield and RUE from rotations 1-3, increase in RUE under shade and increased lag phase in regrowth), especially when accompanied by little changes in plant morphology, measured as foliage angle, extinction coefficient, L/S ratio, STH, leaf Pn rate at saturation and node appearance. Likely, these responses indicate that there was an increase in shoot/root ratio under shade, caused by carbohydrate partitioning and translocation of root reserves accumulated before the experiment started, and this would explain the increase in RUE under cloth and slats compared with full sun.

Lucerne development (Figure 3.13) was apparently unaffected by shading. The phyllochron (Table 3.08) was similar between the three light regimes. The similar daily temperatures measured above the canopy (Figure 3.03) in the full sun and under shade may have contributed to this lack of response, despite the changes observed between day and night temperatures. Plants under cloth and slats flowered only once in Rotation 2, whereas in full sun flowering was observed from Rotations 1-3. This was an indication that shaded plants were possibly affected by less carbohydrate available for growing the flowering buds.

Indeed, there were little differences in lucerne morphology between plants growing under shade cloth and wooden slats in this experiment. In this short-term study, the greatest difference was in the stem size classes. Although statistically the results for stem classes never showed significant differences between the two artificial shading treatments, field data suggested that plants under slats had a greater variation in stem sizes than under the cloth and in full sun. In fact, plants under slats showed some of the stems as long as those observed in full sunlight. This was not detected in the results because the longest class size (> 0.2 m) was limited to distinguish long stems between the light regimes. It would be expected, if a stratified GAI analysis had been performed, that the slatted plants would have presented a greater GAI in the uppermost stratum than plants under cloth conditions. Potentially, this would be a disadvantage for light distribution within the canopy under slats if leaves of the upper stratum were not more vertically dispersed. As overall canopy architecture was unchanged with the 3 light regimes, this could partially explain the greater RUE observed under cloth compared with slats from Rotation 1 to 3. The increase and decrease of photosynthetic activity during the sun and shade periods under slats was not determined in this study, but it may greatly explain the advantage for plants growing under cloth compared with under slats. Data from the literature (Peri *et al.*, 2002) suggests that maximum leaf Pn rate actually decreased gradually after leaving the sun and entering the shade period under a slatted structure.

3.5-Points to be addressed

Based on the temporal radiation differences between shade cloth and slats, it seems likely that lucerne leaves under the intermittent (slat) regime changes its photosynthetic activity from the full sun to the heavy shade periods (and vice-versa). At this stage, results would agree with McCree & Loomis (1969) that it is valid to use leaf photosynthetic rates determined in continuous shade conditions for the alternating sun/shade regime. However, if yield differences are likely to appear between the continuous and intermittent regimes in a long-term study or at distinct regrowth periods, then it is critical to know the plant photosynthetic activity during both the full sun and shade periods under slats. For the next experiment, the focus should also concentrate on a long-term agronomic and physiological analysis under the two artificial shade structures and under trees compared with an full sun condition.

Because lucerne is used as an indicator crop to determine shading effects, it appears necessary to maintain this analysis over different seasons and at distinct regrowth periods. After shoot removal, lucerne regrowth is a complex process in which the interaction of environmental factors (light, air and soil temperatures) and endogenous plant factors (root reserve levels, number of remaining active meristems) determines the final herbage yield (Richards, 1993; Volenec *et al.*, 1996; Lemaire, 2001). In this 'pilot' study, both artificial shading treatments were imposed after summer to a well-established lucerne crop, which was previously growing in full sunlight conditions. To obtain conclusive results, it is essential to perform further investigation on recently established plants with shade imposed at the beginning of its growing season.

In this chapter, the use of two artificial shade structures as an experimental methodology to resemble the radiation environment of an agroforestry system has been investigated. Despite the results indicating a useful potential to use either cloth or slat structures for agroforestry research purposes, the accuracy of the methods to simulate yield of understorey vegetation from a real agroforestry system is unknown. Further study should address a comparison between lucerne growing under the two artificial materials and under trees at equivalent light transmissivity levels.

Additional measurements of photosynthesis activity during shade and sun periods under the intermittent regime and morphological responses, such as stem classes, L/S ratio, internode length and stem height, in a long-term study are necessary to obtain more conclusive differences between the two artificial shade methods. In the next chapter, these measurements are again performed for a young lucerne crop, theoretically more sensitive to root reserves changes, and compared with plants grown in a non-irrigated agroforestry system during distinct seasons.

3.6-Conclusions

Lucerne plant responses submitted to different soil water and radiation conditions in a short-term led to the following conclusions:

1- The typical physical radiation characteristics (light flux, light periodicity and spectral composition) of an agroforestry system were better simulated by a wooden slatted than a plastic shade cloth structure.

2- Irrigation increased lucerne crop yields in full sunlight proportionally to the increase in SWC during water stress periods. However, irrigation had little effect under artificial shade environment and light was the primary factor that limited yield increases in this particular experiment.

3- Canopy architecture was similar and it was unaffected by water status and light regimes. Mean foliage angle was 45°, with a K value of 0.82 and a critical GAI of 3.6 for all treatments.

4- Artificial shading reduced the number of stems, GAI and DM growth compared with full sunlight. There are indications that a decrease in root carbohydrate reserves would be involved with shading effects on lucerne growth.

5- The reduction in crop yield and growth rates under artificial shading was lower than the decline in PPFD transmission compared with full sun condition, because of the greater RUE under the artificial shade structures compared with full sun.

6- There were only slight morphological differences between plants growing under shade cloth and wooden slat structures, but there were indications that differences in the proportion of stem classes may occur over a longer study period.

CHAPTER 4

Lucerne growth and development under artificial and tree shade

4.1- Introduction

In Chapter 3, the assessment of regimes for light intensity, light periodicity and spectral composition, using artificial shade structures for agroforestry research, was highlighted. Specifically, plastic cloth and wooden slats produced distinct radiation environments, but lucerne crop responses were similar over the short experimental period.

In this chapter, crop responses to the two artificial shading methods are assessed over a longer term throughout different seasons. Another objective is to determine if sun/shade intervals of 1-2 hours can improve the utilization of light energy under this intermittent light regime compared with continuous shade (Rabinowith, 1956, Section 2.1.5.3). In addition, agronomic and physiological responses of lucerne under the two artificial shade structures will be compared directly with those observed in an agroforestry system. Thus the aims of this experiment are: (i) to investigate the patterns of radiation of an agroforestry area and compare it with the two artificial shade materials; (ii) to extend the crop results of cloth and slats methods by adding tree shade levels and (iii) to determine the yield potential of lucerne under a shade environment.

4.2- Materials and methods

4.2.1- Site description

4.2.1.1- Site history

This study was conducted at the Lincoln University agroforestry area, located in Canterbury, New Zealand (43° 38'S and 172° 28'E). The area was established in July 1990 with five *Pinus radiata* genotypes and six understorey pasture treatments: 'WL 325' lucerne (*Medicago sativa*), 'Maru' phalaris (*Phalaris aquatica*) + clovers, 'Wana' cocksfoot (*Dactylis glomerata*) + clovers, 'Yatsyn' perennial ryegrass (*Lolium perenne*) + clovers, 'Yatsyn' perennial ryegrass and bare ground, in a split-plot design with three replicates. Full details of the establishment were reported by Mead *et al.* (1993).

The trees were planted at 7.0 m (between rows) x 1.4 m (within a row) spacing (1000 stems ha^{-1}) in an east-west direction. Strips of 1 m wide centred on tree rows were sprayed with hexazinone at 2.5 kg a.i. ha^{-1} in the spring of 1990 and 1991 to aid tree establishment. Therefore, experimental plots under trees had only 86% of their area occupied by sown pastures. The total area planted in trees was 5.2 ha with 18 pasture plots of 46.2 x 42.0 m (0.194 ha) each.

The pine trees were periodically thinned to a final stocking of 200 stems ha^{-1} (Table 4.01). Annual pruning (Table 4.01) controlled the diameter over stubs (DOS) and left a similar amount of crown between trees. In 1997, all trees were pruned to a final height of 6 m. Pruning residues were removed from all plots. Tree crown closure had not occurred at age 10 years. Additional details of the forestry practices were reported by Chang & Mead (2002). A view of the agroforestry experiment at age 9 years is shown in Plate 4.01.

An adjacent area of 1 ha in a full sun was used to establish the same 18 pasture treatments in September 1990. Each experimental plot was 27.5 x 18 m (0.05 ha). All pastures were cut for silage in the open and under trees in the first two growing seasons to avoid livestock damage

damage to the seedling trees. Sheep flocks have subsequently rotationally grazed both pasture treatments in the open and under trees since 1993, with no further herbage conservation.

Table 4.01- Silvicultural thinning and pruning procedures for the Lincoln University agroforestry area since trees were established in 1990.

	Thinning procedures			
	1992	1993	1994	1996
Age (years)	2.5	3.5	4.5	6.5
Stocking (stems ha^{-1})	800	600	400	200
Mean tree height (m)	1.3	2.6	4.3	8.6
	Pruning procedures			
	1994	1995	1996	1997
Age (years)	4.5	5.5	6.5	7.5
Pruning height (m)	1.4[1]	1.7[1]	3.7[1]	6.0[2]

1. Pruning to a crown length of 4 m (biological criteria)
2. Pruning to 6 m height from ground (silvicultural criteria)

Plate 4.01. A view of the lucerne pasture in the Lincoln University agroforestry experiment in summer 2000.

4.2.1.2- Tree development

At the commencement of the current study, in August 1999, the diameter at breast height (DBH) outside bark was measured using a tape and ladder and total height (Ht) using a digital hypsometer (Forestor Vertex, Sweden). Tree measurements were taken annually in three lucerne replicates at 9 and 10 years in winter (Table 4.02). From these measurements, basal area per hectare (BA), mean crown length (MCL) and total crown length per hectare (TCL) were estimated (Table 4.02).

Table 4.02- Summary of the main dasometric variables of radiata pine grown in lucerne plots at the Lincoln University agroforestry area at ages 9 (1999) and 10 (2000). Tree stocking was 200 stems ha^{-1} for both years. Values are mean of 3 replicates.

Year	**DBH (mm)**	**Ht (m)**	**BA (m^2 ha^{-1})**	**MCL (m)**	**TCL (m ha^{-1})**
1999	229	11.0	8.2	5.5	1100
SD	*7.4*	*0.45*	*0.53*	*0.55*	*110.0*
2000	256	12.5	10.4	6.5	1300
SD	*6.7*	*0.51*	*0.54*	*0.51*	*102.0*

DBH= diameter at breast height (1.4 m from ground); Ht= total tree height; BA= basal area (BA= DBH^2*π]/4 * 200); MCL= mean crown length (MCL= Ht – 6); TCL= total crown length per hectare (TCL= MCL*200); SD= standard deviations

4.2.1.3- Soil

The soil is classified as a Templeton silt loam in the New Zealand soil classification system (Udic Haplusteps in the U.S. Soil Taxonomy system). and consists of 1-2 m of fine alluvial sediments over gravels. The typical profile texture form consists of 1-2 m of fine alluvial sediments over gravels with a uniform textured layer of varying thickness (but less than 60 cm), underlain by a texturally layered portion in the B horizon and below. Textures in the layered portion ranged from heavy silt loams to sands. Gravels were found below 160 cm depth (Karageorgis *et al.*, 1984; Adams, unpublished data). It is medium to free-draining with a moderate capacity to hold moisture at 320 mm in the top one meter (Watt & Burgham, 1992). The site has only slight changes in topography, but there is variation in depth to the underlying gravels (Mead *et al.*, 1993). The soil is considered as one of the most productive cropping soils in the Canterbury plains and is used for annual crops, ryegrass and white clover seed production and grazing. The experimental area was cropped with peas (*Pisum sativa*) in the 1989/1990 season, prior to establishment.

Thirty soil cores (300 mm diameter x 150 mm depth) were taken at random within each 'Kaituna' lucerne plot in full sun and under trees at the beginning and at the end of the experiment in September 1999 and April 2001, respectively (Table 4.03). Soil nutrients between lucerne plots in the full sun and under trees were similar. Potassium (K) and magnesium (Mg) levels were optimal for maximum pasture production in sedimentary soils (Morton & Roberts, 1999), but the pH decreased from 6.0 and 5.8 in 1999 to 5.4 and 5.6 in open and under trees, respectively, by 2001. Sulphate sulphur [S (SO_4)] was below the target values in 1999, but increased to the optimum level in 2001. Soil nutrient levels for Olsen phosphorus (P), calcium (Ca) and sodium (Na) were always below the optimal levels for maximum pasture production. No fertilisers were applied during the experimental period to be consistent with the long-term experimental protocol for the Lincoln University agroforestry area.

Table 4.03- Soil nutrient levels to 150 mm depth for 'Kaituna' lucerne plots in the full sun and under trees sampled at the beginning (1999) and at the end (2001) of the experiment in the Lincoln University agroforestry area. Soil tests were performed using the Ministry of Agriculture and Fisheries Quick Test (MAF QT) procedures.

Treatment	**Year**	**Ca**[1]	**K**[1]	**Mg**[2]	**Na**[1]	**P**[3]	**S (SO_4)**[4]	**pH**[5]
		----------m.e. 100 g^{-1} soil--------				μg ml^{-1}	ppm	
Full sun	1999	5.62	0.46	0.92	0.19	7	3	6.0
	2001	5.00	0.51	0.84	0.17	7	7	5.6
Under trees	1999	5.00	0.46	0.80	0.15	9	4	5.8
	2001	4.38	0.51	0.80	0.15	10	9	5.4

1. Ammonium acetate extraction:AA determination test method; 2. Ammonium acetate extraction test method; 3. Olsen extraction:colorimetry test method; 4. Potassium phosphate extraction:IC test method; 5. 1:2.1 V/V water slurry test method (AgResearch, Lincoln, New Zealand).

4.2.1.4- Climate

The climate description and long term mean (LTM) meteorological data for the experimental site are described in Section 3.2.1. Actual air temperatures were recorded onsite in the open and under trees, using a digital temperature sensor (TDC-01A, Monitor Sensors, Queensland, Australia) located 1.5 m above ground and logged every 6 minutes. Other meteorological data (rainfall, Penmann evapotranspiration and windrun) used for the open treatments were obtained from the Broadfields Meteorological Station, which is located 2 km north of the agroforestry area (Table 4.04).

Mean monthly air temperatures were similar in the full sun and under trees over the experimental period (Figure 4.01). The mean daily temperature was 11.4 ± 3.39 °C under trees and 11.2 ± 3.3 °C in the full sun over the experimental period. On a typical winter day at the experimental site, mean daily temperature was 0.4 °C warmer under trees than in the open with maximum differences of 1.9 °C at 3.00 h (Figure 4.01a). Similar results were observed for a typical summer day (Figure 4.01b) when mean daily temperature was 0.6 °C warmer than in the open and maximum differences were 1.6 °C between 10.00 and 3.00 h.

Annual rainfall (Figure 4.02) was similar to the long-term mean (659 mm) in 1999 (625 mm) and 2000 (668 mm), but below (419 mm) in 2001. Monthly rainfall at the experimental site was below the long-term means (Table 3.01, Section 3.2.1) from April to May 1999 and from December 2000 to March 2001.

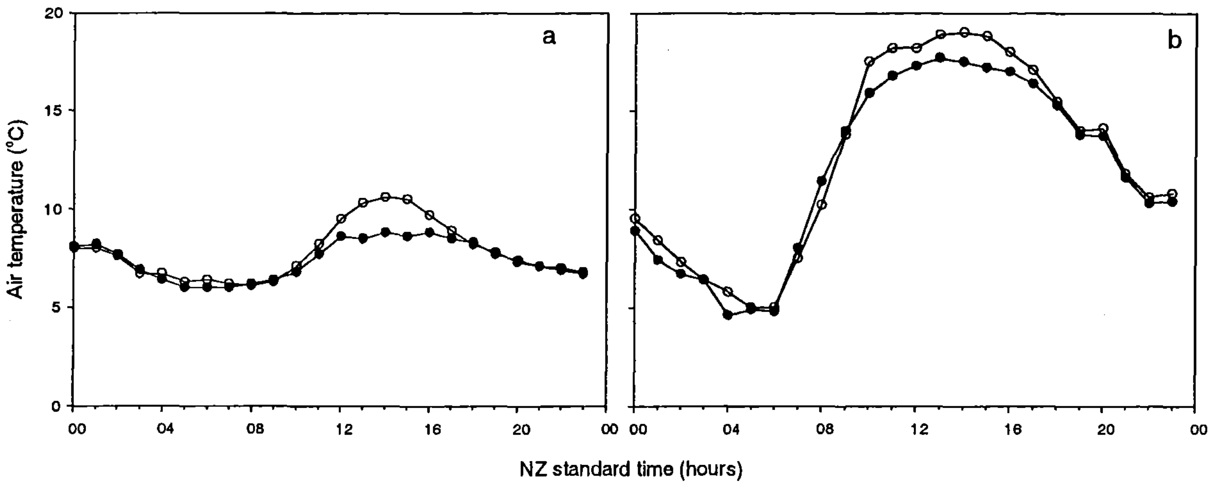

Figure 4.01. Diurnal air temperature under the trees (o) and in the open (•) on a typical sunny a) winter (16 July 2000) and b) summer (1 February 2001) day at the Lincoln University agroforestry experiment.

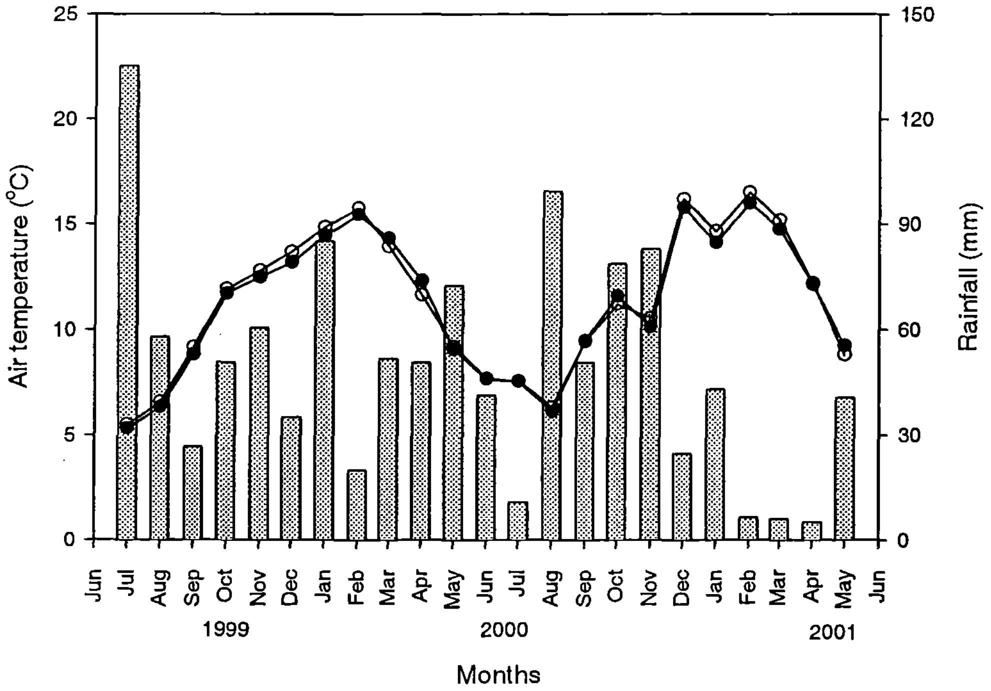

Figure 4.02. Mean air temperature (°C) and monthly rainfall (▨) measured in the full sun (•) and in the agroforestry site (o) during the experimental period for Broadfields Meteorological Station (Lincoln, New Zealand).

Table 4.04- Actual total global solar radiation (SR) (MJm^{-2}), maximum (Tmax), minimum (Tmin) and mean (Tmean) air temperatures (°C), total Penmann evapotranspiration (ET) (mm), mean windrun (km d^{-1}) and total rainfall (mm) recorded in an full sun at the Broadfields Meteorological Station (Lincoln, New Zealand) from March 1999 to March 2001.

Data*	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar
	1999										2000		
SR	478.2	292.4	213.6	161.2	148.7	262.2	417.1	521.9	601.8	742.7	660.7	553	517.3
ET	107.7	59.9	55.5	29.1	27.7	44.1	74.1	97.1	100.5	133.6	120.6	113	95.8
Tmax	21.6	16.5	16.8	12.1	10.5	12	14.8	17.3	17.3	18.9	19.5	21.6	19.5
Tmin	12.2	8.1	5.2	1.8	2.4	2.4	4.4	8.1	9	8.6	10.8	11.3	9.3
Tmean	16.5	11.9	11.2	6.6	6.7	6.9	9.4	12.2	12.9	13.4	14.8	15.9	14
Windrun	340.9	252.02	280.6	211.14	258.43	231.05	284.7	331.1	361.8	334.8	295.5	351.2	319
Rainfall	56.1	36.3	23.6	69.1	135.1	58	26.6	50.9	60.5	35.1	85	19.9	51.8

Data	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar
	2000										2001		
SR	517.3	293	169.2	177.9	152.4	231.5	361.6	564.3	684.9	786.8	712.9	516.2	465
ET	95.8	56.3	41.7	-0.5	32.4	47.5	71.9	107.4	115.6	172.7	140.7	107.5	111.1
Tmax	19.5	17.2	14.8	12.8	12.1	12.6	15	17.4	16.2	22.3	20.1	22.8	20.9
Tmin	9.3	7.8	5	3.7	3.8	2.2	5.3	6.6	5.3	11.4	9.1	11.5	9.8
Tmean	14	12	9.9	8.3	7.9	7.4	10.1	12	10.8	16.9	14.7	16.5	15.2
Windrun	319	240.2	335.1	353.9	271.6	278.4	370.8	440.7	365.7	456.9	390.1	358.6	380.2
Rainfall	51.8	50.6	72.4	41.4	10.8	99.4	50.6	78.6	82.8	24.6	43	6.4	6

* Meteorological data units: rainfall and ET (mm), air temperature (°C), SR (MJ m^{-2}) and windrun (km d^{-1})

Soil temperature was measured in the full sun and under tree treatments, using two thermistor sensors (KTY/110, Cooltronics, Christchurch, New Zealand) permanently set at 0.10 m below ground in Replicate 3. The sensors were individually calibrated to a 0.1 °C mercury thermometer. Readings were taken at one minute intervals, the averages were calculated hourly and data were stored by dataloggers. Mean monthly soil temperatures (Figure 4.03) were typically warmer under trees than in full sun, particularly in spring and summer periods, reaching a maximum difference of 2.1 °C by January 2001. In autumn and winter, mean soil temperatures under the trees and in the open were similar.

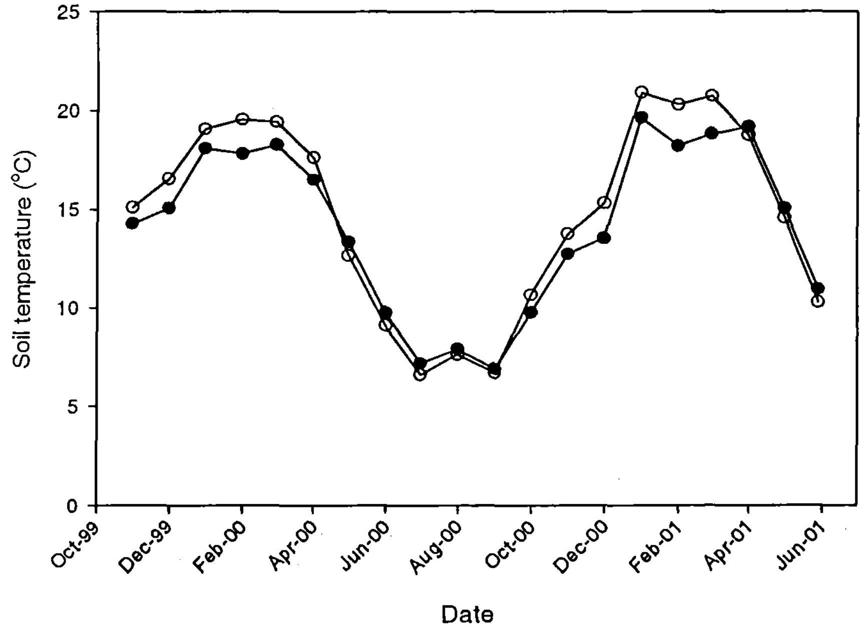

Figure 4.03. Mean monthly soil temperature (°C) measured 10 cm below ground in full sun (●) and in the agroforestry site (○) during the experimental period in Canterbury, New Zealand.

4.2.2- Treatments and experimental design

4.2.2.1- Preparation of experimental plots

Of all pasture treatments, lucerne and cocksfoot showed the greatest persistence and production under trees over the 9 experimental years (Chang *et al.*, unpublished data; Varella *et al.*, 2001). Therefore, for this study, a second set of 'Kaituna' lucerne (winter semi-dormant cultivar) treatments was established to replace phalaris plots in both full sun and under trees. The phalaris was sprayed with Glyphosate 360 (*Nufarm glyphosate* 360) at 1.5 l i.a. ha^{-1} plus a surfactant (*Pulse penetrant*) diluted at 0.1% in January and February 1999. Then, 'Kaituna' lucerne was directly drilled in a 150 mm rows at 7 kg ha^{-1} in both the open and under trees in March 1999.

4.2.2.2- Treatments and design

The present experiment used the six recently established 'Kaituna' lucerne plots (three in the full sun and three under trees) from September 1999 to March 2001. The experimental design was a split-plot randomised block with the main plots as covering status (with or without radiata pine trees cover) and sub-plots the artificial shade structures (none, shade cloth or wooden slats) in three replicates. This imposed six light regimes to lucerne plants:
I- Trees (T);
II- Shade cloth installed under trees (T+CL);
III- Wooden slats installed under trees (T+SL).
IV- Full sunlight (FS);
V- Shade cloth installed in the open (FS+CL);
VI- Wooden slats installed in the open (FS+SL);

Details of the shade structures construction were as described in Section 3.2.3.1. Shade cloth and slatted structures were set permanently in lucerne plots on 9th September 1999. A view of the experimental site and details of the shade structures in full sun and under trees are shown in Plates 4.02 and 4.03, respectively. The artificial shade structures were set in the middle of middle of the 7.0 m wide inter-row under trees and in the centre of open field plots, both in an east-west direction. Subplot study area was 5 x 15 m. The shade cloth covered a 2.3 x 1.8 m area and wooden slats covered an adjacent 2.4 x 5.2 m area. The control subplot consisted of no artificial shading, located adjacent to the shade structures and covered a 2.5 x 5 m area.

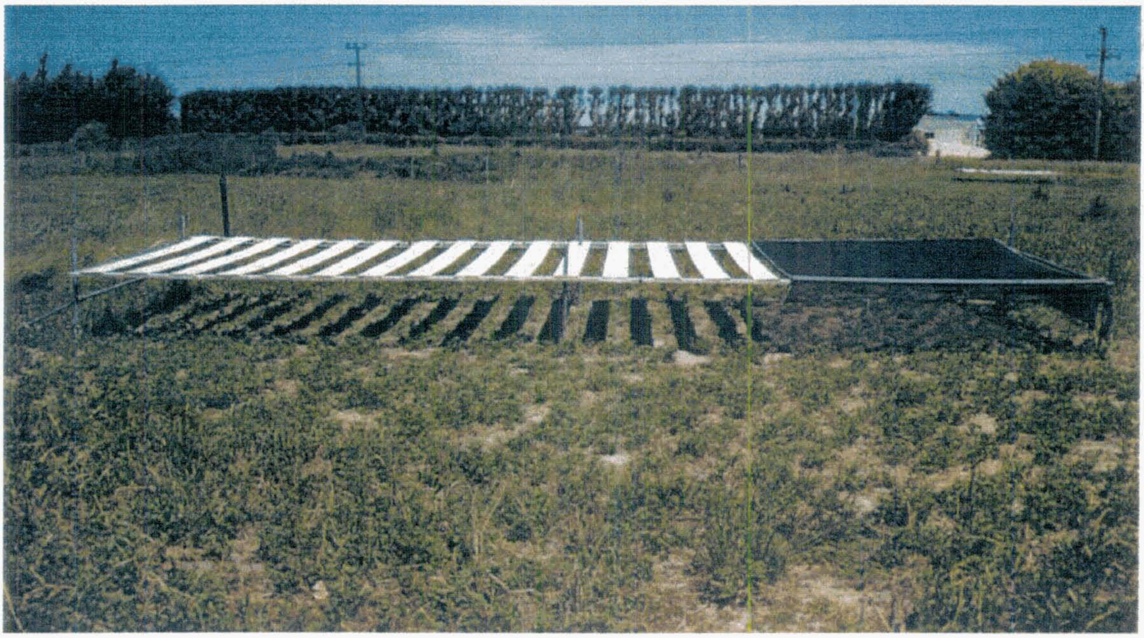

Plate 4.02. A view of the shade structures installed in the open field adjacent to the Lincoln University agroforestry experiment.

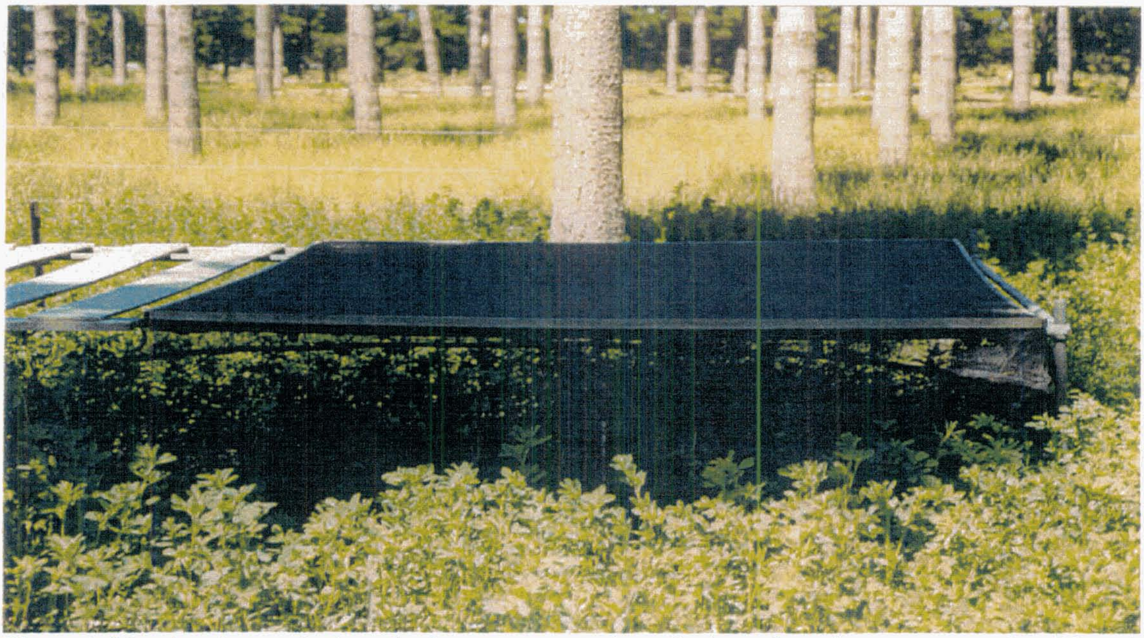

Plate 4.03. A view of the shade structures installed under the trees at the Lincoln University agroforestry experiment.

4.2.3- Site management

4.2.3.1- Grazing management

After being grazed in June 1999, all lucerne plots were trimmed before the first growing season, on 15 August 1999, and remaining herbage was left in the field. Experimental plots were grazed from 29 September 1999 to 30 March 2001, except during the winter period (May to September 2000) because the cultivars used were semi-dormant (Table 4.05). In summer 2001, there were only 2 grazing rotations (Jan and Mar) because of the low soil water content and slow lucerne crop growth rates. Two flocks of shorn Coopworth ewe lambs were rotationally grazed in the three 'Kaituna" and three 'WL325' lucerne plots in the open and under trees for 6±2 days (36±12 days regrowth). The timing of each grazing was a compromise between optimal development stage for lucerne persistence and nutritive value. Lucerne plants were allowed to fully flower (Stage 6; Fick & Mueller, 1989) at least once in summer. Shade structures were removed for the grazing period. To avoid overgrazing and plant damage, subplot areas were only grazed for the last 2±1 days in each grazing period, having been fenced off for the previous 4 days. Post-grazing residual shoots were trimmed just above crown height in all plots as described in Section 3.2.4.2. An electric fence was set up around the study areas to prevent early grazing.

Lucerne plots were rotationally grazed with a single flock in the full sun and another under trees. Thus, there were 1-2 week differences in regrowth time for crops between the three replicates, but rotation length was equivalent for all rotations, except the first one. Therefore, for this chapter, replicate differences are acknowledged, but assumed as differences in rotation time. The mean value of the three replicates and differences among treatments are the main focus.

Table 4.05- Sheep grazing period, stocking rate and 'Kaituna' lucerne rotation length at the agroforestry experiment from July 1999 to March 2001.

Rotation	Replicate	Rotation period (residual to final cut)	Rotation length	Grazing duration	Lambs per plot†	
			-----------days---------		FS*	T**
1	1	15 Aug -29 Sept 1999	45	6	8	31
1	2	15 Aug-05 Oct 1999	51	7	8	31
1	3	15 Aug-12 Oct 1999	58	6	8	31
2	1	05 Oct-16 Nov 1999	42	8	5	26
2	2	12 Oct-24 Nov 1999	43	8	5	26
2	3	18 Oct-02 Dec 1999	45	7	5	26
3	1	24 Nov 1999-02 Jan 2000	39	6	5	23
3	2	02 Dec 1999-08 Jan 2000	37	7	5	23
3	3	09 Dec 1999-15 Jan 2000	37	7	5	23
4	1	08 Jan-18 Feb 2000	41	7	7	21
4	2	15 Jan-25 Feb Mar 2000	41	7	8	21
4	3	22 Jan-04 Mar 2000	42	7	8	18
5	1	25 Feb-17 Apr 2000	52	7	5	13
5	2	03 Mar-24 Apr 2000	52	5	5	13
5	3	11 Mar -28 Apr 2000	48	5	5	13
1	1	24 Apr-04 Oct 2000	163	7	6	26
1	2	28 Apr-11 Oct 2000	166	7	8	21
1	3	03 May-18 Oct 2000	168	7	8	21
2	1	11 Oct-20 Nov 2000	40	8	9	21
2	2	18 Oct-28 Nov 2000	41	7	8	19
2	3	25 Oct-06 Dec 2000	42	8	8	19
3	1	28 Nov 2000-04 Jan 2001	37	7	7	19
3	2	05 Dec 2000 11 Jan 2001	37	6	7	19
3	3	14 Dec 2000-17 Jan 2001	34	6	7	19
4	1	11 Jan-19 Mar 2001	67	4	8	13
4	2	17 Jan-25 Mar 2001	67	6	8	13
4	3	23 Jan-30 Mar 2001	66	6	8	13

† Sheep stocking rate per plot and grazing duration were equivalent for lucerne 'Kaituna' and 'WL325' plots.
* Full sun (FS) plots measured 0.05 ha each;** Trees (T) plots measured 0.2 ha each

Sheep stocking rate was adjusted when necessary after each liveweight measurement (37±5 day intervals) to ensure a similar pasture allowance for both flocks. Calculations of stocking rate were made based on a minimal pasture intake rate of 1.5-2.0 kg DM per lamb per day (Milligan *et al.*, 1987; Rattray *et al.*, 1987). Mean stocking rate observed over the experimental period in the full sun was 21±6 hd ha^{-1} d^{-1} and under trees, 16±4 hd ha^{-1} d^{-1} per rotation. Mean actual pasture allowance was 3.3±1.4 kg DM hd^{-1} d^{-1} in full sun and 2.9±1.0 kg DM hd^{-1} d^{-1} under trees over the experimental period. Details of pre and post grazing pasture mass, pasture allowance and apparent intake rate per measured period are shown in Appendix 3.

Liveweight gains were always greater in the full sun than under trees (Appendix 3). Mean gain per head was 229±40 g hd^{-1} d^{-1} in open and 171±51 g hd^{-1} d^{-1} under trees over the experimental period, and mean liveweight gain per area were 5.3±1.4 and 2.6±1.1 kg ha^{-1} d^{-1} in full sun and under trees, respectively.

4.2.3.2- Weed control

All 'Kaituna' and 'WL325' lucerne plots were sprayed with *Spinnaker* (imazethapyr 240 g i.a. $litre^{-1}$) at 400 ml ha^{-1} of commercial product on 10th August 1999. On 16th June 2000, *Atradex* (atrazine 900 g i.a. kg^{-1}) at 1.1 kg ha^{-1} of commercial dosage and *Gramoxone* (paraquat 250 g a.i. $litre^{-1}$) at 3 l ha^{-1} were both applied immediately after grazing in the whole plot area.

Herbicides effectively controlled grasses, but some broadleaf weeds persisted in particular during the first spring season (from October to December 1999). The mean infestation for this period was 21.6±8.7 % in full sun and 18.8±5.7 % (dry weight basis) under trees. The most frequently observed weeds in the study area were hawksbeard (*Crepis capillaris*), dandelions (*Taraxacum officinale*), narrow-leaved plantain (*Plantago lanceolata*) and clovers (*Trifolium repens, T. pratense, T. subterraneum*) particularly in the full sun plots. By the second spring, weed control had reduced weeds to a maximum of 3±1.2 % in the full sun and 1.0±1.1 % under trees.

4.2.4- Measurements

4.2.4.1- Physical environment

Radiation:

The PPFD of shaded treatments was monitored with 3 quantum sensors (LI-190SB, Lincoln, USA) placed in the centre of the space between adjacent tree rows. One was periodically installed above and another below the shade structures under trees (T, T+CL and T+SL) and the third installed permanently in full sunlight (FS) conditions. Under trees, the two sensors were alternated from under cloth to under slats every 15 days and both were rotated between replicates every 30 days. PPFD was continuously recorded every 30 seconds and averaged for 15 minute intervals by a datataker under trees and another in the full sun (DT100, Roseville, Australia) over the experimental period. Radiation transmissivities under the shaded environments were calculated on a daily PPFD basis.

Spectral radiation was measured with a portable Spectroradiometer LI-1800 (LI-COR Inc., Lincoln, USA) as described in Section 3.2.3.1. Readings were the average of five scans and were taken between the wavelengths of 300 and 1100 nm at 5 nm intervals. Measurements were performed on three occasions: on 7th March 2000 for a partial overcast day at 12.00 PM (51.6° solar angle), on 10th October 2000 for a sunny day at 12.00 PM (52.6° solar angle) and on 11th October 2000 for a cloudy day at 12.00 PM. On all occasions, spectral radiation was taken in each of the ten light regime conditions:

Tree area:
I- under trees during sun period (T sun)
II- under trees during shade period (T sh)
III- under trees+cloth during sun period (T+CL sun)
IV- under trees+cloth during shade period (T+CL sh)
V- under tree+slats during sun period (T+SL sun)
VI- under trees+slats during shade period (T+SL sh)
Open area:
VII- full sunlight (FS)
VIII- under shade cloth (FS+CL)
IX- under slats during sun period (FS+SL sun)
X- under slats during shade period (FS+SL sh)

The differences in spectral radiation between treatments focuses on the proportions of blue (B= 400-500 nm), red (R= 600-700 nm) and far-red (FR= 700-800 nm) wavelengths to the total short wave radiation (PPFD+FR= 400-800 nm) as used by Bell *et al.* (2000).

Soil water content:

Metal rods measuring 0.5 m long were installed permanently in the centre of each treatment for all replicates to measure soil water content (volumetric base), using a TDR (Time Domain Reflectometer Trase system, Model 6050X1, Soilmoisture Equipment Corp., Santa Barbara, USA). Soil moisture readings were taken at 7-10 day intervals in all experimental plots.

4.2.4.2- Agronomic measurements

Dry matter yield:

The herbage dry matter (DM) yield was measured prior to sheep grazing at the end of each regrowth period. Samples were cut from a 0.2 m^2 quadrat at about 0.05 m above ground level and above plant crown. The number of DM cuts was reduced compared with the previous experiment to avoid undesirable effects of frequent cuts on lucerne regrowth. From the main sample, a randomised sub-sample of at least 100 g fresh matter (FM) was selected to count the number of stems, to separate into stem class sizes and to measure leaf to stem ratio as described in Section 3.2.5.1.

Green area index and radiation use

Green area index (GAI) was measured using a LAI-2000 canopy analyser (LI-COR Inc., Lincoln, USA) at 7-10 day intervals as described in Section 3.2.5.2. To avoid reading noise, particularly in the fluctuating light regimes (SL, T and T+SL), GAI measurements were taken only in diffuse sky conditions (overcast days or clear days at low solar angles).

Calculations for canopy radiation interception and the extinction coefficient (K) used data collected from the canopy analyser and followed methods described in Section 3.2.5.2. Estimations of RUE for treatments in each rotation were based on final DM yield and PPFD intercepted by canopy at the final harvest (RUE= final DM yield/accumulated PARi by crop from residual to final cut), as described in Section 3.2.5.3.

Phenological development

Five dominant stems from different plants were marked in the centre of each treatment to measure stem height (STH), number of fully expanded nodes (NOD), time to bud appearance and node number of the flowering bud (PFLOW) as described in Section 3.2.5.5. New plants were marked at the beginning of each rotation. Results for phenological development in this chapter focus on the phyllochron and time to flowering.

4.2.4.3- Physiological measurements

Leaf net photosynthesis rate

Potential leaf Pn rate (µmol CO_2 m^{-2} s^{-1}) was measured on three of the youngest fully expanded leaves per treatment at the late vegetative stage for rotation periods from November 1999 to November 2000. Measurements were performed at an artificial light flux (PPFD) of 1000 µmol photons m^{-2} s^{-1}, using the portable infra-red gas analyser (LI-6400, LI-COR Inc., Nebraska). Equipment settings and field procedures were as described in Section 3.2.5.4. Readings were taken in each of the 10 different light regimes as listed in Section 4.2.5.1.

In addition, photosynthetic light response curves were measured at the end of each rotation from November 1999 to November 2000. Measurements were performed at seven PPFD levels: 0, 100, 250, 500, 750, 1000 and 2000 µmol photons m^{-2} s^{-1}, using the "Auto Light Curve Program". The minimum wait time used to stabilise readings, before taking measurements, was 60 seconds or 5% coefficient of variation (CV) for each PPFD level. For the photosynthetic light curves, a non-rectangular hyperbola (Section 2.1.5, Equation 3) was fitted and the main parameters (*Pmax*= maximum photosynthetic rate and α= photosynthetic efficiency) were obtained from the plotted equation.

4.2.5- Statistical analysis

Results for all variables were analysed using a split-plot analysis of variance (ANOVA), where covering status (with or without trees cover) was the main plot and shade structures (control, shade cloth and wooden slats) the sub-plots, with 3 replicates. This analysis was performed on individual dates as measured in the field. A complementary ANOVA was performed for all variables using a split-split plot analysis, where the sub-sub-plot was the date of measurement (time), to identify seasonal differences. In both cases, means were compared whenever treatment effects in the ANOVA were significant ($P<0.05$). Means separation was then based on the Fisher's protected least significant difference test (LSD) at 5% probability. Agronomic and physiological data between replicates were analysed in each rotation for equivalent regrowth time. The statistical analysis was also performed for the average values over the 9 rotation periods. For the photosynthetic curves, a statistical analysis was performed separately for *Pmax* and α parameters, after fitting the non-rectangular hyperbola equation. The statistical package used was the GENSTAT 5, release 4.1 (Lawes Agricultural Trust, IACR, Rothamsted, UK).

4.3- Results

4.3.1- Physical environment

4.3.1.1- Solar radiation

Photosynthetic photon flux density (PPFD)

The PPFD transmissions under the shade treatments for different seasons are summarized in Table 4.06. Radiation passing through the radiata pine trees was slightly greater than mean transmission observed under the two artificial shade structures in the full sun. They had a mean PPFD transmissivity of 42% and 46% under FS+CL and FS+SL, respectively, in summer. Under trees (T), the mean PPFD measured was 55% compared with FS and reached a maximum of 93% transmissivity (1871 μmol photons m^{-2} s^{-1}) during the sun period (11.00 AM) and a minimum of 9% (184 μmol photons m^{-2} s^{-1}) during the shade period (12.00 PM) in a clear summer day. As expected, mean radiation transmission decreased proportionally under T+CL to 22% (maximum of 976 μmol photons m^{-2} s^{-1} and minimum of 44 μmol photons m^{-2} s^{-1}) and to 23% (maximum of 1136 μmol photons m^{-2} s^{-1} and minimum of 41 μmol photons m^{-2} s^{-1}) under T+SL compared with the full sun in summer.

Radiation transmitted under the shade structures and trees declined from summer to winter (Table 4.06). For example, PPFD measured under trees decreased from 55% in summer to 47% in spring and 45% in winter compared with FS. The decrease of PPFD transmission observed over seasons was lower for the two artificial shade structures in the full sun than that observed under trees. PPFD under slats declined from 46% in summer to 41% in winter and under cloth from 42 to 40% compared with FS. The consequence was that the PPFD transmissivity under T became even closer to the FS+CL and FS+SL treatments as sun angle declined. In overcast sky conditions, radiation transmission increased slightly under all shade treatments compared with a clear sunny day.

Table 4.06. Mean daily PPFD transmissivities (relative to full sunlight treatment) measured under shade cloth (FS+CL), wooden slats (FS+SL), radiata pine trees (T), trees+cloth (T+CL) and trees+slats (T+SL) for typical sunny days in different seasons and for a diffuse overcast day in summer. Values in parenthesis indicate the maximum sun angle when PPFD was measured.

Treatment	Summer*	Autumn*	Winter*	Spring*	Diffuse**
			%		
FS	100	100	100	100	100
FS+CL	42 (65°)	40 (54°)	40 (24°)	40 (52°)	43 (56°)
FS+SL	46 (66°)	45 (43°)	41 (23°)	45 (52°)	51 (61°)
T	55 (70°)	48 (50°)	45 (23°)	47 (55°)	58 (70°)
T+CL	22 (70°)	15 (50°)	10 (24°)	16 (55°)	23 (50°)
T+SL	23 (70°)	16 (53°)	13 (23°)	18 (61°)	25 (70°)

* PPFD measured in clear suuny sky days; ** PPFD measured in a summer overcast day.

Temporal patterns

Besides the FS+CL and FS+SL treatments used in the first experiment (Section 3.3.1.1), three new light regimes were imposed under trees (T, T+CL and T+SL). An intermittent light regime was observed under T (Figure 4.04), with a maximum of 2.45 hours of full sun and 1.30 hours of heavy shade in summer at noontime. In the spring, the maximum sun period was 1.45 hours and maximum shade period was 1.15 hours. This was different from the intermittent regime observed under the FS+SL structure (Section 3.3.1.1), which produced equivalent periods of sun and shade over the day. The shade cloth structure set under trees (T+CL) produced a similar temporal pattern as that observed under T on sunny days (Figure 4.04*a*). During the sun period, T+CL transmitted a similar amount of PPFD to that measured under FS+CL treatment (45% PPFD), but during the shade period caused by tree shade, the transmissivity was consistent with that observed in the tree shade alone (4%). The T+SL treatment (Figure 4.03*b*) produced an intermittent light regime with a maximum of 45 minutes in sun and 3.30 hours in shade in summer. The maximum PPFD transmissivity measured under the T+SL treatment was 48% during the sun period and 5% during the shade period compared with FS. The pattern of light regime for both T+CL and T+SL was similar to those in the full sun for overcast days (Figure 4.04*bd*).

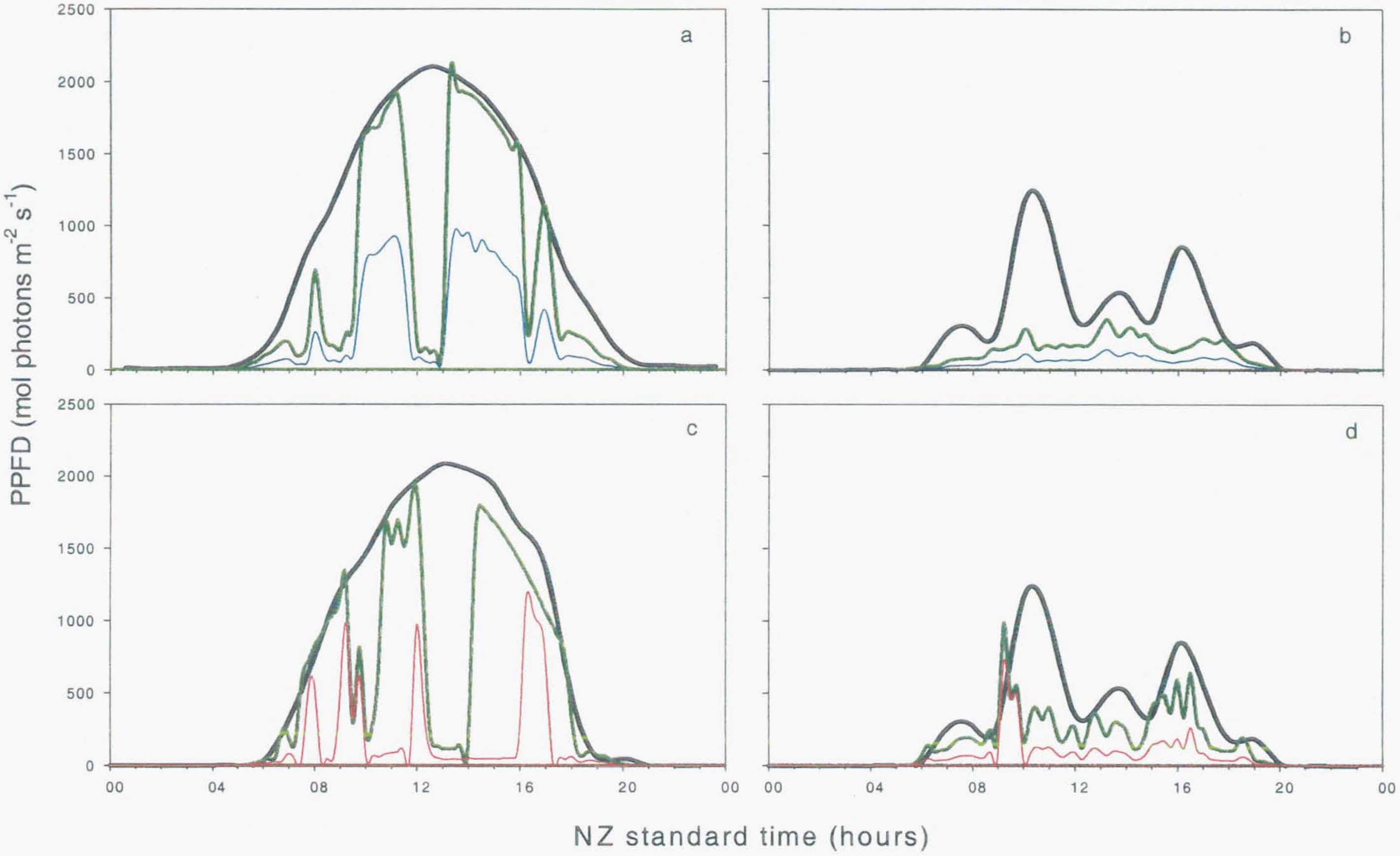

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Figure 4.04- Photosynthetic photon flux density (PPFD) at the centre of tree inter-rows measured in full sunlight (——), under radiata pine trees (——), trees + cloth (……….) and trees + slats (——) for typical clear sunny (*ac*) and overcast (*bd*) days in summer at Canterbury, New Zealand.

Spectral composition

Radiation spectral composition (Table 4.07) on a clear and sunny day for FS+CL (42% transmissivity) caused no change in the proportions of B, R and FR wavelengths compared with FS treatment and with the other treatments exposed to direct sunlight (FS+SL sun, T sun and T+SL sun). However, both slatted (5% transmissivity) and tree shade (9% transmissivity) increased the proportions of B and FR light and decreased the amount of R wavelength. There was more FR light under tree shade (T sh, T+CL and T+SL sh) than under FS+SL sh treatment. The consequence was that R/FR ratio reduced under T sh (0.64) compared with FS (1.31), but B/FR increased. The B/FR ratio was greatest for the FS+SL sh and Tsh treatment (0.64) and lowest for the FS+SL sun and T+SL sun treatment (0.48). The R/FR ratio was similar for FS (1.31) and FS+CL (1.28), FS+SL sun (1.26), T sun (1.23) and T+CL sun (1.24), but decreased under FS+SL sh (0.74), T sh (0.64) and T+SL sh (0.46).

As diffuse sky conditions increased, spectral irradiance differences among treatments reduced. It was not possible to identify the shadow patches under the intermittent regimes on an overcast day and differences between treatments for B and R wavelengths were less evident than on clear sunny days. Overall ratios decreased in the cloudy day compared with those in the clear sky condition. However, the FS+CL treatment continued to approach the FS spectrum. The FR radiation was also greater for the FS+SL sh T and T+SL compared with FS and FS+CL treatments. The R/FR was slightly lower under T (1.01) and FS+SL (1.07) than in FS (1.15) treatment.

Table 4.07. Spectrum ratios between blue (B), red (R) and far-red (FR) to photosynthetic photon flux plus far-red (PPFDFR), blue to far-red (B/FR) and red to far-red (R/FR) measured in different light regimes on sunny (10 Oct 2000), partially cloudy (7 Mar 2000) and cloudy (11 Oct 2000) sky conditions in Canterbury, New Zealand.

Treatment**	B*/PPFDFR*	R*/PPFDFR	FR*/PPFDFR	B/FR	R/FR
7 March 2000: sunny-cloudy					
FS	0.216	0.280	0.269	0.802	1.041
FS+CL	0.214	0.283	0.267	0.802	1.059
FS+SL sun	0.205	0.285	0.278	0.738	1.025
FS+SL sh	0.213	0.276	0.283	0.753	0.975
T sun	0.215	0.274	0.274	0.785	0.999
T sh	0.215	0.269	0.286	0.753	0.942
T+CL sh	0.211	0.271	0.289	0.731	0.938
T+SL sun	0.203	0.268	0.309	0.657	0.868
T+SL sh	0.207	0.277	0.286	0.724	0.969
10 October 2000: sunny					
FS	0.147	0.342	0.262	0.561	1.307
FS+CL	0.146	0.341	0.266	0.547	1.285
FS+SL sun	0.139	0.344	0.272	0.512	1.262
FS+SL sh	0.210	0.236	0.319	0.659	0.739
T sun	0.139	0.340	0.277	0.502	1.228
T sh	0.212	0.218	0.339	0.626	0.644
T+CL sun	0.140	0.342	0.275	0.508	1.243
T+CL sh	0.203	0.207	0.370	0.548	0.560
T+SL sun	0.133	0.340	0.288	0.461	1.178
T+SL sh	0.207	0.182	0.395	0.524	0.461
11 October 2000: cloudy					
FS	0.148	0.326	0.284	0.520	1.146
FS+CL	0.146	0.324	0.290	0.504	1.117
FS+SL	0.142	0.321	0.301	0.471	1.066
T	0.140	0.315	0.312	0.448	1.008
T+CL	0.145	0.322	0.295	0.490	1.092
T+SL	0.140	0.318	0.308	0.455	1.033

* PPFDFR= 400-800 nm; B= 400-500 nm; R= 600-700 nm; FR= 700-800 nm.

** FS- full sunlight; CL- shade cloth; SLsun- slats during sun period; SLsh- slats during shade period; Tsun- trees during sun period; Tsh- trees during shade period; T+CLsh- trees+cloth during shade period; T+SLsun- trees+slats during the sun period; T+SLsh- trees+slats during the shade period.

4.3.1.2- Soil water content (SWC)

The SWC was above 24% in spring for all treatments, but on occasion declined below 20% in summer and autumn (Figure 4.05). There were indications of low soil water extraction by plants from February to March 2000. The lowest SWC of the experimental period was in March 2001 (<15% in both the FS and under T), although the SWC continued to decline, indicating that plants were still extracting soil water. Surprisingly, SWC was not different (P>0.29) between the FS and T over the experimental period, including the dry seasons. There was 3-5% more (P<0.003) SWC under the artificial shade structures than in the FS and T in the last rotation period in March 2001. No differences between the shade cloth and wooden slats for SWC were observed.

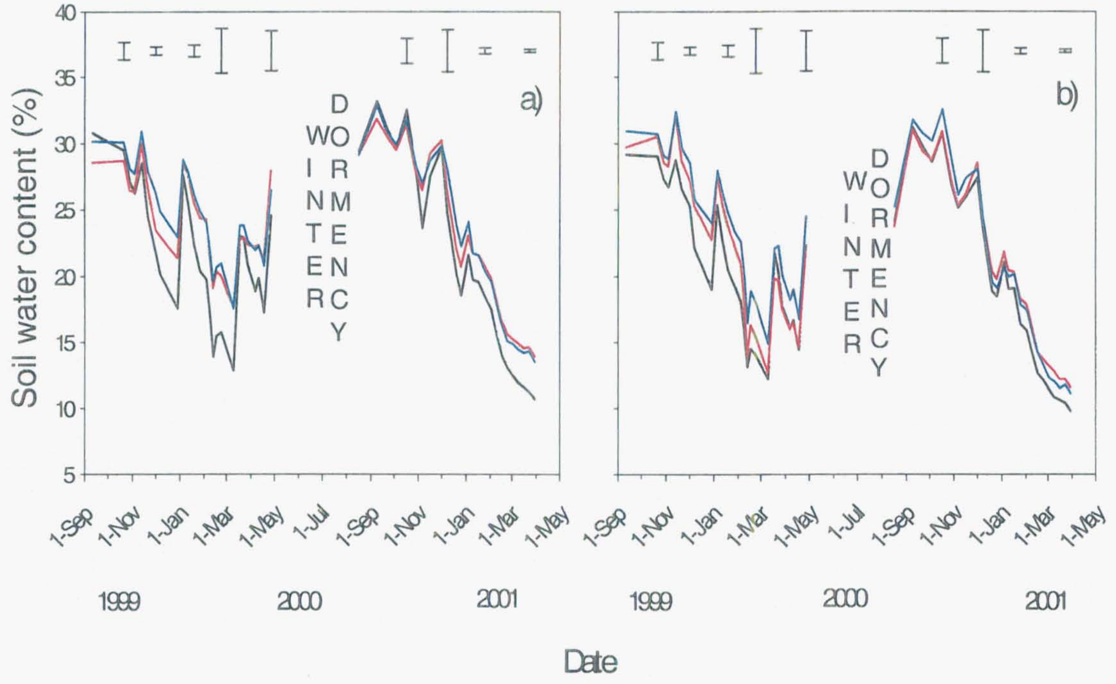

Figure 4.05. Mean soil volumetric water content (%) of the top 0.5 m measured with the Time Domain Reflectometer (TDR) in the open field (*a*) and under trees (*b*) for three light regimes: no shade structures (—), shade cloth (—) and wooden slats (—) from September 1999 to March 2001. Bars indicate standard error of means (SEM) by the end of each rotation length. Lucerne winter-dormancy period was from May to September 2000.

4.3.2- Plant agronomic response

4.3.2.1- Herbage dry matter yield (DM)

DM increased from September to December, then declined in summer periods (January to March) in both growing seasons (Figure 4.06). Lucerne annual DM decreased ($P<0.003$) by 30% under the trees (10.8 t ha^{-1}) compared with full sunlight (15.4 t ha^{-1}) over 5 rotations from October 1999 to March 2000. Annual DM was also greater ($P<0.001$) under trees (10.8 t ha^{-1}) than under FS+CL (8.5 t ha^{-1}) and under FS+SL (8.9 t ha^{-1}) in the first growing season. Plants under the cloth and slatted shade decreased ($P<0.001$) in total DM yield by 45% and 42%, respectively, compared with FS in the first year. Lucerne DM declined 51% under T+CL (5.4 t ha^{-1}) and 42% under T+SL (6.3 t ha^{-1}) compared with the T treatment. In the second year (from October 2000 to March 2001), there were only 4 lucerne rotations and differences between treatments were similar to those in the previous growing period. However, annual DM production from all treatments under the trees decreased ($P<0.001$) compared with the first year period. The annual DM under trees (8.6 t ha^{-1}) decreased ($P<0.02$) by 45% compared with FS (15.7 t ha^{-1}) with further reduction ($P<0.001$) under T+CL (3.1 t ha^{-1}) and T+SL (3.6 t ha^{-1}) compared with under the T for the second growing season. Yields under FS+CL (9.0 t ha^{-1}) and FS+SL (9.2 t ha^{-1}) were similar to that under T.

No significant differences in lucerne DM were observed between the two artificial shade structures installed either in the full sun or under trees. DM production under both cloth and slats was similar to the agroforestry treatment. In the first growing season, plant yield under the FS+CL was on average 78% of that observed in T treatment, whereas under the FS+SL it was 85%. Differences in DM yield between the two artificial shade materials and trees were minimal for the second growing season. Plants yielded more ($P<0.03$) under T than under FS+SL on three occasions: November 1999, January 2000 and October 2000. On the other hand, DM yield under T was greater ($P=0.01$) than FS+CL in January and February 2000.

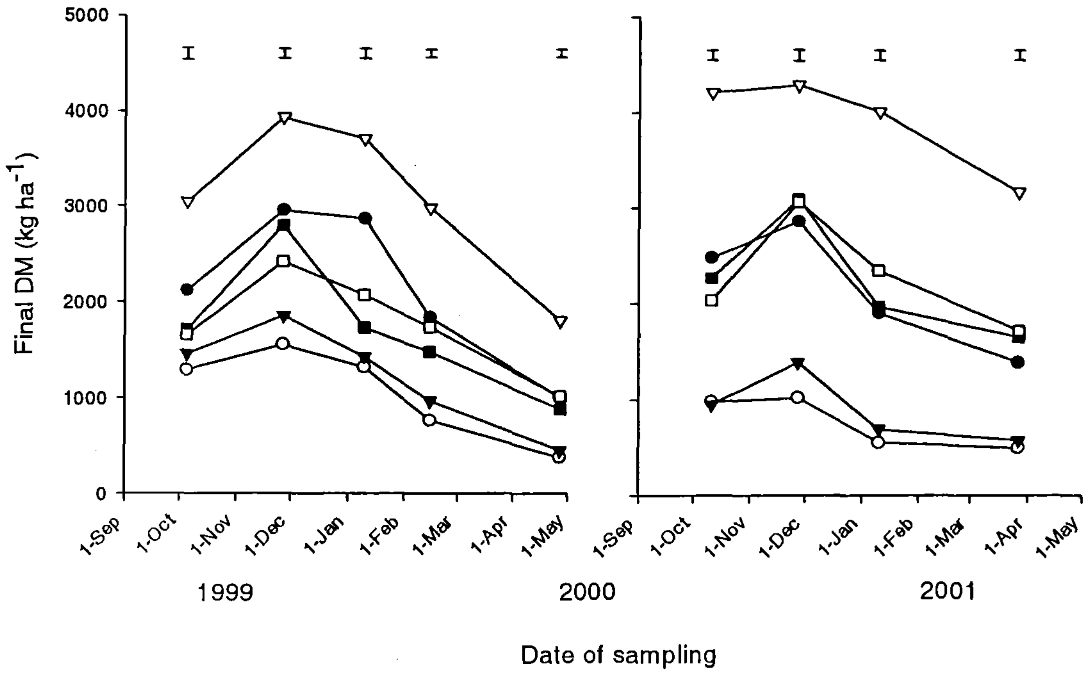

Figure 4.06. Mean final herbage dry matter yield (DM) for lucerne grown in six different light regimes: full sunlight (▽), shade cloth (■), wooden slats (□), radiata pine trees (●), trees+cloth (○) and trees+slats (▼). Data are averages of 3 replicates collected from October 1999 to March 2001 and bars indicate the standard error of means (SEM). No data was collected from May to September 1999, when lucerne was in winter-dormancy.

4.3.2.2- Green area index (GAI)

Lucerne annual GAI in FS was greater ($P<0.006$) than the 5 shaded treatments (Figure 4.07). Plants under trees decreased total GAI by 29% compared with FS in the first year and by 42% in the second experimental year. Total GAI was greater ($P<0.001$) under the T than under the FS+CL and FS+SL in the first growing season, but they were all the same in the second growing season. In the 1999-2000 season, total cumulative GAI was 18.5 in FS, 13.2 under T, 11.1 under FS+CL and 11.8 under FS+SL over 5 lucerne rotations. In the second growing season, total cumulative GAI was 18.9 in FS, 10.9 under T, 11.2 under FS+CL and 11.5 under FS+SL over 4 lucerne rotations. The heavy shaded treatments T+CL and T+SL reduced total GAI production from the first growing season (GAI= 8.4 and 9.7, respectively) to the second growing season (GAI= 5.4 and 6.2, respectively).

Final GAI measurements at the end of each rotation followed the same pattern as DM yield, with a peak of production between September and December, and then declining in March-April for all treatments. Final GAI in FS was always greater (P<0.07) than other treatments. Tree shading decreased lucerne final GAI compared with FS progressively from 24% at the beginning of the experiment (October 1999) to 58% in April 2000 (P<0.07) and 52% in the March 2001 (P<0.04). Final GAI was greater (P=0.05) under the natural shade (T) than the two artificial shade regimes (FS+CL and FS+SL) only for the first three rotations in 1999. In subsequent rotations, no significant differences (P>0.10) between the natural and artificial shade regimes were observed for final GAI.

Plants under shade had a slower (P<0.02) GAI expansion from defoliation time to the first harvest (lag phase) compared with full sun crop for all rotations, except in April 2000. In the second growing period, the most shaded treatments (T+CL and T+SL) had a slower (P<0.03) GAI recovery after defoliation than the intermediate shade treatments (FS+CL, FS+SL and T). No significant differences (P>0.10) for initial GAI expansion between the T and the two artificial shades (FS+CL and FS+SL) were observed. The exception was in the second Rotation of 1999 and in the last two rotations of the experiment, when T was slower (P<0.03) to recovery after defoliation than FS+CL and FS+SL.

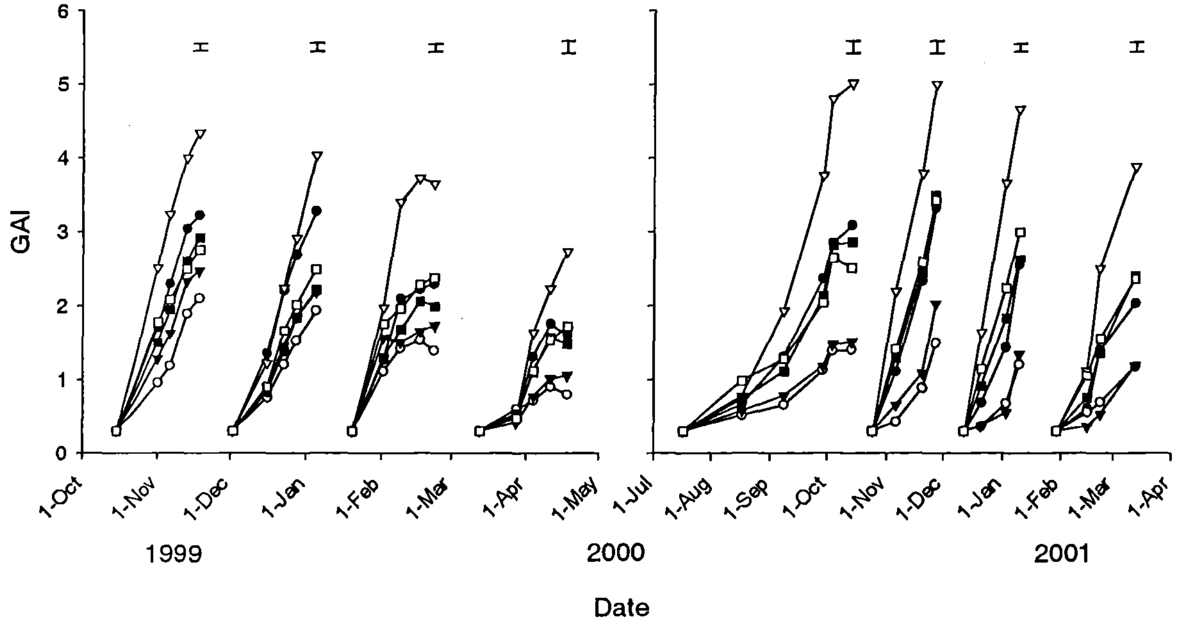

Figure 4.07. Mean green area index (GAI) for lucerne grown in six different light regimes: full sunlight (▽), shade cloth (■), wooden slats (□), radiata pine trees (●), trees+cloth (○) and trees+slats (▼). Data are averages of the 3 replicates at equivalent regrowth time and were collected from October 1999 to March 2001. Bars indicate the standard error of means (SEM) for final readings. No data were collected from May to September 1999, when lucerne was in winter-dormancy.

4.3.2.3- Number of stems

Changes in the mean number of stems (Figure 4.08) were consistent with results from the final canopy GAI. Mean number of stems per m^2 was 804 in FS, which was greater ($P<0.001$) than under FS+CL (493 stems m^{-2}) and FS+SL (476 stems m^{-2}). The mean numbers of stems for the T+CL and T+SL treatments were 344 and 359 stems m^{-2}, respectively, compared with 523 under trees. The number of stems under T was greater ($P=0.002$) than under the two artificial shade regimes for the first three rotations, but equivalent for the subsequent rotations. No differences ($P>0.095$) in mean number of stems between the shade cloth and slatted treatment were observed. In the second growing period, there was an apparent grouping in the number of stems among treatments. The full sun plants (858 stems m^{-2}) had a greater ($P<0.001$) number of stems than the three intermediate shade levels (511 stems m^{-2}), whereas the two most shaded regimes had the lowest stem population (338 stems m^{-2}).

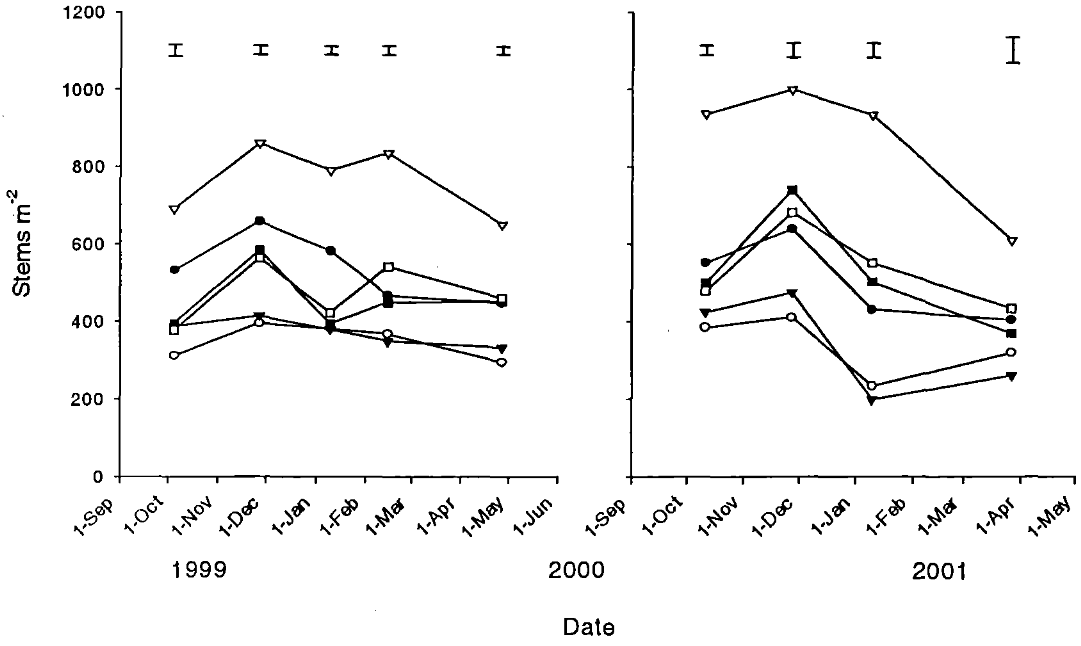

Figure 4.08. Mean stems number measured at the final harvest for lucerne grown in six different light regimes: full sunlight (▽), shade cloth (■), wooden slats (□), radiata pine trees (●), trees+cloth (○) and trees+slats (▼). Data are averages of 3 replicates collected from October 1999 to March 2001 and bars indicate the standard error of means (SEM). No data were collected from May to September 1999, when lucerne was in winter-dormancy.

4.3.2.4- Canopy architecture and radiation interception

Estimates of the extinction coefficient (Figure 4.09*b*) showed equivalent (P>0.29) lucerne canopy architectures for the six light regimes over the experimental period with a mean K= 0.84. This resulted in a similar pattern of radiation interception (PPFDi) by the canopy (Figure 4.09*a*) between treatments. That is, the lucerne canopy intercepted 95% of the incoming radiation (critical GAI) at a mean GAI= 3.6 for all treatments (P>0.28). Lucerne in the FS treatment reached the critical GAI in all rotations, except in the autumn 2000 when maximum GAI was 2.8. In contrast, critical GAI under the 5 shaded regimes was never achieved (Tables 4.08 and 4.09). For example, when mean GAI was 3.6 in full sun (95% PPFDi), FS+CL was 2.2 (85% PPFDi), FS+SL was 2.4 (85% PPFDi), T was 2.7 (88% PPFDi), T+CL was 1.6 (73% PPFDi) and T+SL was 1.9 (77% PPFDi) for the first growing season (Table 4.08). Similar difference among treatments was observed in the second season for full sun plots, but overall GAI declined under the tree covering treatments (Table 4.09).

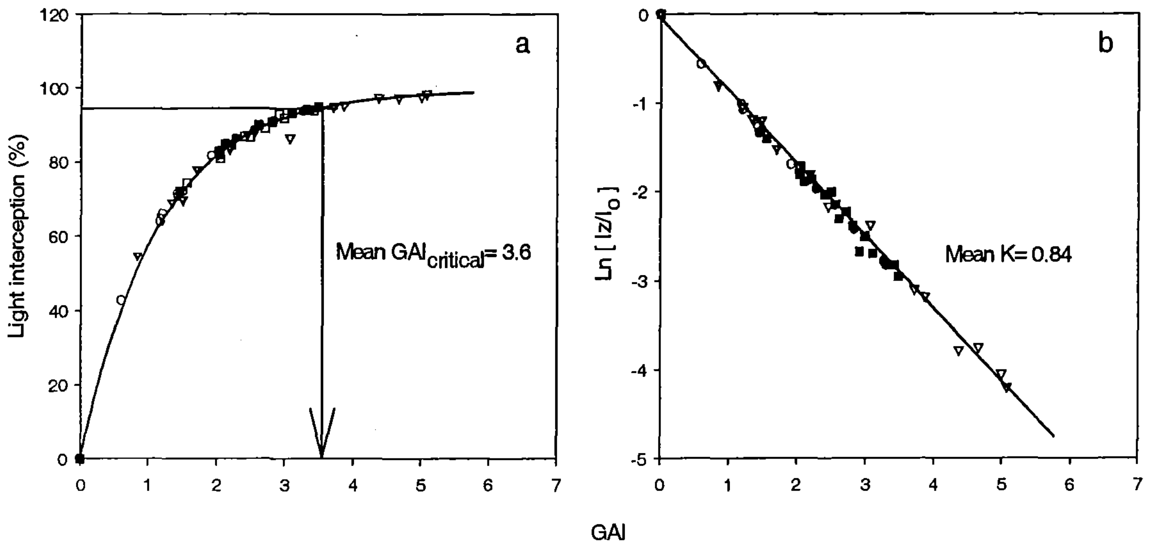

Figure 4.09. Radiation interception (Iz/Io) within lucerne canopy (*a*) and natural log of Iz/Io (*b*) against green area index (GAI) in six different light regimes: full sunlight (▽), shade cloth (■), wooden slats (□), radiata pine trees (●), trees+cloth (○) and trees+slats (▼) measured over the experimental period. The extinction coefficient (K) was calculated as the slope of lines in graph *b* (Section 3.2.5.2). Arrow indicates when 95% of the incoming radiation was intercepted by canopy (critical GAI). Data are the averages of the 3 replicates over the experimental period.

Table 4.08. Mean GAI, regrowth and relative amount of PPFD intercepted (PPFDi) by lucerne canopy under the six light regimes when full sun plants reached the critical GAI*

(GAI= 3.6). Data are averages of 3 replicates over the 5 experimental rotations in the first growing season at Canterbury, New Zealand. Statistics were performed for GAI.

Rotation period**	**Treatment**	**GAI**	**Regrowth (days)**	**PPFDi (%)**	**F probl.† (p<F)**
15Oct-18Nov 99:	FS	3.60	28	95.0	
	FS+CL	2.28	28	86.11	
	FS+SL	2.29	28	86.22	
	T	2.68	28	89.80	
	T+CL	1.55	28	74.62	
	T+SL	2.00	28	82.59	**0.050 (0.135)**
02Dec 99-05Jan 00 :	FS	3.60	36	95.0	
	FS+CL	2.07	36	83.56	
	FS+SL	2.30	36	86.33	
	T	3.11	36	92.51	
	T+CL	1.77	36	78.93	
	T+SL	2.13	36	84.34	**0.001 (0.111)**
20Jan-23Feb 00 :	FS	3.60	26	95.0	
	FS+CL	1.71	26	77.84	
	FS+SL	1.95	26	81.86	
	T	2.06	26	83.42	
	T+CL	1.43	26	71.87	
	T+SL	1.48	26	73.05	**0.025 (0.150)**
13Mar-18Apr 00:	FS	2.81	38	90.74	
	FS+CL	1.74	38	78.39	
	FS+SL	1.78	38	79.10	
	T	1.73	38	78.21	
	T+CL	0.84	38	52.91	
	T+SL	1.05	38	60.87	**0.001 (0.144)**

* Critical GAI occurs when canopy intercepts 95 % of the total incoming radiation;

** Rotation period is the average of the 3 replicates (Table 4.05).

† is the F probability for the interaction Cover*Shade on GAI. The SEM is shown in parenthesis.

Table 4.09. Mean GAI, regrowth and relative amount of PPFD intercepted (PPFDi) by lucerne canopy under the six light regimes when full sun plants reached the critical GAI*

(GAI= 3.6). Data are averages of 3 replicates over the 4 experimental rotations in the second growing season at Canterbury, New Zealand. Statistics were performed for GAI.

Rotation period**	Treatment	GAI	Regrowth (days)	PPFDi (%)	F probl.† (p<F)
17Jul-14Oct 00:	FS	3.60	153	95.0	
	FS+CL	2.05	153	83.29	
	FS+SL	2.03	153	83.01	
	T	2.30	153	86.33	
	T+CL	1.07	153	61.55	
	T+SL	1.17	153	64.77	**0.001 (0.100)**
25Oct-27Nov 00:	FS	3.60	31	95.0	
	FS+CL	2.42	31	87.56	
	FS+SL	2.56	31	88.83	
	T	2.31	31	86.44	
	T+CL	0.85	31	53.32	
	T+SL	1.15	31	64.15	**0.001 (0.176)**
12Dec 00-10Jan 01:	FS	3.60	26	95.0	
	FS+CL	1.84	26	80.13	
	FS+SL	2.26	26	85.89	
	T	1.47	26	72.82	
	T+CL	0.70	26	46.68	
	T+SL	0.61	26	42.23	**0.003 (0.096)**
30Jan-13Mar 01:	FS	3.60	41	95.0	
	FS+CL	2.12	41	84.21	
	FS+SL	2.12	41	84.21	
	T	1.86	41	80.45	
	T+CL	1.05	41	60.87	
	T+SL	0.96	41	57.64	**0.03 (0.159)**

* Critical GAI occurs when canopy intercepts 95 % of the total incoming radiation;

** Rotation period is the average of the 3 replicates (Table 4.05).

† is the F probability for the interaction Cover*Shade on GAI. The SEM is shown in parenthesis.

4.3.2.5- Radiation use efficiency (RUE)

The RUE for plants grown in FS was always less than those calculated under the 5 shaded treatments (Figure 4.10). The mean RUE in FS was 0.8 g DM MJ^{-1} PAR, which was lower ($P<0.001$) than under FS+CL (1.3 g DM MJ^{-1} PAR), and under both FS+SL and T (1.2 g DM MJ^{-1} PAR). The most shaded treatments reduced RUE from 3.3 g DM MJ^{-1} PAR in the first rotation to 1.7 g DM MJ^{-1} PAR by January 2000 and then it stabilized. Mean RUE was the same for T+CL and T+SL with a value of 1.3 g DM MJ^{-1} PAR over the experimental period, excluding the first two rotations. For all other treatments RUE declined ($P<0.001$) consistently from spring to autumn in both seasons.

In full sun conditions, RUE under shade cloth was greater ($P< 0.02$) than under slats at the beginning of both seasons (November 1999 and October 2000). In all other rotations, there were no differences between FS+CL and FS+SL treatments (Figure 4.10). Plants grown under the trees usually showed similar RUE to those under the two artificial shading treatments. The exception was in the last experimental rotation (April 2001), when lucerne under T and in full sun had the lowest ($P<0.005$) RUE (0.6 g DM MJ^{-1} PAR) among treatments.

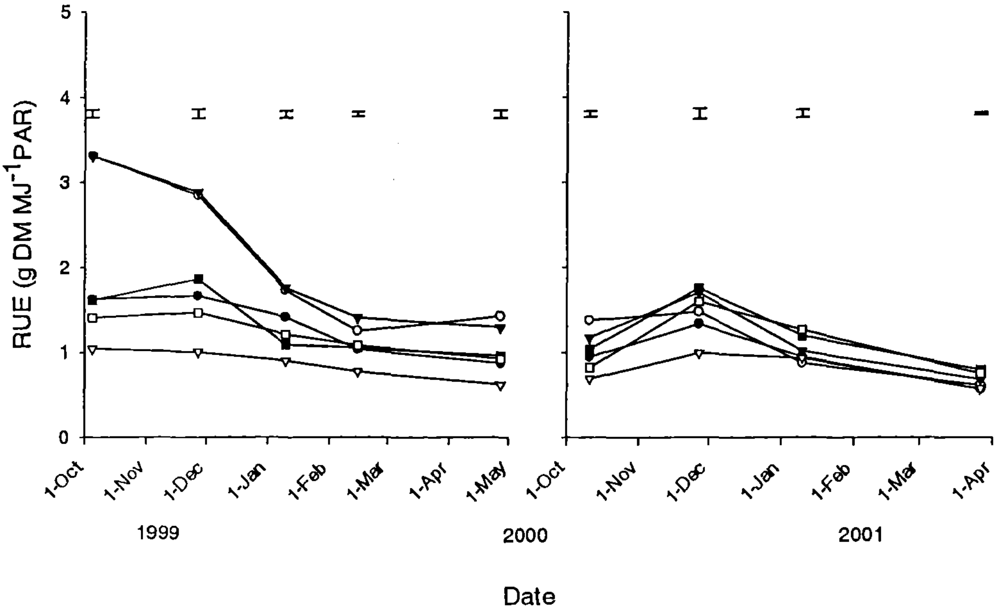

Figure 4.10. Mean radiation use efficiency (RUE) calculated for each final harvest for lucerne crops grown in six different light regimes: full sunlight (▽), shade cloth (■), wooden slats (□), radiata pine trees (●), trees+cloth (○) and trees+slats (▼). Data are averages of 3 replicates collected from October 1999 to March 2001 and bars indicate the standard error of means (SEM). No data was collected from May to September 1999, when lucerne was in winter-dormancy.

4.3.2.6- Instantaneous net photosynthesis rate potential (Pn)

The Pn at 1000 μmol photons m^{-2} s^{-1} was measured separately during the sun and shade periods under the intermittent light regimes and also in the continuous radiation treatments (Figure 4.11). In all six rotations, there were differences ($0.001<P<0.03$) between treatments for Pn rate. Net photosynthesis was usually highest (36-40 μmol CO_2 m^{-2} s^{-1}) for FS, FS+SL sun, T sun, and T+SL sun and lowest (14-26 μmol CO_2 m^{-2} s^{-1}) for FS+SL sh, T sh, T+CL sh and T+SL sh treatments. Leaves under shade cloth treatments (FS+CL and T+CL sun) showed an intermediate mean photosynthetic activity (27-34 μmol CO_2 m^{-2} s^{-1}), but were frequently not different ($P>0.05$) from that Pn measured in full sunlight, as found from January to March 2000 and January 2001. Plants exposed to the alternating sun/shade regimes (FS+SL, T, T+CL and T+SL) showed a decrease in Pn between periods of full sun and full shade, which was less proportional to the reduction in PPFD. For example, under FS+SL, leaf Pn ranged from 40 μmol CO_2 m^{-2} s^{-1} during the sun period to 26 μmol CO_2 m^{-2} s^{-1} during the shaded period in January 2000. Similarly, leaf Pn changed from 35 μmol CO_2 m^{-2} s^{-1} during the sunny period under trees to 22 μmol CO_2 m^{-2} s^{-1} during the tree shade period.

For the following analysis, a weighted mean of Pn was calculated between both sun and shade periods under all the intermittent treatments based on the mean length of time leaves were exposed to each radiation condition (Section 4.3.1.1). For example, plants were exposed to approximately 60% (2.45 h) of the diurnal time in full sun and 40% (1.30 h) in shade under the T and T+CL treatments, whereas under T+SL and FS+SL the time was equally 50% in shade and in full sun. The Pn for leaves in FS was higher ($0.001<P<0.01$) than the two artificial shade regimes in all rotations, except in February 2000, when no difference was observed between the six light regimes ($P>0.16$). Leaf Pn rate under T was usually similar ($P>0.05$) to those under FS+CL and FS+SL. Leaf Pn was higher ($0.003<P<0.02$) in FS compared with T in the first two rotations, but remained similar over the following rotations.

Leaf photosynthetic response curves were also generated prior to grazing in 6 of the 9 rotations. The results taken in autumn-spring (Figure 4.12) and summer (Figure 4.13) confirmed the lower ($P<0.001$) leaf Pn response during the shade compared with the sun period for plants submitted to the intermittent light regimes (T and FS+SL), particularly at high PPFD levels. The Pn in the continuous light regimes (FS and FS+CL) showed the same photosynthetic response (Table 4.11). Lucerne top leaves under the 6 light treatments never saturated at the maximum PPFD of 2000 μmol photons m^{-2} s^{-1}. The Pmax, estimated from the asymptotic light curves, was always similar ($0.05<P<0.36$) between FS, FS+SL sun and T sun treatments over the experimental period (Table 4.10), with a mean value of 41.3 μmol CO_2 m^{-2} s^{-1}. Likewise, average Pmax for treatments under heavy shade (FS+SL sh, T, T+CL sh and T+SL sh) was similar and consistently lower than in sun treatments ($0.05<P<0.36$) at about 28.9 μmol CO_2 m^{-2} s^{-1} over the experimental rotations.

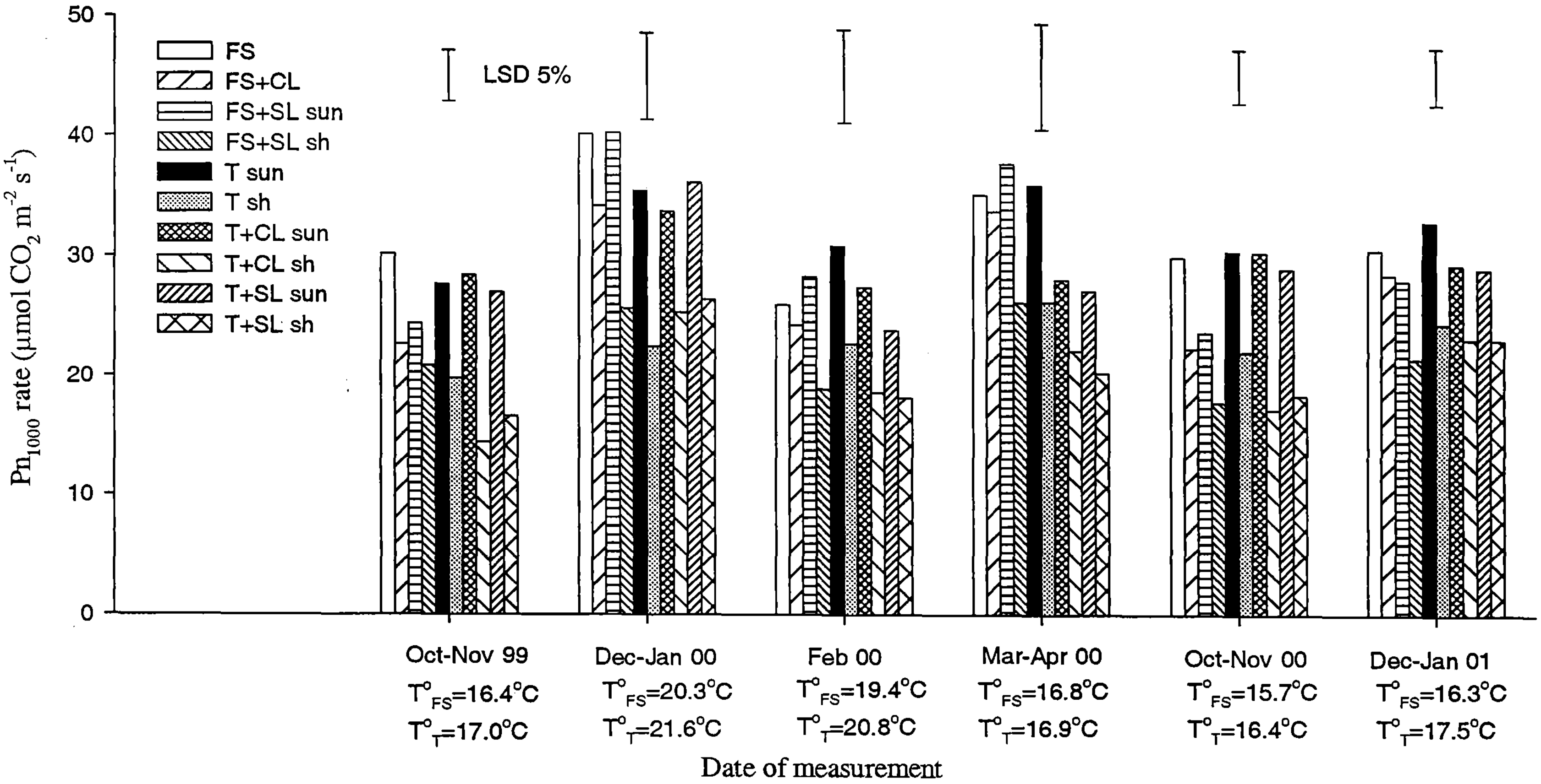

Figure 4.11. Mean net photosynthesis rate at 1000 µmol photons m^{-2} s^{-1} (Pn_{1000}) of the youngest fully expanded leaf in lucerne plots. Measurements were performed for 10 light regimes, during the late vegetative stage and at noon time, for six consecutive rotations: FS (full sunlight), FS+CL (shade cloth), FS+SL sun (slats sunny period), FS+SL sh (slats shaded period), T sun (tree sunny), T sh (tree shaded), T+CL sun (tree+cloth sunny), T+CL sh (tree+cloth shaded), T+SL sun (tree+slats sunny) and T+SL sh (tree+slats shaded). Mean air temperatures in full ($T°_{FS}$) and under trees ($T°_{T}$) at the moment Pn rate was measured are shown at the bottom of the graph. Data are averages of 3 replicates and error bars on the top indicate the least significant difference (LSD) between means at α=0.05.

The weighted mean analysis among treatments (Table 4.10) indicated that top leaf Pmax was generally similar between FS, FS+CL and FS+SL. The exception was in February ($P=0.02$) and April 2000 ($P<0.001$), when Pmax declined under the slatted regimes compared with full sun and cloth treatments. The Pmax for top leaves was equivalent ($0.09<P<0.99$) between T and the two artificial shade regimes in the open over the experimental period. However, calculations for the averaged leaf Pmax over the 6 rotations showed that treatments without artificial shading (FS and T) had higher Pmax ($P=0.002$) compared with those with artificial shade (FS+CL, FS+CL, T+CL and T+SL). Plants under FS+CL and FS+SL had a mean leaf Pmax of 35.6 μmol CO_2 m^{-2} s^{-1} compared with 42.7 μmol CO_2 m^{-2} s^{-1} for FS. Pmax under T (36.6 μmol CO_2 m^{-2} s^{-1}) was higher than under T+CL and T+SL (30.8 μmol CO_2 m^{-2} s^{-1}).

Leaf photosynthetic efficiency (α) was calculated as the slope of the linear part of the light curves shown in Figures 4.12 and 4.13 and was calculated from the asymptotic fitted curves. The analysis (Table 4.11) showed that leaves under heavy shaded treatments (FS+SLsh, Tsh, T+CLsh and T+SLsh) had a mean α (0.015 mg CO_2 J^{-1}) lower ($P=0.02$) than those observed (0.017 mg CO_2 J^{-1}) under high radiation (FS, FS+CL, FS+SLsun, Tsun and T+SLsun) over the 6 rotations. However, the weighted mean for α was equivalent ($P>0.26$) among treatments over the 6 rotations, with a mean value of 0.016 mg CO_2 J^{-1}. The exception was on February and April 2000, when leaves under FS+SL had a lower ($0.005<P<0.05$) α compared with FS and FS+CL.

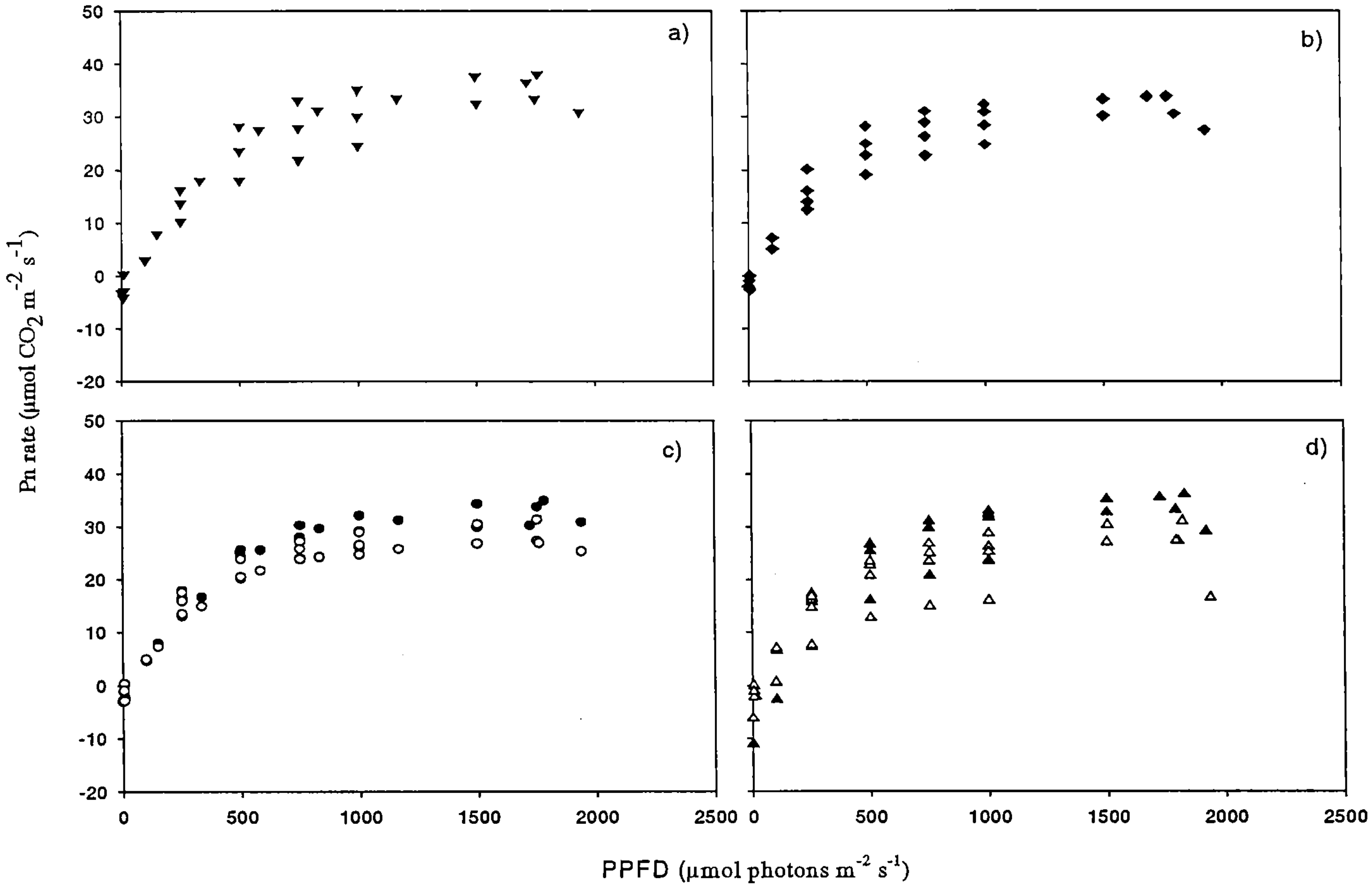

Figure 4.12. Mean leaf net photosynthetic light response curves (Pn) measured under 6 different light regimes during the spring (Nov 1999, Oct and Nov 2000) and autumn (Apr 2000) experimental periods: *a*-full sunlight (▼), *b*-shade cloth (◆), *c*-sunny period under slats (●), *c*- shade period under slats (○), *d*-sunny period under trees (▲) and *d*-shade period under trees (△). Data are averages of the 3 replicates. Dates of measurements and statistical analyses are indicated in Table 4.10.

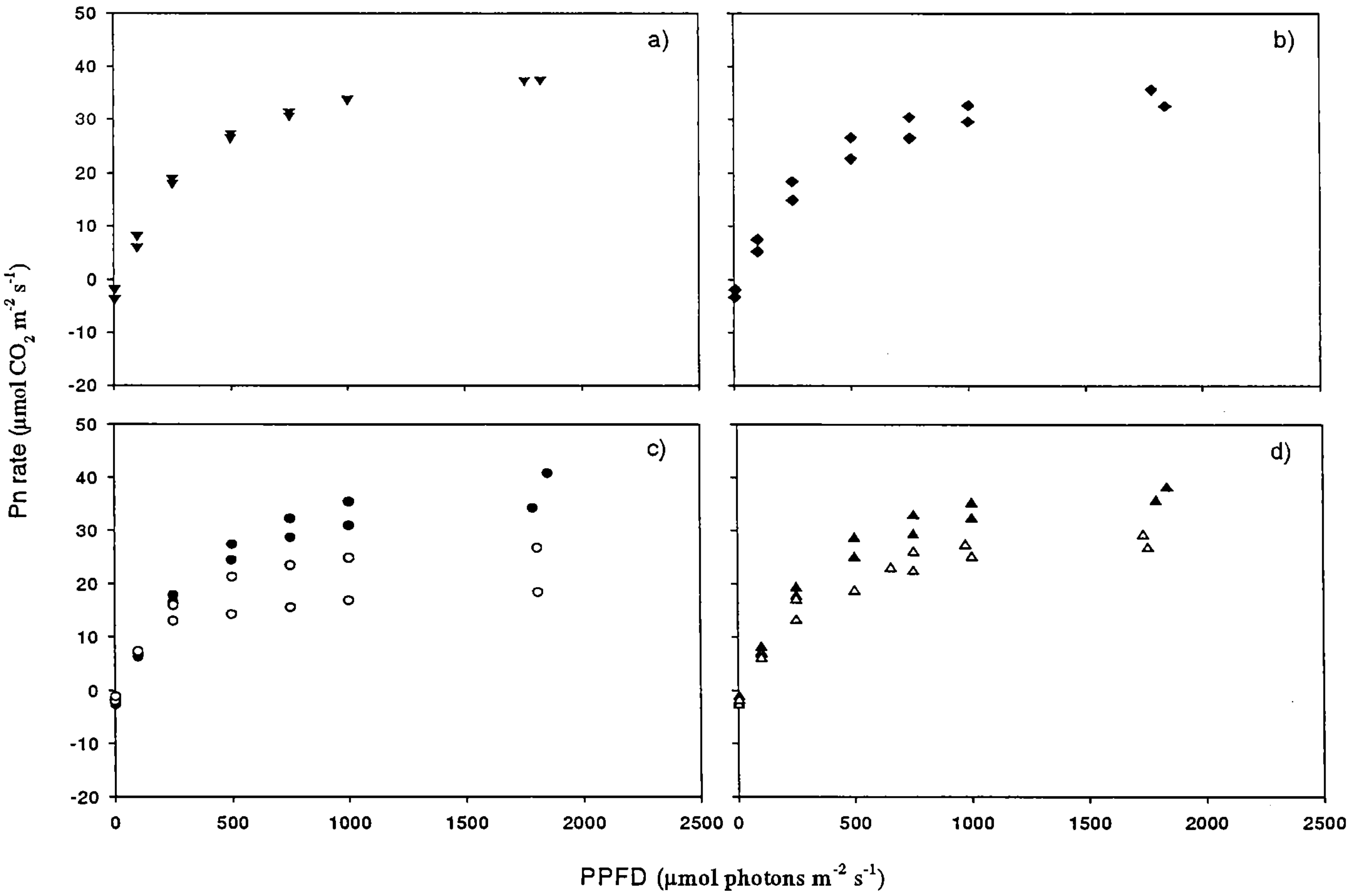

Figure 4.13. Mean leaf net photosynthetic light response curves (Pn) measured under 6 different light regimes during the summer (Jan and Feb 2000) experimental periods: *a*-full sunlight (▼), *b*-shade cloth (◆), *c*-sunny period under slats (●), *c*- shade period under slats (○), *d*-sunny period under trees (▲) and *d*- shade period under trees (△). Data are averages of the 3 replicates. Dates of measurements and statistical analyses are indicated in Table 4.10.

Table 4.10. Leaf Pmax (maximum gross photosynthesis rate) from asymptotic light curves for 10 different light regimes during 6 consecutive rotations: full sunlight (FS), shade cloth (FS+CL), slats sunny period (FS+SLsun), slats shaded period (FS+SLsh), tree sunny (Tsun), tree shaded (Tsh), tree+cloth sunny (T+CLsun), tree+cloth shaded (T+CLsh), tree+slats sunny (T+SLsun) and tree+slats shaded (T+SLsh). Mean values are the weighted averages for the sun and shade periods under all the intermittent regimes or the actual reading in continuous treatments. Data are averages of the 3 replicates.

Treatment	**Nov 99**	**Jan 00**	**Feb 00**	**Apr 00**	**Oct 00**	**Nov 00**
			--------°C--------			
Temp$_{FS}$*	16.4	20.3	19.4	16.8	12.7	13.3
Temp$_{T}$*	17.0	21.6	20.8	16.9	13.4	14.5
			--------µmol CO_2 m^{-2} s^{-1}--------			
T sun	47.3	43.4	40.9	41.4	36.4	38.6
T sh	23.9	29.3	29.8	35.0	30.7	30.5
T+CL sun	28.2	33.9	34.3	27.3	39.8	34.6
T+CL sh	23.0	27.7	28.0	25.9	34.3	28.2
T+SL sun	31.8	37.1	34.6	24.6	43.0	28.6
T+SL sh	23.2	27.3	28.0	23.2	32.5	34.8
FS	45.7	44.8	44.1	41.4	44.6	35.9
FS+CL	34.1	32.7	41.6	36.4	35.5	38.4
FS+SL sun	40.0	52.1	40.2	32.5	39.8	33.6
FS+SL sh	29.1	31.8	31.6	28.9	36.6	32.7
Means:						
T	*37.9*	*37.7*	*36.5*	*38.8*	*34.0*	*35.3*
T+CL	*26.1*	*31.4*	*31.8*	*26.7*	*37.6*	*32.0*
T+SL	*27.5*	*32.1*	*31.3*	*23.8*	*37.7*	*31.6*
FS	*45.7*	*44.8*	*44.1*	*41.3*	*44.5*	*36.0*
FS+CL	*34.1*	*32.7*	*41.5*	*36.4*	*35.5*	*38.3*
FS+SL	*34.6*	*41.9*	*35.9*	*30.7*	*38.2*	*33.2*
P<f						
Cover(C)**	**0.37**	**0.35**	**0.29**	**0.07**	**0.45**	**0.14**
Shade(S)**	**0.02**	**0.08**	**0.02**	**<0.001**	**0.60**	**0.47**
C*S	**0.99**	**0.49**	**0.18**	**0.27**	**0.09**	**0.55**
SEM†	**2.46**	**2.46**	**1.81**	**1.45**	**3.06**	**0.84**
LSD‡ (5%)	**8.04**	**8.01**	**5.91**	**4.63**	**10.70**	**5.09**

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* Mean air temperature in full sunlight (TempFS) and under trees (TempT) between 1100 and 1400 h when Pn rates were measured

** Statistics performed for mean values. Main plots (cover): Tree or full sun; Subplots (shade): no artificial shade, cloth or slats.

† SEM is the standard error of means for the lowest P<f test

‡ LSD is the least significant difference (LSD) at α=0.05 for the lowest P<f test.

Table 4.11. Leaf photosynthetic efficiency (α) calculated from the asymptotic light curves for 10 different light regimes during 6 consecutive rotations: full sunlight (FS), shade cloth (FS+CL), slats sunny period (FS+SLsun), slats shaded period (FS+SLsh), tree sunny (Tsun), tree shaded (Tsh), tree+cloth sunny (T+CLsun), tree+cloth shaded (T+CLsh), tree+slats sunny (T+SLsun) and tree+slats shaded (T+SLsh). Mean values are the weighted averages for the sun and shade periods under all the intermittent regimes or the actual reading in continuous treatments. Data are averages of the 3 replicates.

Treatment	**Nov 99**	**Jan 00**	**Feb 00**	**Apr 00**	**Oct 00**	**Nov 00**
	°C					
Temp$_{FS}$*	16.4	20.3	19.4	16.8	12.7	13.3
Temp$_{T}$*	17.0	21.6	20.8	16.9	13.4	14.5
	mg CO_2 J^{-1}					
T sun	0.021	0.021	0.017	0.019	0.017	0.014
T sh	0.013	0.014	0.013	0.018	0.014	0.015
T+CL sun	0.013	0.017	0.012	0.016	0.017	0.016
T+CL sh	0.014	0.018	0.015	0.014	0.019	0.017
T+SL sun	0.015	0.021	0.017	0.013	0.022	0.016
T+SL sh	0.016	0.015	0.018	0.011	0.017	0.017
FS	0.015	0.018	0.019	0.019	0.016	0.017
FS+CL	0.014	0.018	0.021	0.019	0.015	0.016
FS+SL sun	0.018	0.022	0.019	0.017	0.019	0.017
FS+SL sh	0.014	0.020	0.011	0.017	0.017	0.014
Means:						
T	*0.017*	*0.018*	*0.015*	*0.018*	*0.015*	*0.014*
T+CL	*0.013*	*0.017*	*0.013*	*0.015*	*0.018*	*0.016*
T+SL	*0.016*	*0.018*	*0.018*	*0.012*	*0.019*	*0.017*
FS	*0.014*	*0.018*	*0.019*	*0.019*	*0.016*	*0.017*
FS+CL	*0.014*	*0.018*	*0.021*	*0.019*	*0.015*	*0.016*
FS+SL	*0.016*	*0.021*	*0.015*	*0.017*	*0.018*	*0.016*
P<f						
Cover(C)**	**0.64**	**0.21**	**0.46**	**0.03**	**0.39**	**0.54**
Shade(S)**	**0.20**	**0.43**	**0.90**	**0.005**	**0.05**	**0.75**
C*S	**0.15**	**0.62**	**0.05**	**0.10**	**0.34**	**0.38**
SEM†	**0.0015**	**0.0006**	**0.0026**	**0.0006**	**0.0008**	**0.0011**
LSD‡ (5%)	**0.0052**	**0.0035**	**0.0104**	**0.0026**	**0.0040**	**0.0034**

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* Mean air temperature in full sunlight (TempFS) and under trees (TempT) between 1100 and 1400 h when Pn rates were measured

** Statistics performed for mean values. Main plots (cover): Tree or full sun; Subplots (shade): no artificial shade, cloth or slats.

† SEM is the standard error of means for the lowest P<f test

‡ LSD is the least significant difference (LSD) at α=0.05 for the lowest P<f test

4.3.2.6- Plant morphology

Stem classes

As described in Section 3.3.2.4, stems were classified within three different classes. Plants grown in FS and under T had a higher (P< 0.01) number of long (>20 cm) stems than under the two artificial shade structures over the 9 rotations. For example, the mean percentage of long stems was 71% for treatments without artificial shading (FS and T), 66% for slatted (FS+SL and T+SL) and 64% for shade cloth (FS+CL and T+CL) treatments. No differences (P>0.14) were observed for medium (10-20 cm) stem size between treatments with or without artificial shading, which were all about 22%. Plants under shade cloth showed a higher (P<0.001) number of short (<10 cm) stems (15%) than all other treatments (9% in FS and T and 11% under slatted treatments). Plates 4.04 and 4.05 show a view of the morphological changes between plants grown the shade cloth and slats plants.

Stem height (STH)

The tallest (P<0.001) stems were observed under the trees and slatted treatments (Tables 4.12 and 4.13). The mean STH was 0.52 m for T and FS+SL, but 0.46 m in FS and under shade cloth over the experimental period. In addition, mean STH was taller (P<0.001) under T+SL (0.48 m) than under T+CL (0.46 m). The individual analysis for each rotation showed that plants were usually taller (P=0.05) under FS+SL than under FS+CL, but closer to T regime. The exceptions (P>0.14) occurred in March (mean STH=0.27 m) 2000 rotation, when no differences (P>0.20) were observed among treatments, and on March 2001 (P>0.31) when plants under T (0.44 m) had a similar STH to the two artificial shading structures (0.49 m).

Internode length (INTNOD)

Mean INTNOD for plants at the final harvest (Tables 4.12 and 4.13) was longer (P<0.001) under the slats (45 mm) than under cloth (41 mm) and full sunlight (41 mm) over the experimental period. Overall, plants under trees (46 mm) had longer (P<0.001) INTNOD than in full sun and under shade cloth (41 mm). Plants under T showed similar (P>0.06) mean INTNOD to those under the FS+SL treatment over the experimental period. Again the exception was on March 2000, when plant INTNOD was shorter (P<0.02) under T (25 mm) compared with FS (33 mm) treatment. On March 2001 rotation, the difference between T (37 mm) and FS (39 mm) treatments was not significant (P>0.06).

Plate 4.04. A view of the morphological changes under the shade cloth structure in summer at the open site.

Plate 4.05. A view of the morphological changes under the wooden slats structure in summer at the open site.

Leaf to stem (L/S) ratio

Changes in L/S ratio followed a similar pattern and was exponentially related to STH (Figure 4.14). Differences in leaf to stem ratio between treatments were usually observed in spring rotations, but remained the same over summer-autumn seasons (Tables 4.12 and 4.13). The mean L/S ratio was higher ($P<0.03$) in FS (0.75) and FS+CL (0.76) than under FS+SL (0.70) and T (0.69). Plants under T+SL showed lower L/S ratio (0.71) than plants grown under the T+CL regime (0.75).

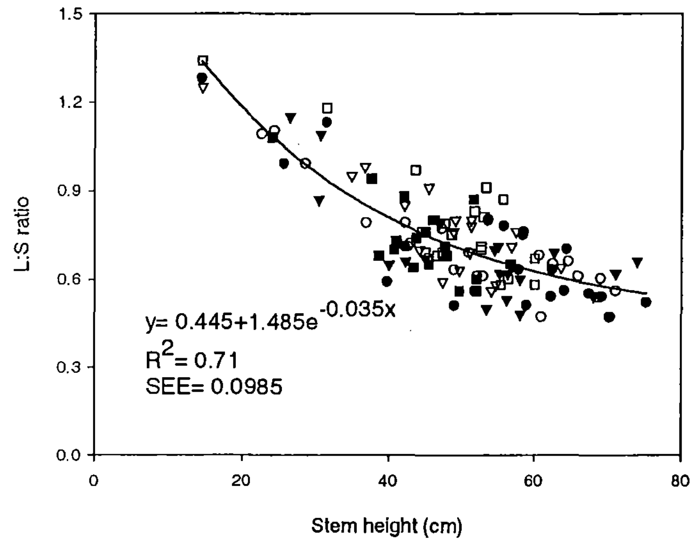

Figure 4.14. Leaf to stem (L:S) ratio plotted against stem height at the final harvest for lucerne canopy grown in six different light regimes: full sunlight (▽), shade cloth (■), wooden slats (□), radiata pine trees (●), trees+cloth (○) and trees+slats (▼). Graph included data from the 3 replicates collected from October 1999 to March 2001. Regression line is plotted for all data and SEE indicates the standard error of estimate for the regression.

Table 4.12. Mean stem height (STH), internode length (INTNOD) and leaf to stem (L/S) ratio at the end of each rotation for lucerne canopy under the six different light regimes. Data are averages of 3 replicates over the 5 experimental rotations in the first growing season at Canterbury, New Zealand.

Rotation*	Treatment	STH (m)	INTNOD (mm)	L/S ratio
15Aug-05Oct 99:	FS	0.48	48.63	0.82
	FS+CL	0.42	41.47	0.78
	FS+SL	0.51	51.37	0.81
	T	0.58	59.70	0.76
	T+CL	0.51	51.33	0.62
	T+SL	0.55	51.57	0.55
	F probl. † (SEM)	**0.002 (0.011)**	**0.002 (2.313)**	**0.053 (0.034)**
15Oct-18Nov 99:	FS	0.46	40.20	0.64
	FS+CL	0.45	40.73	0.63
	FS+SL	0.53	45.50	0.69
	T	0.62	51.93	0.54
	T+CL	0.63	52.60	0.59
	T+SL	0.59	51.27	0.60
	F probl. (SEM)	**0.024 (0.042)**	**0.080 (2.904)**	**0.034 (0.02)**
02Dec 99-05Jan 00:	FS	0.55	47.80	0.68
	FS+CL	0.45	46.37	0.63
	FS+SL	0.51	49.93	0.68
	T	0.69	57.37	0.56
	T+CL	0.66	57.13	0.62
	T+SL	0.71	62.47	0.61
	F probl. (SEM)	**0.008 (0.046)**	**0.051 (3.000)**	**0.118 (0.031)**
20Jan-23Feb 00:	FS	0.50	48.91	0.80
	FS+CL	0.48	45.90	0.81
	FS+SL	0.51	50.25	0.85
	T	0.53	54.63	0.74
	T+CL	0.44	46.71	0.76
	T+SL	0.55	53.14	0.73
	F probl. (SEM)	**0.152 (0.032)**	**0.221 (2.890)**	**0.204 (0.036)**
13Mar-18Apr 00:	FS	0.29	33.14	1.06
	FS+CL	0.26	29.19	1.00
	FS+SL	0.30	35.89	1.16
	T	0.23	25.33	1.13
	T+CL	0.25	28.33	1.02
	T+SL	0.29	32.70	1.04
	F probl. (SEM)	**0.196 (0.049)**	**0.016 (16.670)**	**0.256 (0.052)**

* Rotation period is the average of the 3 replicates (Table 4.05).

† The F probability and the standard error of means (SEM) are shown for all variables.

Table 4.13. Mean stem height (STH), internode length (INTNOD) and leaf to stem (L:S) ratio at the end of each rotation for lucerne canopy under the six different light regimes. Data are averages of 3 replicates over the 4 experimental rotations in the second growing season at Canterbury, New Zealand.

Rotation*	**Treatment**	**STH (m)**	**INTNOD (mm)**	**L/S ratio**
17Jul-14Oct 00:	FS	0.41	25.07	0.66
	FS+CL	0.46	33.40	0.71
	FS+SL	0.51	37.03	0.65
	T	0.47	28.40	0.55
	T+CL	0.37	22.30	0.74
	T+SL	0.36	21.30	0.65
	F probl. † (SEM)	**0.052 (0.041)**	**0.010 (2.279)**	**0.020 (0.020)**
25Oct-27Nov 00:	FS	0.52	44.61	0.65
	FS+CL	0.52	44.10	0.64
	FS+SL	0.60	52.13	0.58
	T	0.62	54.22	0.55
	T+CL	0.55	47.60	0.65
	T+SL	0.53	45.74	0.66
	F probl. (SEM)	**0.041 (0.032)**	**0.086 (3.392)**	**0.007 (0.020)**
12Dec 00-10Jan 01	FS	0.48	42.02	0.73
	FS+CL	0.54	46.63	0.71
	FS+SL	0.60	50.80	0.64
	T	0.54	47.74	0.67
	T+CL	0.41	42.41	0.80
	T+SL	0.45	43.33	0.76
	F probl. (SEM)	**0.001 (0.022)**	**0.081 (2.552)**	**0.001 (0.022)**
30Jan-13Mar 01:	FS	0.44	39.72	0.80
	FS+CL	0.49	37.62	0.81
	FS+SL	0.49	35.07	0.85
	T	0.45	36.87	0.74
	T+CL	0.35	25.83	0.76
	T+SL	0.38	27.47	0.73
	F probl. (SEM)	**0.008(0.0184)**	**0.036 (1.354)**	**0.204 (0.036)**
MEAN for the experimental period	*FS*	*0.46*	*41.03*	*0.78*
	FS+CL	*0.46*	*40.53*	*0.76*
	FS+SL	*0.51*	*45.23*	*0.70*
	T	*0.54*	*46.23*	*0.69*
	T+CL	*0.46*	*41.60*	*0.75*
	T+SL	*0.49*	*43.23*	*0.71*
	F probl. (SEM)	**0.001 (0.014)**	**0.001 (0.948)**	**0.014 (0.031)**

* Rotation period is the average of the 3 replicates (Table 4.05).

† The F probability and the standard error of means (SEM) are shown for all variables

4.3.2.7- Plant development

Calculations for the phyllochron were based on air temperatures collected from full sun and trees, assuming no changes in mean daily temperatures under the artificial shaded structures (Table 4.14). Although phyllochron seemed to increase under tree regimes compared with full sun during shortage of soil water, the mean phyllochron was the same ($P>0.14$) for all six light regimes over the 9 experimental rotations (42 °C day) and values increased from spring to autumn seasons for all treatments ($P<0.001$).

Mean daily air temperature was 0.2-0.5 °C warmer under trees than in full sun in spring and summer rotations, but in autumn and winter mean temperature was inverted and full sun was 0.1-0.3 °C warmer than under trees (Figures 4.01 and 4.02). Plants flowered in full sunlight and under trees from November to March in both growing seasons. Full sunlight plants accumulated 452 °C day to reach late bud (Stage 4, according to Fick and Mueller, 1989) while under trees plants were at early bud (Stage 3) in November rotations. In January and February of both growing seasons, full sun plants accumulated 401 and 505 °C day to be at late flowering (Stage 6), respectively, whereas plants under the T were only at late bud (Stage 4). With this same summer temperature accumulation, plants under the two artificial shading structures reached the early bud (Stage 3). No flowering buds were observed in the T+CL and T+SL treatments over the experimental period.

Table 4.14. The mean phyllochron (°C day) of lucerne stems in six light regimes over 9 rotations in Canterbury, New Zealand and from October 1999 to March 2001.

Treat.	**Oct**	**Nov**	**Jan**	**Feb**	**Apr**	**Oct**	**Nov**	**Jan**	**Mar**	***Mean***
	-----1999-----		-----2000-----					-----2001-----		
	-----°C day-----									
*TT**	*354*	*452*	*401*	*505*	*550*	*541*	*359*	*469*	*843*	
T	36	38	33	52	58	31	32	41	59	*42*
T+CL	35	38	35	53	62	32	31	45	56	*44*
T+SL	33	39	35	49	62	31	31	48	62	*43*
FS	35	41	35	49	52	32	31	41	58	*41*
FS+CL	34	41	41	48	54	40	31	40	60	*43*
FS+SL	35	39	40	49	54	40	31	39	56	*42*
Mean	*35*	*39*	*37*	*50*	*57*	*34*	*31*	*42*	*59*	
P<F										
Cover**	**0.99**	**0.22**	**0.11**	**0.17**	**0.03**	**0.03**	**0.74**	**0.03**	**0.08**	*0.23*
Shade**	**0.17**	**0.67**	**0.01**	**0.84**	**0.23**	**0.002**	**0.98**	**0.21**	**0.93**	*0.14*
C*S	**0.17**	**0.55**	**0.09**	**0.66**	**0.83**	**0.01**	**0.90**	**0.07**	**0.16**	*0.94*
SEM †	**1.78**	**0.75**	**0.68**	**0.79**	**0.20**	**1.08**	**1.36**	**0.62**	**0.12**	*0.50*

* Mean thermal time (TT) accumulated individually for each replicate from the residual to the final DM cut. Mean air temperatures in full sunlight and under trees are indicated in Figure 4.01, Section 4.2.1.3.

** Main plots (cover): Tree and full sun; Subplots (shade): no artificial shade, cloth and slats.

† SEM is the standard error of means for the lowest P<f test

4.4- Discussion

4.4.1- Radiation environment

4.4.1.1- Light flux and temporal patterns

The two artificial shade structures set in the open successfully mimiced the quantity of PPFD transmission observed under the agroforestry site over the seasons. However, the temporal pattern and spectral composition under slats were closer to that observed under trees than from shade cloth. The mean PPFD transmission over the seasons was 41% under FS+CL, 44% under FS+SL and 48% under T compared with full sun (Table 4.06).

The alternating periods of sun and shade under FS+SL were equivalent at 120 minutes at noontime (Section 3.3.1.1, Figure 3.02), but plants under T were exposed to a double period of full sun (2.45 hours) and approximately the same of shade (1.30 hours) compared with slats at maximum solar elevation (Figure 4.04). The sun and shade time course was inversed at low solar angle elevations under T, when 30 minutes of full sun and 165 minutes of shade was observed, whereas under FS+SL there were 50 minutes of light and 40 minutes of shade. The differences in temporal pattern between FS+SL and T were a consequence of the distinct shapes of the shade sources (conical tree crown versus long wood slat), tree canopy discontinuity and the additional presence of tree trunks in the agroforestry site. Change in the temporal pattern of radiation is an important issue in agroforestry research as it influences the daily canopy photosynthesis (Pearcy, 1990) of understorey vegetation. The periodicity of radiation was previously discussed for sunfleck/ shade events of forest environments (Pearcy, 1988), but it has usually been omitted in most agroforestry publications.

4.4.1.2- Spectral composition

Plants under the intermittent regimes (trees and slats) experienced different spectral composition from those in the continuous treatments during the shade period, but grew in equivalent spectral conditions during the sun period (Table 4.07). The shade cloth structure always had similar B/FR and R/FR ratios to the full sunlight conditions on sunny and overcast days. This result partially disagrees with early observations by Gaskin (1965) who found that shade cloth produced similar light quality (proportions of blue and red wavelengths) to tree shade when light transmission was above 25% compared with full sunlight. However, the results agree with more recent data from Devkota *et al.* (1997), who reported a similar R/FR ratio between black shade cloth with 43, 27, 18 and 14% and full light conditions. In addition, proportions of R and B light were always the same between T sun and FS+SL sun or between T sh and FS+SL sh. The ratios of B/FR and R/FR observed in FS and under trees were consistent with those reported by Bell *et al.* (2000) under coniferous and deciduous tree shade. The R/FR ratio was equivalent between the slatted and trees regimes, but they are explained differently. The red photon light originating primarily from direct irradiance was blocked and decreased at the low PPFD transmissions during the shade phase under slats. The same decline of R wavelength was observed under trees, but this was also because of tree canopy absorption. The FR was greater under trees than under the slats because direct FR penetrated tree canopies, but not the wooden slats. The heavy shaded treatments (T+CL and T+SL) produced similar temporal variation of spectral composition to slats and under trees, but plants were exposed to a longer period in shade with low R/FR ratios.

Overall results indicate that lucerne was submitted to equivalent radiation environments either under trees or slats. Therefore, plants morphogenetic changes would basically depend on the time scales of phytochrome-mediated responses during the shade period under the intermittent regimes. In the present experiment, R/FR ratio exceeded 1.0 in FS, FS+CL and during the sun periods under the intermittent regimes, but reduced to 0.4-0.7 during the heavy shaded periods. Likewise, Turnbull & Yates (1993) found that the R/FR ratios were between 0.3 and 0.6 during the shade, but exceed 1.0 during the sun periods under a subtropical rainforest. These authors observed that the time length under shade is critical for the magnitude of plant morphogenetic changes. The dependent effect of spectral composition and temporal variation of radiation on plant morphology under intermittent light regimes will be discussed in further Section (4.4.1.5). In summary, the spectral composition under the slatted structure was closer to that observed under trees than that from shade cloth.

4.4.2- Lucerne crop responses

4.4.2.1- DM yield

The DM yield changed progressively under shade treatments with regrowth periods (Table 4.06). In the second season, three distinct treatment groups were observed: (i) high PPFD (FS), (ii) intermediate PPFD levels (FS+CL, FS+SL and T) and (iii) low PPFD levels (T+CL and T+SL). DM yield decreased 30% and 45% under T compared with FS in the first and second season, respectively, but in both seasons mean daily PPFD (Table 4.06) was reduced by 52% on clear sunny conditions. A similar pattern of response under the other shade treatments was observed in this study.

Under shade, the progressive decrease of DM yield observed over the experimental period was probably associated with a continuous decline in root reserves and preferential allocation of carbon assimilates to shoot growth (Lemaire, 2001). Similar decline in DM yields and growth rates under the two artificial shade materials were observed in non-irrigated plots in the first experiment (Chapter 3, Section 3.4.4.2). Plants under the two heavy shaded treatments were severely affected by the decrease in PPFD. Therefore, the initial indication is that plants compensated the low PPFD levels by increasing remobilisation to above ground biomass. Results agreed with Lin *et al.* (2001) who observed that the dry weight of lucerne cultivars grown in greenhouse declined between 24-15% under 50% shade cloth and between 55-39% under 80% shade compared with full sun (2000 μmol photons m^{-2} s^{-1} at noon).

4.4.2.2- Canopy GAI

Results for total and final canopy GAI (Figure 4.07) were consistent with the DM yields and associated with the decline in the number of stems (Figure 4.08). By the end of summer periods, when SWC dropped below 15% in the top 0.5 m soil depth (Figure 4.05), lucerne GAI was more affected under competition from trees than in the full sun. This was the only time when plants under FS+CL and FS+SL had greater GAI than those under T. However, in the other rotations, when SWC was sufficient, DM yield and canopy GAI expansion seemed to be driven primarily by the radiation environment. This suggests a possible interaction between soil water and radiation competition for lucerne growth under trees. That is, lucerne growth declined more severely when low soil moisture (SWC<15%) caused by tree roots competition was combined with shading. In this case, DM yield decreased beyond the reduction in PPFD transmission. In contrast, when SWC was sufficient, lucerne DM yield decreased less than the reduction in PPFD.

Under the two heaviest shade treatments, lucerne plants never developed sufficient GAI for full light interception and relative reductions in DM was mainly limited by the low radiation environment. Competition for water and radiation resources has been identified as the main limitation for understorey species growth in agroforestry systems (Ong *et al.*, 1996). These results contrast with Yunusa *et al.* (1995) for the Lincoln area, when lucerne was competitive with young radiata trees (2-3 years old) in summer and had increased DM yield compared with the full sun. However, lucerne DM yield decreased compared with the open in spring, when soil moisture was not limiting and tree crown shade was severe. Obviously, the 9 years old trees in the present study had a greater advantage in competition for light and water with the lucerne understorey than the 2-3 year old trees.

The differences in slopes of GAI expansion after defoliation (Figure 4.07) indicate that under shade there was a lag in new green area expansion. Canopy GAI expanded to intercept most of the radiation available (PPFDi= 95%) in FS (Figure 4.08a, Tables 4.08 and 4.09), while radiation interception under the two artificial shade structures (PPFDi= 78-89%) and under T (PPFDi= 72-92%) never reached the critical GAI of 3.6. In addition, plants under T+CL and T+SL were estimated to intercept only 42-65% of the available PPFD in the second season. Thus, subsequent growth rates were greatly affected by reduced canopy photosynthesis. It is important to highlight that canopy architecture was unaffected by light regimes, with a mean K of 0.84 over the experimental period (Figure 4.08b). This result agrees with that found in the previous chapter when plants showed a mean K of 0.82 for all treatments. Although plants can eventually change canopy architecture under shade (Trenbath & Angus, 1975; Heichel *et al.*, 1988; Peri, 2002) or in severe water stress conditions (Moran *et al.*, 1989), the lucerne strategy under shade actually seemed to adjust GAI expansion until the irradiance penetrating the most shaded leaves equalled their compensation point. Therefore, the lucerne crop appeared to regulate its GAI expansion to maintain a favourable balance between sink and sources at a particular radiation environment. This response agrees with Givinish (1988) theory that lower levels of irradiance decrease the light that penetrates through a given number of canopy layers, so that shaded plants arrange their leaves in fewer layers than full sun plants.

4.4.2.3- Leaf Pn

Results for instantaneous Pn (Figure 4.11) and estimated Pmax (Table 4.10) confirmed the intermittency light-response effect under the slatted shade structure and under trees compared with the steady-state conditions in the FS and under shade cloth. Photosynthetic activity on top leaves declined consistently from the sun to the shade period under slats and trees over the experimental period (Figures 4.12 and 4.13). This was an indication that top leaves developed the photosynthetic phenomena of induction (gradual rise of photosynthesis after a prolonged shade period from a low initial rate to a steady final level) and deactivation (gradual decrease of photosynthesis from high to low irradiance), as defined by Rabinowitch (1956), under the present alternating sun/shade regimes. Peri *et al.* (2002) found that the decrease of Pmax in cocksfoot leaves, after entering the shade, was an exponential function of the duration in PPFD (at 50% PPFD of full sun) previously experienced. Likewise, these authors reported that the increase of Pmax (induction phase) in the intermittent regime was dependent on the previous time spent under severe shade. In this experiment, Pn measurements were randomly taken during the sun and shade phases under the intermittent regimes and this may explain the variability observed in Pmax (Table 4.10) within the heavy shaded treatments (FS+SLsh, Tsh, T+CLsh and T+SLsh).

Weighted averages for instant Pn, estimated Pmax and α (Section 4.3.2.6) showed that photosynthetic activity on top leaves changed little for plants grown in full sunlight or any other shade regime with more than 50% PPFD transmissivity. Although lucerne leaves were normally non-saturated at a PPFD of 2000 μmol photons m^{-2} s^{-1}, there was only a slight increase between 1000 and 2000 μmol photons m^{-2} s^{-1} (Figures 4.12 and 4.13). This explains the similarities for mean Pmax between FS, FS+CL, FS+SL and T over the duration of the study (Table 4.10). However, full sun exposed leaves (FS, FS+SLsun and Tsun) had higher

Pmax compared with those that were operating in heavy shade (FS+SLsh, Tsh, T+CLsh and T+SLsh). Photosynthetic activity would be expected to drop quickly for leaves at lower layers in all shaded treatments, because they would be operating in a lower part of the photosynthetic light response curves (Figures 4.12 and 4.13).

Data from Figure 4.09 shows that the lucerne crop in full sun intercepted 50% of the available PPFD (~1000 μmol photons m^{-2} s^{-1}) with a cumulative GAI of about 1.0 unit, so leaf photosynthesis activity at any layer less than this GAI level would be expected to change little. For this reason, the overall reduction in instant Pn and Pmax for top leaves under the 50% shade regimes was usually observed to be less than the decrease in DM yield compared with the FS. This result agrees with Evans (1993) who observed that most of the full sunlight was intercepted at the top parts of a lucerne canopy and that 50% interception occurred with a cumulative LAI of about 1.0 in spring. In the current study, for example, mean DM yield under T was reduced 38% compared with full sun, but top leaf mean Pmax decreased about 14% in this treatment over the experimental period. Similar trend was previously reported in Chapter 3 (Section 3.3.2.1, Figure 3.07), when plants under the two artificial shade structures had 40% less DM yield compared with those in FS, whereas instant Pn was reduced by about 14% in non-irrigated conditions (Section 3.3.2.7, Table 3.07). This response is consistent with data from Woodward & Sheehy (1979) in full sun conditions, where they observed a decrease of only 30% in canopy Pn at 100 mm below the top canopy, but a reduction of 70% at 300 mm depth compared with top leaves. According to the authors, this was due to the most efficient distribution of leaf area per unit of canopy height observed at the top canopy parts (cumulative LAI= 2.5). The results of this experiment also agree with Walgenbach & Marten (1981), in glasshouse conditions, who reported a decrease of 29% and 42% in shoot DM for lucerne plants grown for 20 days under 50 and 70% shade cloth, respectively, compared with fully illuminated plants. These authors also reported a decline of only 8% and 16% in total non-structural carbohydrates in the upper 0.10-0.15 m of herbage from plants grown under the two shaded regimes, respectively.

4.4.2.4- Use of radiation

The RUE estimations were similar to those observed in the previous experiment (Chapter 3, Section 3.3.2.6). Plants grown under the shaded regimes typically had greater RUE (Figure 4.10) than those in full sun. In addition, overall RUE values decreased from summer to autumn rotations. The mean RUE of 0.8 g DM MJ^{-1} PAR in full sunlight observed in this study was similar to those found by Khaiti & Lemaire (1992) for seedlings in spring, but lower than those for subsequent summer and autumn regrowth. The lower efficiency of lucerne in the current experiment compared with the literature could be because plants grew without any fertilizer input and irrigation. In addition, the mean RUE reported by Khaiti & Lemaire (1992) was calculated over the different growth periods within the rotation, whereas in the present study RUE was calculated based on the final harvest only, when usually reserves remobilisation to roots is maximal (Keoghan, 1991). Despite the difference, the decrease of RUE in autumn compared with summer rotations observed in the current experiment was consistent with Khaiti & Lemaire (1992) work and indicates more partitioning from shoots to roots in late season as well as slowing of new leaf appearance and growth at lower temperatures. However, estimation of RUE on a whole plant basis (shoot+roots) was shown to be constant over seasons by the same authors and has been reported to be little sensitive to environmental conditions (Monteith, 1989).

The explanation for greater RUE under shade compared with the FS treatment was previously stated as a result of lower decline in DM yield and photosynthesis activity than the reduction in PPFD and a possible increase in the shoot/root ratio. In this study, one evidence of preferential allocation of carbohydrates to shoots rather than roots under shaded treatments was the longer stem lengths compared with full sun plants. The morphological changes in shaded plants, such as in stem height, internode length and L/S ratio, seemed to be affected by the light quality environment and are the most important acclimation response observed on lucerne plants under shade. However, the magnitude of these changes never seemed to play a major role in the canopy growth under low radiation. Indeed, the most likely explanation for lucerne growth efficiency under shaded regimes was associated with the ability of the leaves to maintain its Pn capacity for PPFD above about 1000 μmol photons m^{-2} s^{-1}, which was the averaged light level mostly measured at the top of the canopies under FS+CL, FS+SL and T on clear days in summer. The light saturation point of young lucerne leaves was previously reported to occur at approximately 1/3 to 1/2 of full sunlight conditions (Pearce & Lee, 1969; Wolf & Blaser, 1972; McDowall, 1983; Nelson & Moser, 1994). In this experiment, top leaves were not physiologically light-saturated in most situations, but only small changes were observed between 1000 and 2000 μmol photons m^{-2} s^{-1}. There are few data in the literature concerning the efficient use of radiation in agroforestry areas (Wilson & Ludlow, 1991; Friday & Fownes, 2001). Overall, greater RUE was typically reported for tropical grasses and legumes under shade compared with full sun (Sophanodora, 1989; Ong *et al.*, 1996).

The quick decline in RUE under the most shaded treatments (T+CL and T+SL) between rotations 1 to 3 was probably due to a rapid decrease in root reserves combined with a major instant decline of PPFD levels, causing a lag in new leaf growth after defoliation (Figure 4.07). The same rapid drop of RUE under intermediate shade levels was never observed in this and in the previous experiment, probably because the newly established lucerne plants were less affected by the decline of root reserves at the 50% PPFD transmissivity.

Finally, the RUE of plants was similar between distinct shade regimes at equivalent PPFD levels (FS+CL, FS+SL and T) for most of the study. Plants under T had lower RUE compared with the two artificial shade regimes only in the last rotation, when water and light stress interacted and reduced DM yield more severely in the agroforestry site than in the full sun. The similarities between the two artificial light and the trees regimes were consistent over the two experiments and are at variance with the hypothesis initially stated by Rabinowich (1956) that *long intervals of the order of several hours can improve the utilization of light energy because during the dark "rest period" the plant can recuperate from the injury or exhaustion that often follows a period of intense photosynthesis.* That affirmative might be true for PPFD levels lower than 50% full sunlight. However, this experiment had not exposed plants to artificial shade levels similar to those observed under T+CL and T+SL in order to address this discussion.

4.4.2.5- Plant morphology and development

While no morphological changes were noted in the previous experiment under the two artificial shade structures (Chapter 3, Section 3.3.2.4-5), in this study they were the main differences observed between the shade cloth, slats and trees treatments (Section 4.3.2.6). Plants under the T and FS+SL showed the highest proportion of long size stems, whereas under FS+CL there was a higher proportion of short stems. Plants grown under T and FS+SL were also the tallest, had the greatest internode length and the lowest L:S ratio among treatments. Those changes were caused by the decrease of the R/FR ratio under the intermittent regimes (Table 4.07) compared with FS and FS+CL treatments. Smith (1982) and Ballare *et al.* (1995) previously stated that reduction in the R/FR ratio promotes stem elongation particularly in sun-adapted plants. In this experiment, plants under shade cloth were similar to those in full sunlight and the proportion of far-red light was lower than under trees or slats.

However, the morphological changes observed under the intermittent compared with the continuous regimes were insufficient to affect canopy growth. While a small number of high PPFD events may have a significant influence on the daily average of PPFD under intermittent regimes, they have little influence on the daily R/FR ratio (Turnbull & Yates, 1993). Shading duration (with low R/FR ratio) under the trees and slatted structure was probably not long enough to allow the morphological changes to affect canopy growth. The interaction between light quantity and quality is still unclear, but these results suggest careful analysis for environments with longer shade periods than those observed in this study is required.

Light intensity, spectral composition and periodicity never affected lucerne development over the experimental period (Table 4.14). As expected, the mean phyllochron was equivalent among treatments over the 9 rotations because only a small difference in daily air temperature (Figures 4.01 and 4.02) between the agroforestry and the full sun sites was observed. The phyllochron and its seasonality dependence observed in this study was consistent with data reported by Moot *et al.* (2001) for lucerne in spring and summer (35° C day per node) and in autumn (51° C day per node). However, there was a clear delay in time of flowering with 50%

shading and no reproductive induction observed in the two most shaded plants (Section 4.3.2.7). Reduced flowering was also observed with other understorey plants at low PPFD and low R/FR ratio (Mitchell & Woodward, 1988) and this could possibly be explained by a decrease in carbohydrate allocation to flowering nodes (Ballare *et al.*, 1995).

4.5- Conclusions

Results for a lucerne crop observed under the different light regimes lead to the following conclusions:

1- The wooden slats structure resembled better than the shade cloth the PPFD transmission, light regime (pattern of temporal variation) and spectral composition observed in the agroforestry site.

2- Spectral changes observed under trees and slatted regimes affected plant morphology by increasing the number of long stems, stem height and internode length compared with full sunlight plants. However, those changes influenced little the canopy growth responses.

3- Canopy growth (DM yield and GAI expansion) was mainly affected by the amount of PPFD received by plants. The magnitude of the decrease in canopy growth was less than that in PPFD transmissivity.

4- Mean annual DM yield was 17.5 t ha^{-1} in full sunlight conditions and declined to approximately 10 t ha^{-1} under FS+CL, FS+SL and T, then 3.4 t ha^{-1} under T+CL and 4.1 t ha^{-1} under T+SL. Lucerne yield potential under intermediate shade was superior to most of C_3 pastures reported in the literature.

5- Canopy architecture was unaffected by radiation environment and mean foliage angle had an intermediate dispersal with a mean K of 0.82.

6- Top leaves under the intermittent shade regimes experienced fluctuations in photosynthetic activity, but had steady responses under the continuous shade treatment. The weighted means indicated that they operated at similar photosynthetic rates in FS, FS+CL, FS+SL and T and declined under the two most shaded treatments.

7- The magnitude of the decrease in top leaf Pn was less than the reduction observed in DM yield, suggesting that photosynthesis activity at the intermediate and lower canopy strata was critical under the shade regimes.

8- Light use efficiency was unaffected by radiation periodicity. The mean RUE under the artificial and natural shade regimes was 58% higher than full sun plants.

9- The radiation environment never affected plant node development, but flowering was delayed in the shaded treatments.

Having defined the main field lucerne responses under the different light regimes, in the next chapter, a theoretical analysis will be performed using a canopy net photosynthesis model to observe how the crop would optimize canopy architecture to obtain maximum yields under the intermittent and continuous light regimes. The results of this analysis will assist in determining the actual yield potential of lucerne under light restrictions.

CHAPTER 5

A theoretical canopy photosynthesis model for different light regimes

5.1- Introduction

The wide range of environmental conditions and the large number of plant species found in agricultural systems produce complex canopy responses, which cannot be predicted by a single mathematical model. It is necessary to integrate various sub-models to adequately predict plant growth responses.

One successful example of sub-model integration is that used to predict canopy net photosynthesis rate (Pn) and consequently crop growth rate (de Wit *et al.*, 1970; Acock *et al.*, 1978; Weir *et al.*, 1984; Thornley & Johnson, 2000). This requires integration of sub-models (Section 2.1.5) for (a) canopy radiation interception, (b) light utilisation in canopy gross photosynthesis and (c) partitioning of photosynthates to canopy respiration.

Canopy Pn models can be applied to a number of environmental situations and crops under full continuous radiation. However, for plants growing either under intermittent light, such as in agroforestry and intercropping systems, or under a continuous shade regime, adjustments to these models are required. Thus, the time scale in the canopy Pn models should correctly resemble the alternating sun and shade intervals to produce a reliable plant growth response for this light regime. It has also been reported that shaded plants may adjust their morphological (Wilson & Ludlow, 1991; Buxton & Fales, 1994) and physiological (Rabinowitch, 1956; Loomis *et al.*, 1971) characteristics to maximise photosynthetic activity. Increasing leaf area, changing leaf to stem proportions and adjusting plant architecture are common strategies associated with maximising light interception and consequently optimising photosynthesis in plant communities. Accurate canopy Pn models should also include these plant parameters. Biochemical plant responses are complex to model and they are often not included in canopy Pn models. For the purpose of this study, biochemical adjustments are not included.

Shaded plants in nature may be exposed to either continuous or intermittent light regimes. The few works in the literature which investigate this issue assume that it is valid to compute leaf photosynthesis from continuous radiation for the various fluctuating light conditions, providing the same environmental conditions (McCree & Loomis, 1969; Loomis *et al.*, 1971 and Sager & Giger, 1980). However, this conclusion appears to be unsatisfactory when extended to a canopy photosynthesis level. Efficiency of light interception by different canopy layers and partitioning of photosynthates may produce somewhat different plant responses under the shaded regimes.

The intention of the analyses in this chapter were: (i) to link classic canopy Pn models found in the literature with continuous and intermittent light regimes and make the necessary adjustments to predict canopy growth rate accurately and (ii) to derive the optimum plant architecture required to maximise net canopy photosynthetic activity in each light regime. To achieve this objective, a canopy net photosynthesis model based on radiation interception, gross photosynthesis and total respiration was adjusted to operate in periods of (i) full continuous, (ii) partial continuous and (iii) intermittent light conditions. The model was also adjusted to simulate various canopy architectures by changing randomly distributed leaf angles. The theoretical analyses reported in this chapter are followed by validations from field experiment and are further described in Chapter 6.

5.2- Materials and methods

The general canopy Pn model was an integration of three main sub-models found in the literature: (a) radiation interception on a leaf (b) leaf gross photosynthesis rate and (c) leaf total respiration rate as described in Section 2.1.5. The canopy Pn rate was then obtained by subtracting total respiration from gross photosynthesis rates. Adjustments were proposed to allow adequate simulation of the alternating light regimes described in Chapter 3. The three sub-models were developed in linked Excel (Microsoft Corporation, 1997) spreadsheets and integrated into a general canopy Pn model.

5.2.1- Radiation interception by leaves

The sub-models suggested by Monsi & Saeki (1953) and Warren Wilson (1960) were integrated into a model to estimate the probability of penetration of rays of direct visible light. This integration was suggested by Duncan *et al.* (1967) to estimate the probability of penetration of rays of direct light and gives the opportunity to simulate light penetration with different leaf angles within the canopy profile. This integration reduces the inaccuracy of a single mean K value due to changes in skylight brightness, solar elevation angles and solar tracking movements by leaves. In this canopy Pn model, light penetration was calculated according to the equation (Section 2.1.5):

$$I(z)= I_0 \exp (-LAI*[F'/F]_{\phi, \beta} / \sin\beta) \qquad \text{Equation 2.2}$$

This derivation gives the area of direct light (Iz) from a point source (I_o) penetrating each foliage layer (LAI units) and allows the amount of light penetration to be calculated from various canopy architectures, by changing leaf angles (ϕ), and at different periods of the day, by altering solar elevation angles (β). Expressions to calculate $[F'/F]_{\phi, \beta}$ were also detailed in Section 2.1.5.

In this sub-model, light flux above the canopy (I_o) was used as input data at 5 minute intervals during the day and expressed in μmol photon m^{-2} s^{-1}. Values of I_o were subsequently converted to Watts m^{-2} of ground area, based on the ratio of 1 W m^{-2} of PAR ≈ 4.61 μmol photons m^{-2} s^{-1} (LI-COR Radiation measurement Manual, Lincoln USA). Light attenuation was corrected for the respective solar elevation and leaf angles every 5 minutes. Values of β were derived from equations used to calculate zenith angle (Appendix 4). Calculation of β was for the latitude of 43° 39'S and longitude 172° 28' E (Lincoln, New Zealand) on January 10th 1999 (Figure 5.01). For this specific geographic position, maximum solar elevation was estimated at 68.5° at 12.40 PM local time.

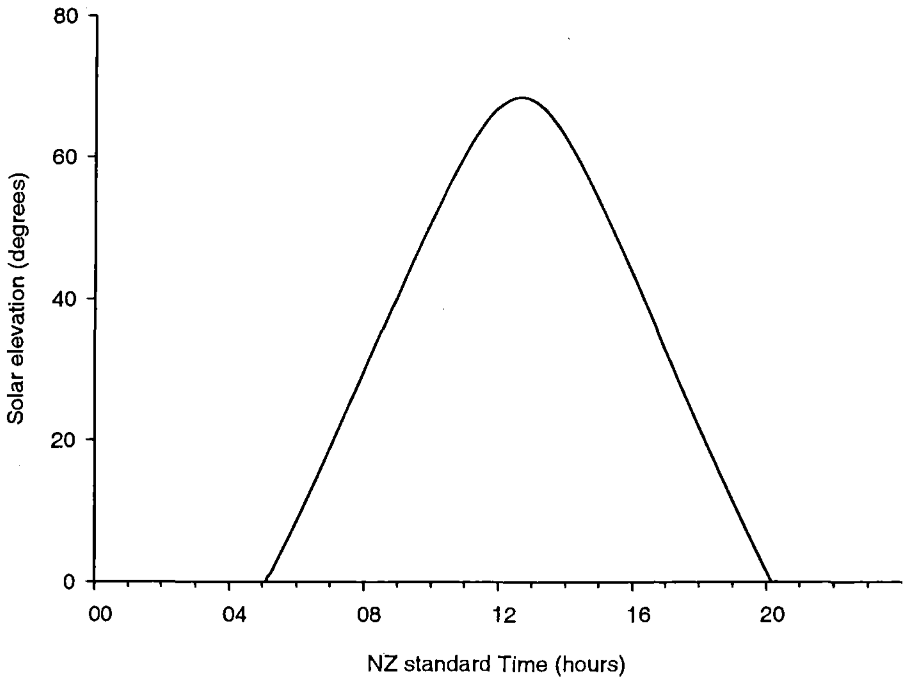

Figure 5.01- An example of calculated daily solar elevation angles for the 10th January 1999 in Canterbury, New Zealand (43° 39'S and 172° 28' E). Mathematical expressions are in Appendix 4.

The amount of direct light penetration was simulated for seven different leaf angles (randomly distributed): 0, 15, 30, 45, 60, 75 and 90°. Values of Iz were calculated for every 0.1 unit of LAI (accumulative) as the light penetrated within the canopy and for 5 minute intervals during the day. This time scale was appropriate to register irradiance alternations, as observed in the intermittent treatment. The lowest LAI value of 0.1 was assumed to be at the top of the canopy and this increased with depth within the canopy. Finally, to compute the area of sunlit leaves within each layer (direct radiation interception), the flux of direct sunlight entering each layer (Iz above the foliage layer) was subtracted from the flux leaving the layer (Iz available at the top of the subsequent lower foliage layer).

Three daily light regimes (Figure 5.02) were used as theoretical input data (I_o) to simulate canopy radiation interception in (i) full continuous light (100% transmissivity), (ii) partial continuous light (50% transmissivity) and (iii) intermittent light (50% transmissivity) with minimum periods of sun/shade of 30 minutes each at early morning and late afternoon and maximum of 120 minutes each at noontime. These theoretical light regimes produced changes in radiation transmissivity and periodicity similar to those described in Chapter 3. The pattern of radiation was similar between the full and the partial continuous radiation whereas the intermittent light produced an alternating full light/heavy shade regime. The sun and shade periods under the intermittent regime produced transmissivity values of 90% and 7% (in PPFD values) compared with the full continuous radiation, respectively. Overall, the full continuous light produced a daily photosynthetic radiation (400-700 nm) of 12.2 MJ m^{-2}, whereas the partial continuous and intermittent regimes produced 6.08 MJ m^{-2}. Mean light transmissivities for both shaded treatments were calculated to be at 50% to facilitate comparisons between light regimes.

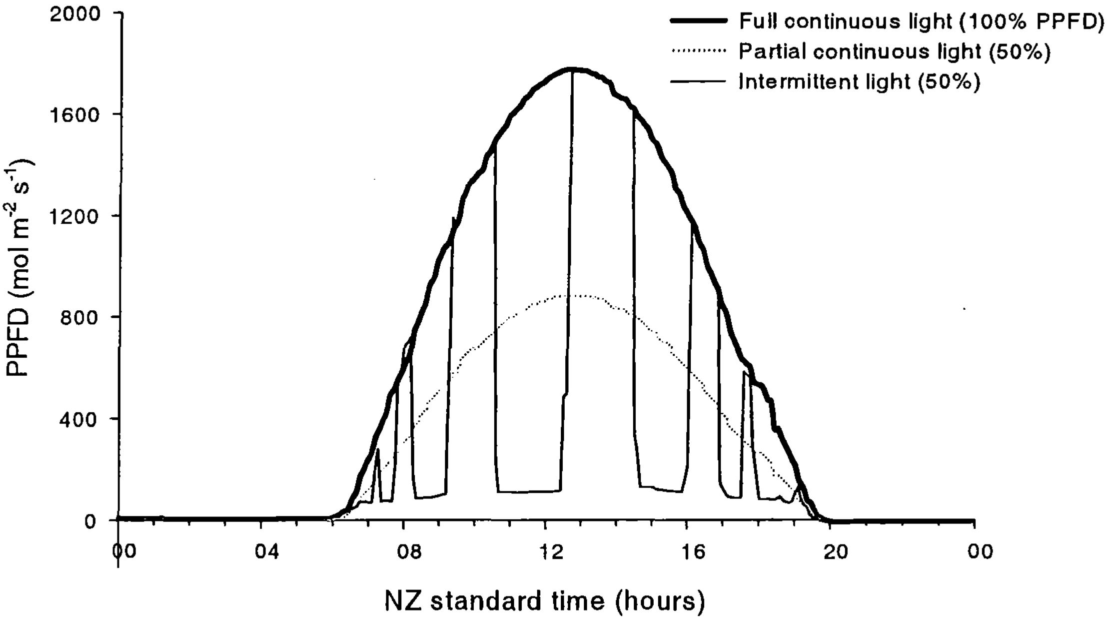

Figure 5.02- Simulated photosynthetic photon flux density (PPFD) in the full continuous light (——), under continuous shade (·········) and intermittent shade (—) on a typical full sun day in Canterbury, New Zealand.

5.2.2- Leaf gross photosynthesis

Leaf gross photosynthesis rate (Pg) was calculated according to Thornley (1976) and Weir *et al.* (1984) as described in Section 2.1.5. The sub-model equation is as follows:

$$Pg = \frac{[Pm + \alpha Iz] - ([Pm + \alpha Iz]^2 - 4\theta\alpha IzPm])^{1/2}}{2\theta}$$ Equation 2.3

This equation implies that gross photosynthetic rate (Pg) is dependent on four main variables: leaf radiation interception (Iz), photosynthetic rate at the saturating point (Pm), photosynthetic efficiency (α) and the ratio of physical to total resistance to CO_2 transfer (θ). The radiation interception of sunlit foliage values (Iz) for ϕ and β angles, as described in the previous section of this chapter, were linked to the Pg equation. For the purpose of this study α=0.017 mg CO_2 J^{-1} PAR and θ=0.72 (dimensionless) were set as constants based on measured light curves from field lucerne leaves. Details of measured light curves are given in Chapter 6. Maximum photosynthesis was calculated according to Thornley & Johnson (2000) equations as described in Section 2.1.5. Initially, maximum photosynthesis rate was corrected based on the growth irradiance within the canopy profile (Pmax').

$$Pmax' = Pm^{o} * [1 - \lambda/2 * (1 - Iz/Io)] \qquad \text{Equation 2.4}$$

Then, values of Pmax' were reduced as mean plant water content (PLWC) decreased as follows:

$$Pm = Pmax' * [1 - c * (1 - PLWC)] \qquad \text{Equation 2.5}$$

Leaf Pm, from Equation 2.5, was the actual value used in Equation 2.3 to calculate Pg. The Pm^{o} was the maximum photosynthesis rate (at 2000 μmol photons m^{-2} s^{-1}) measured in the field for top lucerne leaves. In this Chapter, a standard Pm^{o} value of 1.78 mg CO_2 0.1 m^{-2} s^{-1} for the three light regimes was applied based on field lucerne measurements in the summer. The value for λ was set at 0.7 according to Thornley & Johnson (2000). When plants were free from water stress, PLWC approached unity and when plants were under severe water stress PLWC reached zero. In this chapter, Pm was calculated in well-watered conditions according to field data (PLWC= 0.85). Constant *c*, which was a dimensionless value, reduced Pmax' below its maximum value as PLWC fell below one, and had a value of 2 in this model based on Thornley & Johnson (2000).

After calculating the appropriate values for Iz and Pmax, and setting the values of α and θ, the gross photosynthesis rate was calculated for every 0.1 GAI unit at 5 minute intervals. This gave Pg in units of mg CO_2 0.1 m^{-2} s^{-1}. The sum of Pg values was transformed to a daily basis and to a square meter of ground surface and the outcome was then expressed in g CO_2 m^{-2}ground d^{-1}. Having a known GAI distribution in the plant, it was then possible to simulate Pg at any height within the canopy profile or at different stages of maturity. For interpretations of RUE in this chapter, canopy Pn was also expressed in g carbohydrate equivalent (CH_2O) m^{-2} ground d^{-1} based on the ratio of 1g CO_2 m^{-2} ground d^{-1} $\approx$ 0.65 CH_2O m^{-2} ground d^{-1} (Hay & Walker, 1989). The carbohydrate unit was assumed an approximation of plant dry matter and easily comparable with values reported in the literature.

5.2.3- Total respiration

The third sub-model applied in this study was modified from McCree (1974) to calculate total respiration rate (R) in 5 minute intervals using Equation 2.8 (Section 2.1.5.2):

$$R = a \sum_{t=0}^{t=H} Pg_{(t)} + b\,W\,2^{0.1(Tmax+Tmin/2)} \qquad \text{Equation 2.8}$$

The first part of the equation calculated the growth respiration dependent on the Pg values and the second part assumed the maintenance respiration rate affected by air temperature as described in Section 2.1.5. *H* is the number of 5 minute intervals in a day and *t* is the time course used for calculations of growth respiration. The growth respiration coefficient (*a*) and the maintenance respiration coefficient (*b*) were set as 0.34 (dimensionless) and 0.03 day^{-1}, respectively, in this chapter. These were consistent values reported for non-stressed lucerne in the literature (Shone & Gale, 1983; Hanson, 1978). From data obtained in the field for irrigated lucerne (final harvest) in summer, a relationship between GAI and crop dry weight (W) was calculated and a corresponding W value was set at 7500 mg CO_2 equivalent in every 0.1 unit of GAI for the 3 light regimes. A unit of dry matter was converted to CO_2 equivalent units based on McCree (1974), multiplying by 1.43. The *Tmax* and *Tmin* are the daily maximum and minimum air temperatures, respectively, and were measured in the field.

The mean daily temperature (Tmax + Tmin/2) was set at 15.5° C as measured for 10th January 1999 in Lincoln, New Zealand (Meteorological Data Software by New Zealand Institute for Crop and Food Research Ltd.). Temperatures and coefficients *a* and *b* were kept as constants for all light regimes and maintenance respiration was calculated on a daily basis for every 0.1 unit of GAI within the canopy. Then, the total respiration rate was expressed on a daily basis (g CO_2 m^{-2} ground d^{-1}).

5.2.4- Canopy net photosynthesis

Finally, the three sub-models were integrated into a dynamic model of canopy net photosynthesis (Pn). Daily Pn was calculated as the difference between Pg (Equation 2.3) and R (Equation 2.8) to obtain values in g CO_2 m^{-2}ground d^{-1}. Using this model, it was possible to perform theoretical simulations of Pn at various levels "z" within the canopy under different light intensities and regimes. Also, it was possible to calculate Pn while altering canopy architecture (foliage angles) under different light conditions. In addition, the model offered the flexibility to simulate different field conditions by modifying values for Pmax, α and θ or by changing crop dry weight and mean temperatures.

5.2.5- Radiation use efficiency

Canopy radiation use efficiency (RUE) was calculated from the ratio between daily canopy Pn production (on a carbohydrates basis) and canopy light interception (in MJ PAR per day) for the three light regimes. Canopy Pn production was obtained from the combination of Equations 2.3 and 2.8. Radiation interception was calculated from the amount of area of sunlit leaves as obtained from Equation 2.2.

5.2.6- Simulations performed

In this chapter, a series of simulations were performed to predict the theoretical net photosynthesis efficiency of crops under the three light regimes. To isolate the effects of light regimes on the canopy Pn rate only, all other parameters involved in the mathematical model were maintained as constants. For all simulations, PPFD values were set at 5 minute intervals and light attenuation was calculated according to sun angles observed for the summer 1999 in the latitude of 43° 39'S (Lincoln, New Zealand) (Figure 5.02). Respiration coefficients, W, α and θ were set as previously described in this chapter. Sensitivity analysis for *a* and *b* coefficients and air temperature on total respiration rate were also performed since these parameters may change under shaded environments. The following simulations were performed in this chapter:

Simulation 1: This simulation determined the pattern of radiation interception and penetration with increasing values of canopy LAI in full continuous, partial continuous and intermittent light regimes. Simulations were performed at the maximum solar elevation angle (68.5° at 12.45 PM) for all light regimes, except for the shade period under the intermittent regime (65.3° at 11.45 AM). A random leaf angle was set at 45° for all treatments, which was near the mean of all treatments found in the earlier experiemnts.

Simulation 2: This simulation determined the daily canopy Pn rate against increasing LAI for different growth (*a*) and maintenance (*b*) respiration coefficients in full continuous light regime. The standard *a* coefficient was set at 0.34 and the *b* coefficient was set at 0.03 d^{-1}. Increments and reductions at 25, 50, and 75% for both respiration coefficients were simulated independently to calculate daily canopy Pn rate. Leaf angle was maintained at 45°.

Simulation 3: This simulation determined the sensitivity of canopy Pn rate against LAI for changes on mean air temperature in full and partial continuous light regimes. The standard mean air temperature of 15.5°C was changed ± 2 degrees in both continuous light regimes. Leaf angle was maintained at 45°. The *a* coefficient was set at 0.34 and *b* coefficient at 0.03 d^{-1}.

Simulation 4: This simulation determined the canopy Pn rate against LAI for different light intensities and regimes. PPFD values in the full and partial continuous and intermittent light regimes were used as an input data. In addition, simulations were performed of canopy Pn rate against LAI for 80, 60, 40 and 20% light transmissivity compared with the full continuous regime. Leaf angle was maintained at 45°. The *a* coefficient was set at 0.34 and *b* coefficient at 0.03 d^{-1}.

Simulation 5: This simulation determined the daily canopy Pn rate with increasing LAI for seven leaf angles (randomly distributed) in full, partial continuous and intermittent light regimes: 0, 15, 30, 45, 60, 75 and 90°. The *a* coefficient was set at 0.34 and *b* coefficient at 0.03 d^{-1}.

Simulation 6: This simulation determined the maximum daily canopy Pn rate with different leaf angle dispersals (0, 15, 30, 45, 60, 75 and 90°) for full, partial continuous and intermittent light regimes. It also determined the LAI value at which daily canopy Pn was maximised against leaf angles (optimisation of canopy Pn) for the three light regimes. The *a* coefficient was set at 0.34 and *b* coefficient at 0.03 d^{-1}.

Simulation 7: This simulation determined the canopy radiation use efficiency against LAI for the optimised canopy architecture in the three light regimes. The criteria used to identify the optimised canopy architecture were maximum daily Pn rates combined with greater LAI values.

5.3- Results

5.3.1- Simulation 1- Influence of light regimes

The irradiance available at level z decreased exponentially from the top (LAI 0.1) to the bottom (LAI 8) of the canopy for all treatments (Figure 5.03). The Full continuous light regime and the high light period under intermittent radiation resulted in a similar decline in canopy light penetration. The decrease was slower under partial continuous radiation and the low light period under the intermittent regime (Figure 5.03a). The absolute difference between the full continuous light and shaded conditions was greater for the top layers of the canopy. However, all treatments had 95% of the available light intercepted by the top part of the canopy (LAI 3.6) because of the constant leaf angle applied (Figure 5.03b). This indicated that the light interception model was sensitive to the amount of light rather than light periodicity and that the critical LAI point (when 95% of the above canopy light was intercepted) can be modified with different canopy architecture and solar angle elevations (Equation 2.2). The amount of irradiance available was negligible by LAI 5 in all treatments.

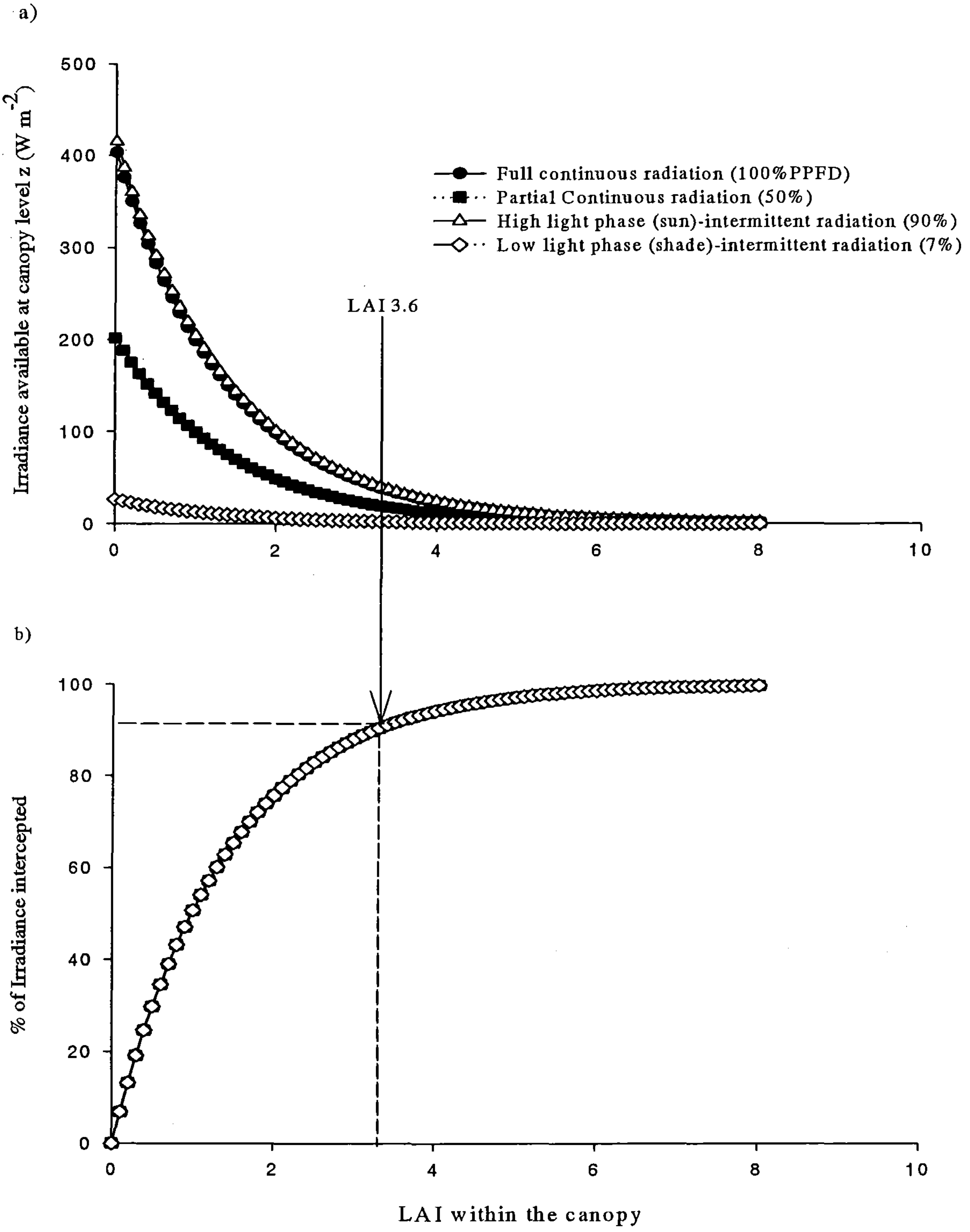

Figure 5.03- **Simulation 1**: light penetration (a) and interceptance (b) against LAI for the three light regimes in a typical sunny day at noontime in Canterbury, New Zealand. Leaf angle was set at 45° for the three light regimes.

5.3.2- Simulation 2- Influence of respiration changes

Figure 5.04 (*a* and *b*) showed that growth and maintenance respiration had a different effect on canopy Pn rate. As expected, canopy Pn rate increased with lower growth and maintenance respiration coefficients. The growth coefficient *a* had a major effect on canopy Pn rate on the high-illuminated upper part of the canopy, whereas changes in coefficient *b* affected net photosynthesis more for the more shaded layers within the canopy (LAI>3.3). The ability to predict canopy Pn rate, using different *a* and *b* coefficients made this model flexible for a range of environmental conditions and crop species.

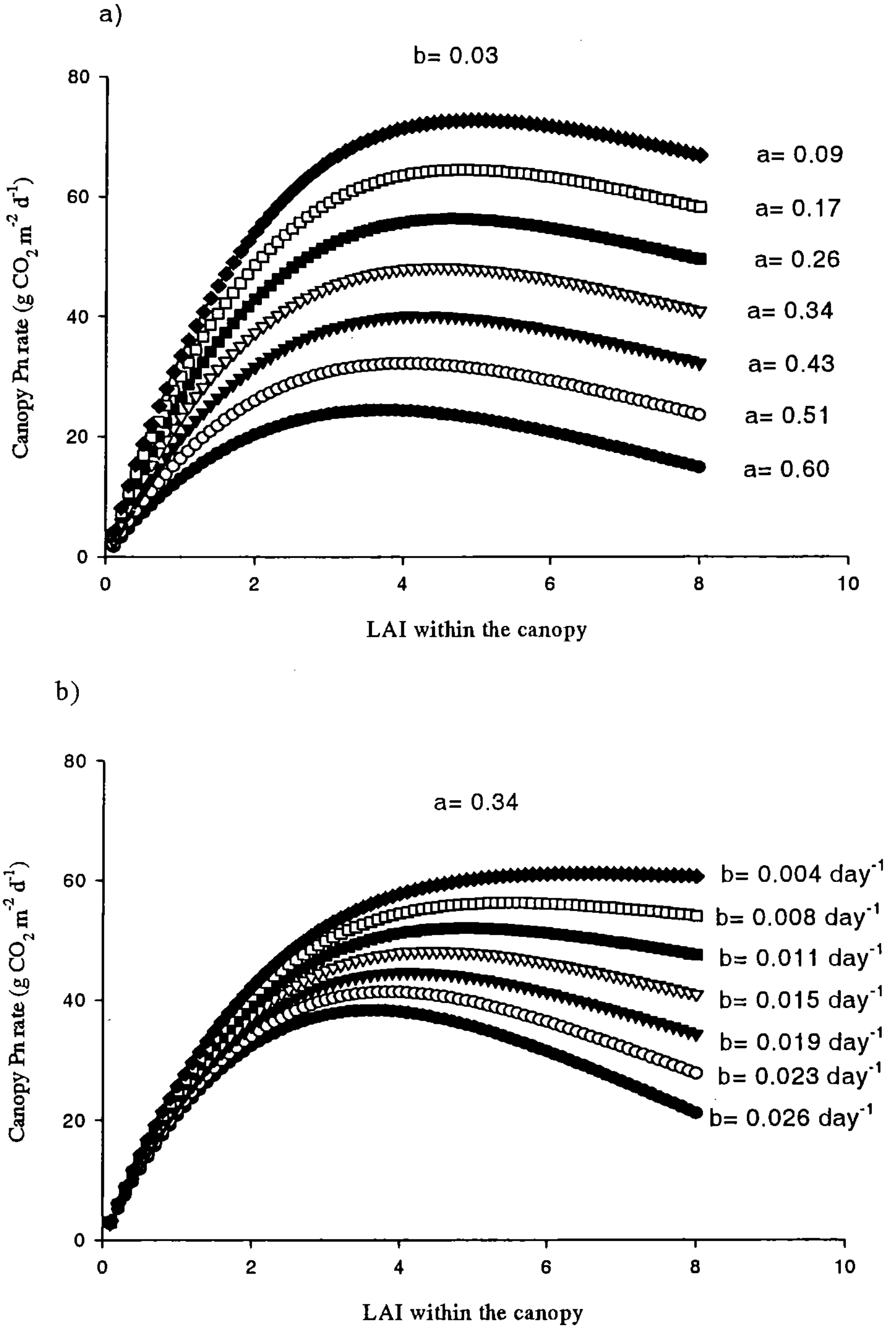

Figure 5.04. **Simulation 2**: daily whole canopy Pn rate against LAI for different growth (a) and maintenance (b) respiration coefficients in full continuous light regime with 45° leaf angle dispersal in Canterbury, New Zealand.

5.3.3- Simulation 3- Influence of air temperature

According to Equation 2.8, mean air temperature exponentially affected canopy maintenance respiration. Figure 5.05 shows that change in air temperature, under both continuous light regimes, affected the lower canopy parts (LAI > 2) more drastically than the upper parts. The temperature effect occurred exactly within the canopy parts where light penetration also decreased. A decrease of 2 °C in mean air temperature (13.5 °C) compared with the standard value (15.5 °C) caused an increase of up to 6 g CO_2 m^{-2} ground d^{-1} on daily canopy Pn rate in either full or partial light regimes. Correspondingly, a 2 °C increase in temperature reduced canopy Pn by a maximum of 7 g CO_2 m^{-2}ground d^{-1}.

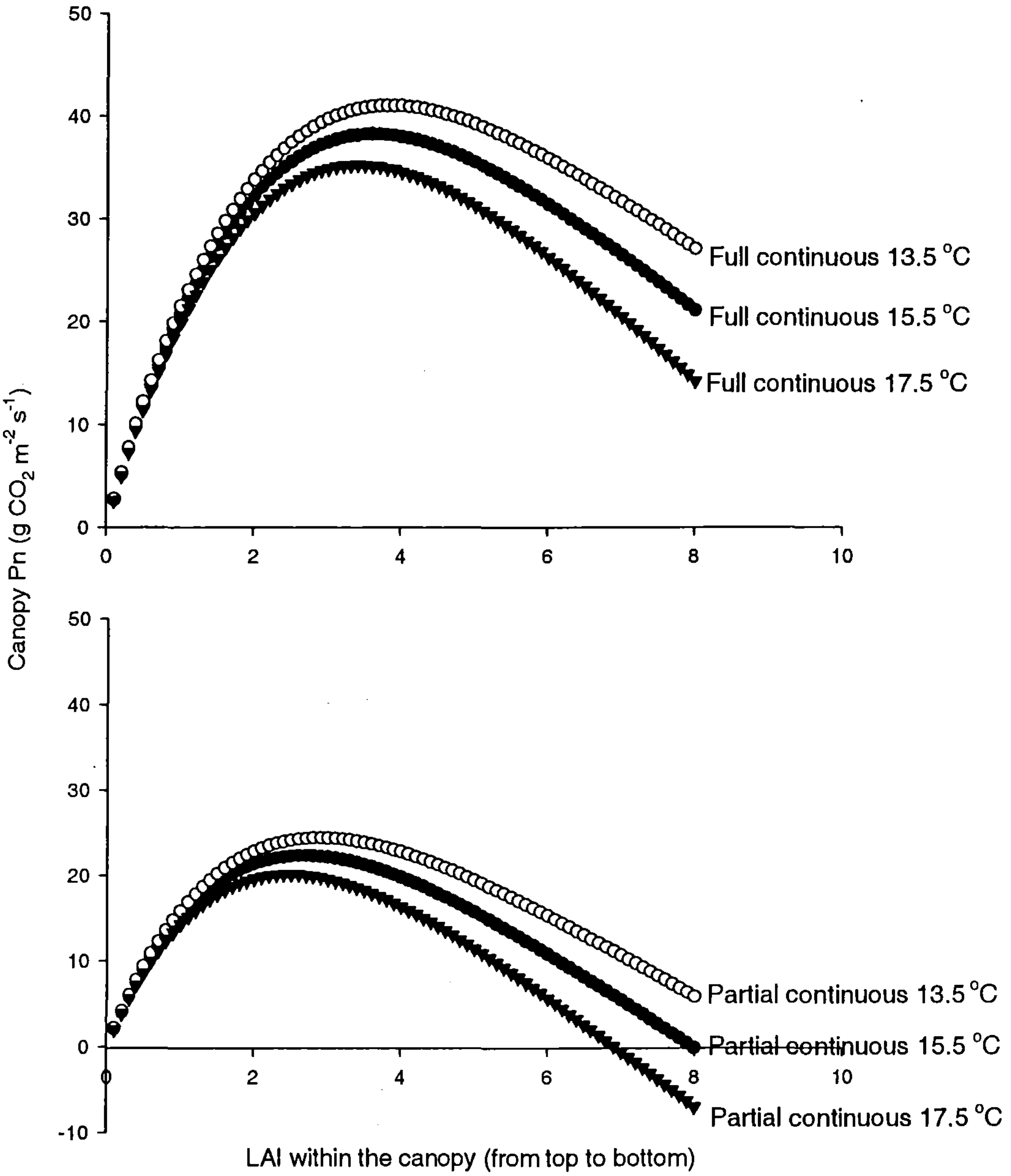

Figure 5.05. **Simulation 3**: whole canopy Pn rate against LAI for different mean daily air temperatures under full (a) and partial (b) continuous light regimes in Canterbury, New Zealand. In a and b respiration coefficients *a* and *b* were set at 0.34 and 0.030 day^{-1}, respectively.

5.3.4- Simulation 4- Influence of shade on whole canopy Pn

Figure 5.06 shows that for all light regimes the accumulative Pn curve increased to an optimum LAI when most of the radiation was intercepted and then decreased as amount of radiation interception by each unit of LAI declined for the lower parts of the canopy. In full continuous light (100% transmissivity), maximum canopy Pn rate was 38.29 g CO_2 m^{-2} d^{-1} at LAI 3.6. Above this LAI level, Pn rates declined as little radiation penetrated to these depths within the canopy and maintenance respiration increased. Maximum canopy Pn rates did not reduce in direct proportion to the decrease in light intensity for the continuous regimes. For instance, the maximum canopy net photosynthesis reached 26.36 g CO_2 m^{-2} d^{-1} or 69% of that predicted in full continuous light regime at LAI 2.9 under 60% light transmissivity. Positive Pn rates were obtained deeper within the canopy (high LAI) for light transmissivities higher than 50% in the continuous regime. In contrast, plants submitted to lower light intensity (40% and 20% transmissivity) were not able to produce positive Pn values at LAI > 6.9 and LAI > 3.8, respectively.

Photosynthesis responses under the intermittent light regime were lower than the 50% continuous light and actually approached the 40% continuous treatment. Daily canopy Pn rates reduced about 39% under the alternating sun/shade regime compared to the partial continuous treatment (50% transmissivity) and a negative Pn value was found at LAI higher than 6.4. In addition, maximum daily Pn rate was obtained at LAI=2.7 under the partial continuous regime, whereas under the intermittent treatment the maximum Pn rate occurred at LAI=2.5.

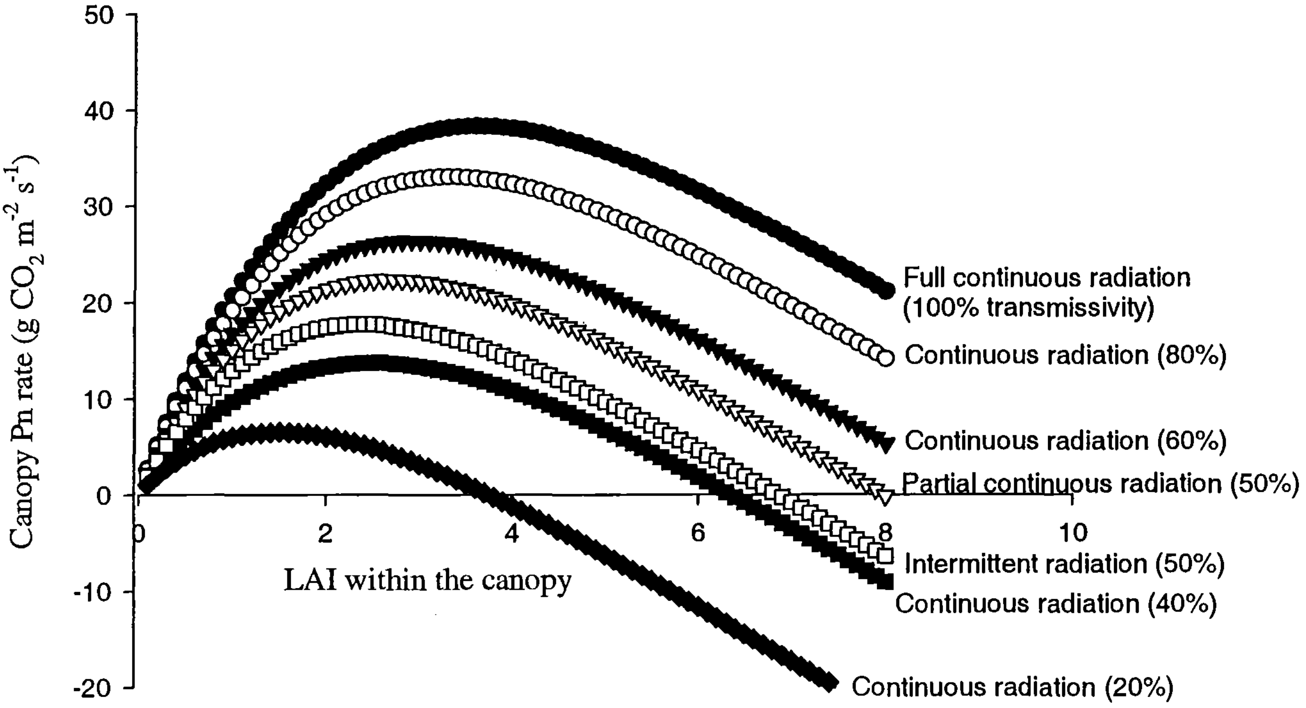

Figure 5.06. **Simulation 4**: whole canopy net photosynthesis rate (Pn) against LAI for different light regimes and intensities. Values in parenthesis mean light transmissivity compared with full continuous light conditions. Simulations were performed with leaf angle set at 45° for all treatments.

5.3.5- Simulation 5- Influence of leaf angle

5.3.5.1- Full continuous radiation (100% transmissivity)

In full continuous light conditions, plant architecture (leaf angles) altered canopy photosynthetic efficiency (Figure 5.07 a and b). In the top layers of the canopy ($LAI \leq 2$), all leaf angles produced similar daily Pn rates. In contrast, greater Pn rates were observed in the lower part of the canopy with more vertical leaf dispositions (> 45 °). Canopy Pn rate for the vertical leaf angle (90 ° dispersal) was greater than that for 45° leaf angle at lower layers (LAI > 3.4), but it was never superior to values obtained for leaf angles of 60 and 75°.

Optimum LAI also varied with leaf angles in the full continuous light regime. For the more horizontal leaf dispersals (0 ° to 30 °) optimum LAI occurred in the upper canopy (LAI 3 to 3.3). In contrast, with vertical leaf dispersal (75 ° to 90 °) the light penetrated deeper within the canopy and the optimum LAI was reached at about 4.5. In this light regime, maximum canopy Pn was greatest for leaves oriented at 75° (40.3 g CO_2 m^{-2} d^{-1} at LAI 4.6). For canopies with simulated horizontal leaf dispersal, the upper layers of the canopy intercepted a large proportion of the light.

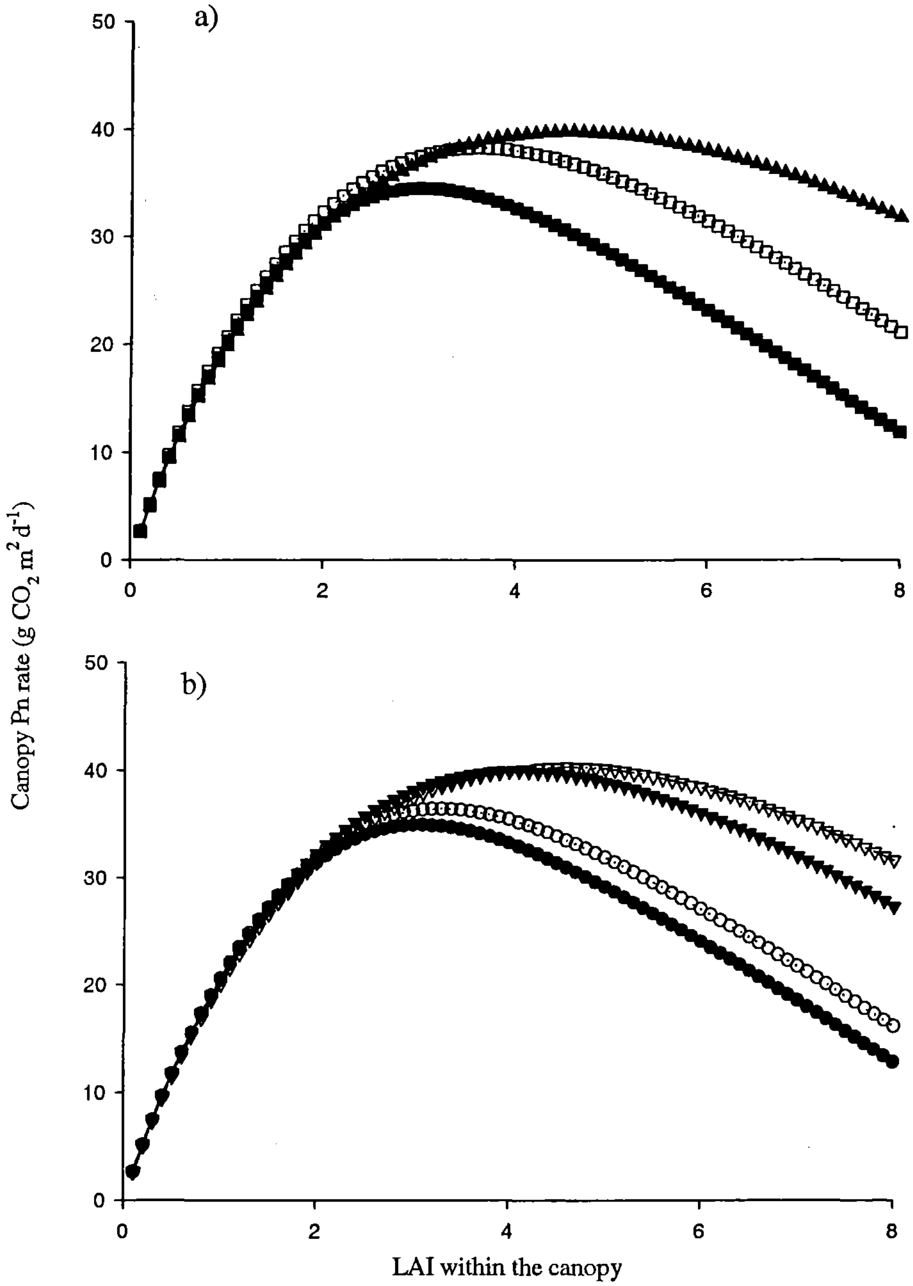

Figure 5.07. **Simulation 5**: daily whole canopy Pn rate against LAI for different canopy architecture (leaf angles) in full continuous light regime (100% transmissivity). Leaf angles were set at 0 (■),45 (□) and 90° (▲) in 5.07a and 15 (•), 30 (○), 60 (▼), 75° (▽) in 5.07b.

5.3.5.2- Partial continuous radiation (50% transmissivity)

Under 50% transmissivity (Figure 5.08 a and b), canopy Pn rates were lower compared with the full continuous light conditions at all leaf angles. Also, differences in canopy Pn rates between leaf angles were less evident than in the full continuous regime. Leaf angle dispersals of 30° and 60° produced similar maximum Pn rates, but critical LAI occurred at different points (LAI 2.5 and 2.9, respectively). Leaf angles of 75° and 90° produced the lowest Pn rates of all simulations in this light regime. However, critical LAI for both analyses occurred deeper within the canopy (LAI 3) compared with the other leaf angles. In contrast to the finding for the fully illuminated plants, under partial continuous radiation the 45° leaf angle resulted in the greatest accumulative Pn value (22.34 g CO_2 m^{-2} d^{-1} at LAI 2.7) of all canopy architecture dispersals. A leaf angle of 60° slightly reduced the maximum canopy Pn rate to 21.95 g CO_2 m^{-2} d^{-1} and the critical LAI occurred at a value of 2.9.

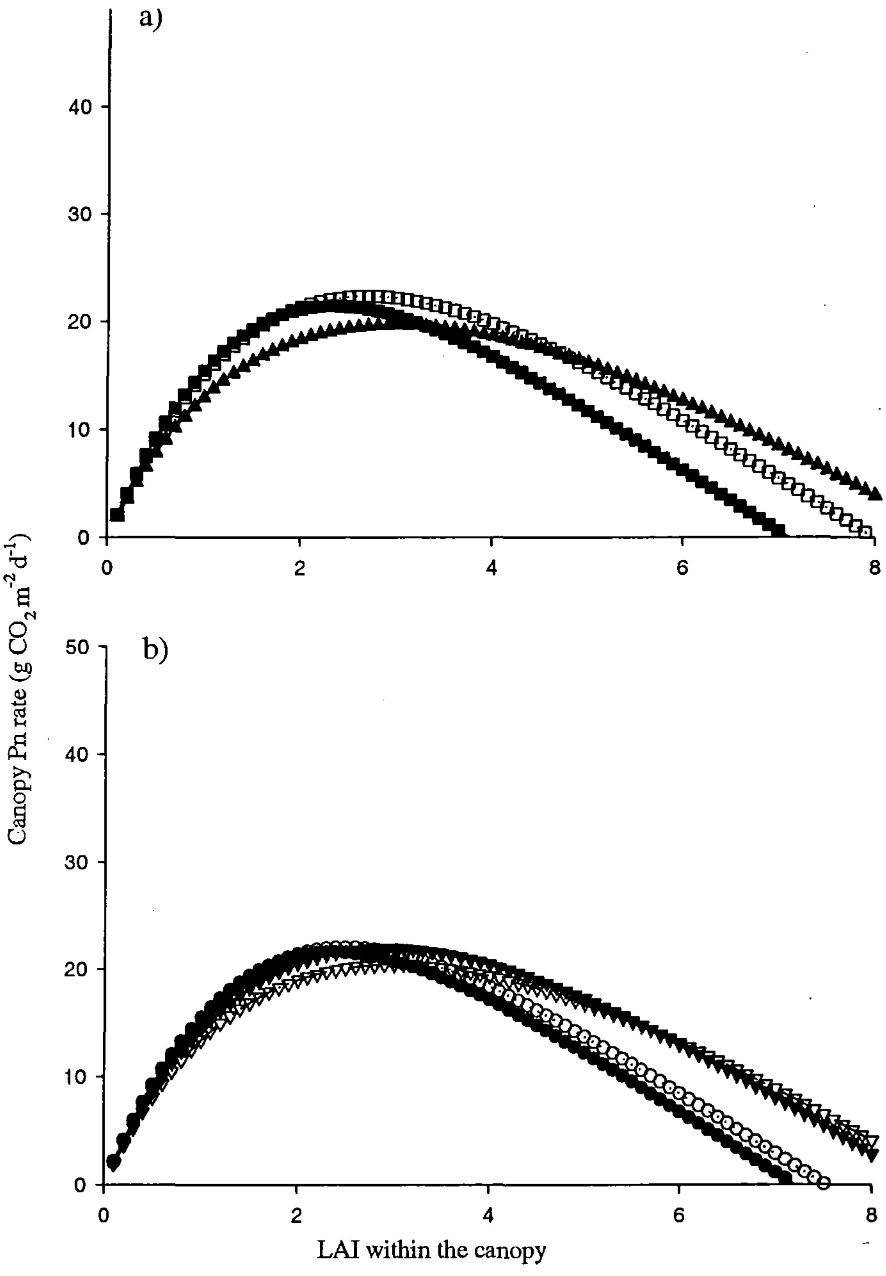

Figure 5.08. **Simulation 5**: daily whole canopy Pn rate against LAI for different canopy architecture (leaf angles) in partial continuous light regime (50% transmissivity). Leaf angles were set at 0 (■),45 (□) and 90° (▲) in 5.08a and 15 (●), 30 (○), 60 (▼), 75° (▽) in 5.08b.

5.3.5.3- Intermittent radiation (50% transmissivity)

Under the intermittent light regime, canopy Pn rates were lower than for the partial continuous radiation. In addition, differences between leaf angle dispersals were of a similar nature, but less evident under the intermittent regime (Figure 5.09 a and b) than the partial continuous light regime. As occurred in the partial continuous treatment, the greatest Pn rate occurred at 45° leaf angle (13.71 g CO_2 m^{-2} d^{-1} at LAI 2.5), but the difference was minimal compared with the 60° leaf angle dispersal. Contrary to the full continuous light, but similar to partial light, a vertical leaves dispositions (75° and 90°) in this light regime resulted in the lowest canopy Pn rates, although radiation penetrated slightly deeper within the canopy (LAI=2.7). Predicted canopy Pn rates were always lower at any leaf angle dispersal under the intermittent than the corresponding partial continuous regime.

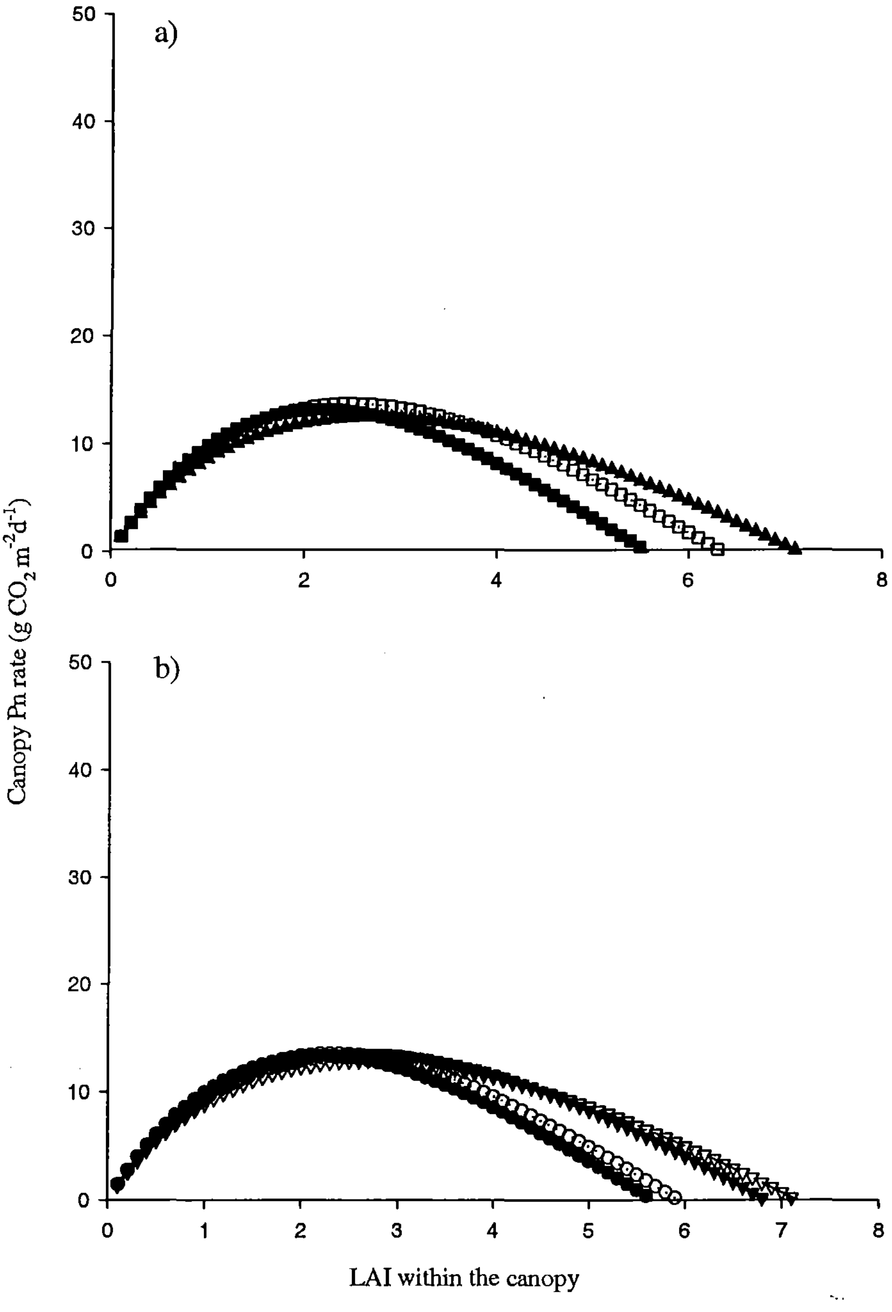

Figure 5.09. **Simulation 5**: daily whole canopy Pn rate against LAI for different canopy architecture (leaf angles) using the intermittent light regime (100% transmissivity). Leaf angles were set at 0 (■),45 (□) and 90° (▲) in 5.09a and 15 (●), 30 (○), 60 (▼), 75° (▽) in 5.09b.

5.3.6- Canopy photosynthesis optimisation

Simulations 1-4 enabled calculations of the optimum canopy architecture in which maximum net photosynthesis was combined with optimum LAI (Figure 5.10). Plants in the full continuous light radiation were most efficient with a leaf angle dispersal of 75°, which resulted in a predicted maximum Pn rate of 40.34 g CO_2 m^{-2} d^{-1} at a LAI of 4.6. With the 90° leaf dispersal, photosynthetic efficiency was reduced because light interception was reduced mainly in the upper parts of the canopy.

For the partial continuous radiation regime, the maximum canopy Pn rate was obtained with leaf angle of 60° when light reached lower layers without compromising photosynthesis (21.95 g CO_2 $m^{-2}.d^{-1}$ at a LAI of 2.9), but virtually there were only small differences from leaf angle 45 to 60°. Similarly, the maximum canopy Pn occurred with a leaf angle of 60° (13.55 g CO_2 $m^{-2}.d^{-1}$ at a LAI of 2.6) under the alternating sun/shade regime, but no virtually no difference was observed for leaf angles changes. Thus, it appeared that the optimum canopy architecture for maximising Pn rate was actually more dependent on the amount of PPFD available than on light regimes. Additionally, optimised canopy Pn under the intermittent regime was much lower compared with the partial continuous regime, though both received equivalent incidence of daily radiation.

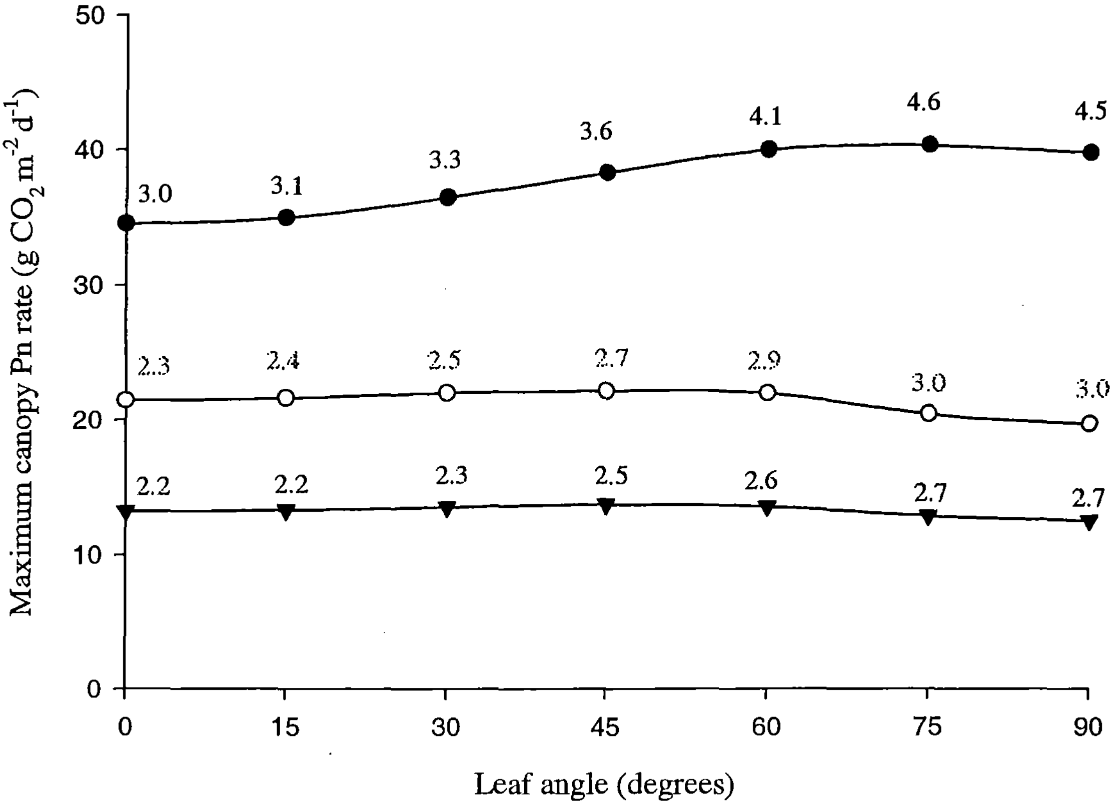

Figure 5.10. **Simulation 6**: predicted maximum canopy Pn rate against leaf angles for full continuous (•), partial continuous (o) and intermittent (▼) light regimes with different leaf angles. Values above each point indicate the LAI at which daily Pn rate was maximal.

5.3.7- Canopy radiation use efficiency

The RUE at the optimum leaf angle was calculated across LAI indices for the three light regimes (Figure 5.11). In full light, RUE was 2.56 g CH_2O MJ^{-1} PAR at the critical LAI 4.6, whereas under partial continuous light RUE increased to 2.96 g CH_2O MJ^{-1} PAR at the critical LAI 2.9. Under the intermittent regime, RUE declined to 1.9 g CH_2O MJ^{-1} PAR at the critical LAI. The RUE in full continuous light decreased slightly with increasing LAI values, whereas for both shaded regimes it declined more quickly after reaching the critical LAI. It is also important to note that the RUE for the partial continuous light regime was greater than the full continuous irradiance in the top parts of the canopy, but this response reversed after reaching LAI= 3.7.

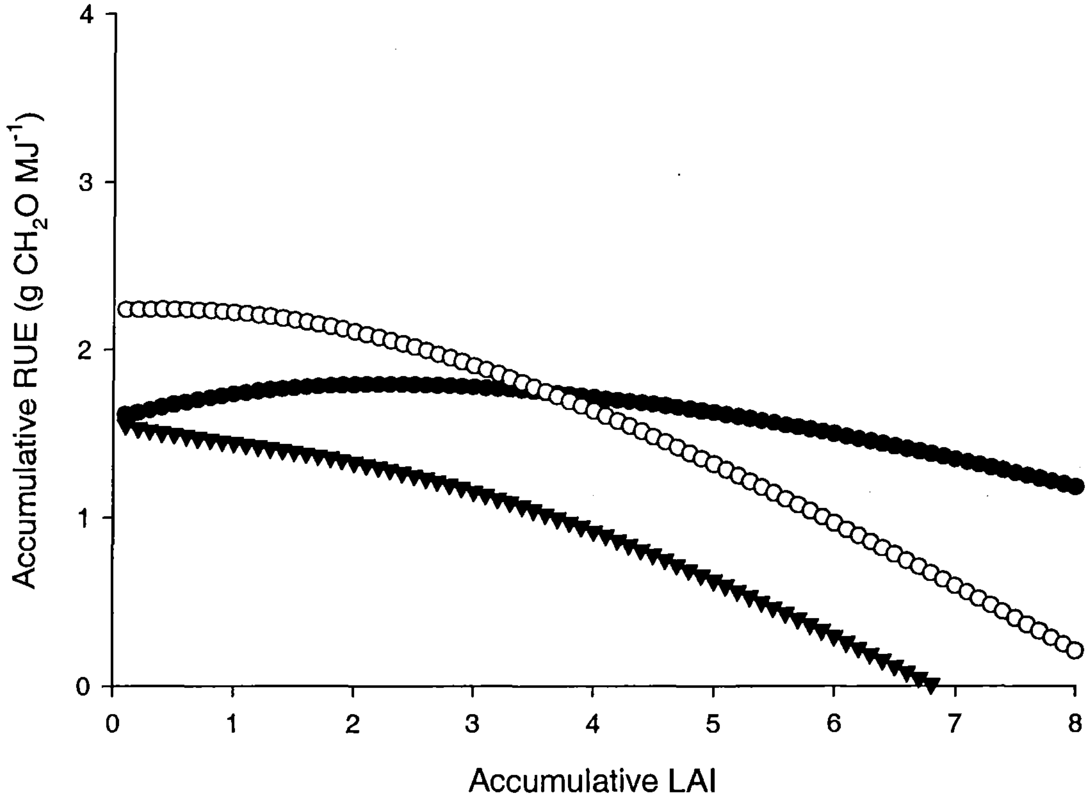

Figure 5.11. **Simulation 7**: radiation use efficiency (RUE) against LAI for optimised canopy architectures under full continuous (●), partial continuous (○) and intermittent (▼) light regimes.

5.4- Discussion

5.4.1- Radiation interception by a canopy

Light distribution within the canopy was similar for the three light regimes simulated, but the amount of radiation available at a given canopy layer (LAI level) differed systematically. Light penetration within the canopy for the intermittent regime showed two distinct responses (Figure 5.03a): (i) during the fully sun period, light penetration was similar to that produced by full continuous radiation regime and (ii) during the shade period, light penetration was negligible, corresponding to only 7% of the full continuous radiation. The mathematical model applied to calculate light distributions (Equation 2.2) produced an immediate switch from full sun to heavy shade condition. Therefore, the length of time in which the canopy was submitted to both full sun and heavy shade conditions was a critical point for simulations using the canopy Pn model. In addition, 95% of the available radiation was intercepted at LAI 3.6 regardless of the light regime and intensity (Figure 5.03b). This indicated that canopy architecture within this LAI range was critical to maximise light interception and quite independent of the amount of PPFD incident on the canopy.

5.4.2- Total canopy respiration

The opportunity to vary the maintenance respiration coefficient is an important tool in this canopy photosynthesis model, because values in the literature can change with air temperature, plant water status and crop weight (Penning de Vries, 1975). Figure 5.04b shows that when coefficient *b* increased, canopy Pn declined and the differences were particularly noted for the lower parts of the canopy (LAI > 3). As the light availability became limited at the lower part of the canopy, the proportional influence of maintenance respiration in relation to the canopy Pn rate increased. Conversely, at the top of the canopy, where light levels are higher, the importance of growth respiration (coefficient *a*) related to canopy Pn rate was greatest. Coefficient a is considered to vary with the type of plant tissue or type of new materials formed in plant growth (Thornley & Johnson, 2000). In the literature, there are a number of *a* and *b* coefficients cited for different plant species and temperature conditions (McCree, 1970; Penning de Vries, 1975, McCree & Silsbury, 1978;

Heichel *et al.* 1988; Hay & Walker, 1989) and for various leaf water potentials (Wilson *et al.*, 1980). It is also necessary to state that this canopy Pn model did not include the rate of change of living material. If a rate of canopy material senescence was applied in this Pn model, as suggested by Thornley & Johnson (2000), a clearer optimum LAI point for the canopy Pn curves might be obtained even for simulations with the lowest *b* coefficient simulations. Therefore, the assumptions of these simulations are only fully valid during the vegetative stage, prior to the canopy reaching the optimum LAI. After this point, the death of plant parts commences and the rate of senescence needs to be included in any model.

According to McCree (1970), air temperature has exponential effects on maintenance respiration rates in plants. There is evidence in the literature (Wong & Wilson, 1980; Ovalle & Avendano, 1988; Chen, 1989, Wilson, 1996) that air temperature changes only slightly in artificial and natural shade environments compared with full sun, but this can be affected by air movement under shade structures or wind conditions. Figure 4 showed the sensitivity of simulated canopy Pn rate to air temperature change. A change of only ±2 °C in air temperature from the ambient value of 15.5 °C caused an effect of up to ±30% on final canopy Pn rates at lower layers for both full and partial continuous light regimes. For the purpose of this theoretical analysis, air temperature was assumed to be equivalent between light regimes.

5.4.3- Light regime effects

In the current model, Pn increased rapidly at the top part of the canopy and passed through a maximum point defined as the optimum LAI. Beyond this point, Pn decreased as light availability was reduced (figure 5.06) and respiration rates increased (Figures 5.04a and b). Having set the canopy architecture constant at 45°, light intensities and periodicity did not change the format of the Pn curve. However, the optimum LAI was obtained deeper within the canopy at higher incident light intensities. At 40 and 20% continuous radiation, the influence of total respiration did not allow the canopy to produce positive Pn rates at LAI > 6.9 and 4.0, respectively.

The comparison between continuous and intermittent regimes at similar light intensity and equivalent leaf angles are also shown in Figure 5.06. The alternating light regime was less efficient than the partial continuous light treatment. These results are consistent with McCree & Loomis (1969) who found that the mean leaf Pn rate in alternating light was always within a few percent of the mean of the photosynthetic rates in a steady light condition. Differences in Pn rate between the two shaded treatments in this model were greater than those reported by McCree & Loomis (1969). The behaviour of the simulation under intermittent light regime, compared with the partial continuous, was associated with the occurrence of a great reduction in photosynthetic activity during the shade period combined with a limited increase during the sun period. Because Iz values were close to 0 PPFD during shade period under the intermittent light, gross photosynthesis was dramatically reduced and the simulated canopy operated at a very low portion of the Pn response curve. On the other side, after leaving the shade period, fully illuminated leaves under the intermittent regime automatically switched to similar Pg rates as simulated for full continuous light regime.

In nature, both the opening of stomata in light and their closure in the shade are not instantaneous. Therefore, the inertia of the stomata is an extra cause of plant growth inhibition or enhancement under an alternating light regime (Rabinowitch, 1956). The same author stated that photosynthesis production could be expected to be higher in alternating light compared with continuous illumination if the periods of shade and sun are very long or very short. This phenomena occurs because during the shade “rest period” leaves can recuperate from the injury or exhaustion that often follows a period of intense photosynthesis. With very short light periods, plants are more efficient under the intermittent light regime because this allows the dark catalytic reactions to run to completion, restoring the photosynthetic apparatus to its full efficiency at the beginning of each sun period (Rabinowitch, 1956). In the analyses performed in this chapter, a minimum of 30 (at lowest solar angle) and a maximum of 120 minutes (at greatest solar angle) were applied for both the sun and shade periods under the intermittent regime. Frequency of light fluctuations used in this analysis could be classified as intermediate compared with those reported by Rabinowitch (1956). It seems likely that, within this time under shade conditions, plants would operate in a more efficient part of the Pn curve than this simulation predicts, because the biochemical photosynthetic apparatus would still have substrate to be synthetised (Peri, 2002). Therefore, predicted canopy Pn rates were likely to be underestimated in this model particularly for shade periods under the intermittent light regime. To correct this problem, a detailed study of Pg light curve responses during the induction period (immediately post the shade period) and during the deactivation period (immediately after commencing the shade period) would be necessary to be included in a comprehensive model.

5.4.4- Canopy architecture effect

The canopy architecture influenced the simulated Pn efficiency (Figures 5.07, 5.08 and 5.09). In full continuous light, vertical leaf dispersal allowed light to penetrate deep within the canopy. As a result, simulated canopy Pn rate at high LAI values was higher for more vertical leaves compared with the horizontal dispersal. This response was associated with greatest radiation intercepted at the top of the canopy for flat leaves and low photosynthetic rates at the bottom portion of the canopy (Figure 5.07). In the full continuous light regime, the greatest photosynthetic rates were obtained at more inclined leaf dispersal (>60°). This result is consistent with Duncan *et al.* (1967) who found that the more nearly horizontal leaves gave the highest Pn rate at low LAI values and that with a LAI > 3.5, the more vertical leaves were most effective. The implication is that plant communities in full light regimes try to distribute evenly the incoming radiation throughout canopy layers to maximise canopy Pn. By increasing leaf angle, particularly at the tops, plants in full light regime thereby maintain most of the leaves operating close to their photosynthetic saturation point.

Net photosynthetic rates under the partial continuous radiation regime (Figure 5.08) were similar for leaf angles between 0 and 60°, but radiation was more efficiently used within the canopy profile with leaf angle dispersal of 60°. The low available radiation under this regime meant that the canopy was more efficient by maintaining intermediate leaf dispersals and a balance of radiation interception between the top and bottom leaf layers.

For the alternating light regime, a similar response to the partial continuous treatment was observed (Figure 5.09), but with less variation between leaf angles. Differences in canopy Pn rates between leaf angle dispersals were also less under the intermittent light regimes because of the low photosynthetic rate produced during the shade periods. Similarly, there were no substantial differences on canopy Pn rates for leaf angles between 0 and 60° under the alternating light regime.

5.4.5- Optimum canopy architecture

Results for optimisation of plant architecture (Figure 5.10) suggest that the advantage of a more vertical leaf angle is greater under high PPFD conditions than in shaded regimes, because the lower canopy layers are still able to operate at a lower portion of the Pn curve. Conversely, intermediate leaf angle dispersal would be photosynthetyically efficient at low light levels, but this would be strongly limited by a critical LAI in which leaves could still achieve positive Pn rates. Although solar tracking by leaves has been reported for some plants, such as lucerne (Heichel *et al.*, 1988; Moran *et al.*, 1989), it follows that random intermediate leaf dispersal is the optimum strategy for plants submitted to an intermittent light regime. In practice, the canopy Pn under the alternating light regime might be enhanced if a longer period of illumination had been simulated, particularly at greater sun angle elevations. Then, canopy Pn responses would approximate the full continuous light conditions and more vertical leaf angles are likely to be the most efficient canopy architecture.

The regimes simulated in this chapter showed that continuous shading produced greater Pn rates than the intermittent regime for all leaf angle dispersals, although photosynthetic values under the alternating regime were likely to have been underestimated. At the optimum canopy architecture (60° leaf angle dispersal) this model produced maximum daily canopy Pn rates 38% lower under the intermittent than under the partial continuous regime. In the real situation, it is possible that adaptation by the plant may make the canopy Pn under the alternating regime approach the rate of the partial continuous treatment. However, the simulations indicate the existence of a potential source of inefficiency within the intermittent light regime. This response confirms the Rabinowitch (1956) hypothesis that plant at intermediate light frequency under the fluctuating light regime can approach but not exceed the rate under the continuous light regime. However, it partially agrees with McCree & Loomis (1969) conclusions that it is valid to compute photosynthesis from leaf photosynthetic rates determined under steady-state light conditions for the various fluctuating light regimes found in the literature.

The greater RUE in the full continuous light regime compared with the shaded continuous regime (Figure 5.11) resulted from the higher photosynthetic rates achieved per unit of light intercepted, particularly at middle and low canopy parts in full sun conditions compared with the partial continuous light regime. In the top layers of the canopy for the full light regime, the RUE was lower than in the partial continuous radiation because leaves were operating above the saturation level, whereas the 50% transmissivity treatment was operating just about Pmax conditions. So, there was an inefficient conversion of light energy into carbon at the top parts of the canopy in full sunlight, although leaves were maintained at 75° angle. However, this response changed at LAI > 3.7, when lower canopy parts in the full continuous light regime were able to intercept sufficient radiation to maintain positive photosynthetic rates whereas under partial continuous regime the photosynthetic efficiency declined dramatically. Another important observation was that the greatest RUE in the full sunlight conditions was obtained at a LAI of 2.4, whereas the critical LAI was 3.6. In other words, the maximum conversion of light to carbon did not occur at the same canopy LAI as the optimum level for net photosynthesis. This results support conclusions of several authors (Duncan *et al.*, 1967; Loomis & Williams, 1969 and Loomis *et al.*, 1971) that there can be a photosynthetic inefficiency in significant parts of the canopy, whenever top leaves operate above light saturation conditions, whereas intermediate and lower leaves still perform at efficient parts of the Pn light curve.

Simulations of RUE under the intermittent regime was consistently lower than the other two continuous radiation treatments at all canopy levels (Figure 5.11) and this did not agree with actual data in experiments 1 and 2. Since daily PPFD interception was similar between the two shaded regimes at all LAI values, this response resulted from the reduced canopy Pn rates simulated under the intermittent light regime. The magnitude of the RUE varied in this theoretical analysis, but the direction of RUE against canopy LAI was the same for both shaded treatments.

5.5- Conclusions

The theoretical results produced in this chapter suggested that:

1. Total light intensity was the main factor that affected canopy net photosynthesis, regardless of the periodicity of light regimes.

2. In full sunlight conditions, a random leaf angle of 75° was optimal to maximise canopy net photosynthesis.

3. Under partial continuous and intermittent light regimes, a random leaf angle of 45-60° was optimal to maximise canopy net photosynthesis.

4. (iv) The automatic switch from heavy shade to full light under the intermittent regime using this canopy model probably increased the cost of fixing carbon particularly during the shade periods and underestimated final daily net photosynthesis rates.

A theoretical framework for testing canopy Pn will be developed in the next chapter for the three light regimes. Then, the theoretical conclusions produced in this analysis will be validated with data collected from the lucerne field experiment reported in Chapter 3.

CHAPTER 6

Validating the canopy net photosynthesis model under different light regimes

6.1- Introduction

The canopy Pn model presented in Chapter 5 was based on mathematical relationships that have previously been developed and validated for crops under natural skylight conditions (de Wit *et al.*, 1970; Marshall & Biscoe, 1981; Weir *et al.*, 1984; Thornley & Johnson, 2000). Both partial continuous and alternating light regimes, caused by fluctuations in daily overcast conditions, may have been simulated during validation periods, but they were not the focus of these studies.

It has not been reported whether the mathematical relationships were valid under alternating light regimes, such as those described in Chapter 5. The theoretical analysis suggested that daily canopy net photosynthesis decreased at a slower rate than the level of PPFD available and as a consequence predictions based on full sunlight were expected to underestimate crop growth rates under both the shaded regimes, through less so for the alternating light regime. Therefore, the aim of this chapter is (i) to test the theoretical assumptions made in Chapter 5 for these light regimes and (ii) verify the accuracy of the proposed canopy Pn model to predict field production under the three light regimes. Further discussion follows about adapting mathematical relationships applied in this canopy Pn model for shaded conditions. The partial continuous and intermittent regimes simulated in this chapter were produced in the field using plastic shade cloth and wooden slat structures, respectively, as described in Chapter 3. Input and validation data for these analyses were obtained from a lucerne crop grown in the field in Canterbury during two consecutive summer rotations under irrigated and non-irrigated conditions.

6.2- Materials and methods

6.2.1- Field experiment description

Canopy Pn rates for a 4 year old lucerne crop were simulated daily for two consecutive summer rotations (January and February 1999). Measured data for comparisons were obtained from an experiment with irrigation (full or none) as the main plots and light regimes as subplots with three replicates. The light regimes imposed on December 12th 1998 were: (i) full continuous (natural sky light), (ii) partial continuous (under black plastic shade cloth) and (iii) intermittent (under wooden slats). The shade cloth treatment allowed a mean daily transmissivity of 40% (in PPFD units) compared with the full sunlight regime in both rotations, whereas the slatted treatment allowed 46% transmissivity. Details of the pattern of these light regimes were previously discussed in Chapter 3. Shade structures were removed immediately prior to grazing and irrigation at the end of each rotation. For the first period of validation (between 23 December 1998 and 13 January 1999), the actual mean soil moisture deficit (SMD) to a maximum extraction depth of 2250 mm was 297 mm (standard deviation ± 20.7) in non-irrigated and 120 mm (standard deviation ± 21.5) in irrigated treatment. In the following rotation (between 20 January 16 February 1999), the mean SMD reached 332 mm (standard deviation ± 12.8) in non-irrigated and 102 mm (standard deviation ± 22.9) in irrigated plots. Methods for calculating SMD during the experiment period were presented in Section 3.2.3.2. Plant water content (PLWC) was estimated from the difference between fresh and dry weight material for all samples collected in the first and second summer rotations. Additional details about the experiment site, lucerne establishment and statistical analysis procedures were previously reported in Chapter 3.

6.2.2- Plant measurements

Lucerne DM samples and GAI were collected at seven day intervals, using methods described in Sections 3.2.5.1 and 3.2.5.2. To facilitate comparisons between predicted and actual values, DM yields were converted to a total carbohydrate (CHO) base. The assumption was that CHO was approximately the result of the subtraction between total

DM and nitrogen plus minerals (P, Ca, Mg and K) content. Lucerne DM samples were harvested at bud stage in the end of the second summer rotation (16 February 1999). From the main sample, sub-samples were obtained for leaves and stems. Total nitrogen and mineral analyses were performed individually for leaves and stems in two replicates for all treatments. Therefore, a relationship was plotted between lucerne GAI and mean weighted shoot CHO production for each treatment.

Canopy architecture was assessed by the extinction coefficient (K) calculated from Beer's law (Equation 2.2, Section 5.2.1). To do this a linear regression between Ln (I/Io) and GAI was plotted for each treatment during the experimental rotations and the slope of this line was K. Light penetration (I/Io) and GAI were obtained from canopy analyser (LAI 2000, LI-COR Inc., Nebraska) measurements in diffuse light conditions. Radiation interception (%) in diffuse light conditions was calculated by subtracting 100 from the radiation penetration value (%). Measurements using the canopy analyser were performed weekly at ground level. The final GAI and light penetration values resulted from the integration of 5 different zenith angles readings (7, 23, 38, 53 and 68°) measured by the canopy analyser.

In addition, a stratified analysis of GAI and mean canopy angle (MCA) was performed at 0.1m canopy height intervals immediately before the final harvest (11th February, 1999) for all treatments, using the canopy analyser. The GAI increment resulted from the subtraction of two consecutive strata readings within the canopy profile. MCA was measured individually at 0.1m canopy height and represented the mean inclination for foliage located above the sensor. MCA resulted from the integration of 5 different zenith angles. When MCA approaches 0, then foliage has a predominant horizontal dispersal, whereas high MCA values means foliage has a vertical dispersal. The mean plant heights in irrigated plots at this stage were 48, 43 and 44 cm in open, shade cloth and slats regimes, respectively. In non-irrigated, plant heights were 36, 38 and 42 cm, respectively (Section 3.3.2.4). Statistical analysis for plant height in all treatments was reported in Section 3.2.6.

6.2.2.1- Statistical analysis for plant growth

From the relationship of GAI against total shoot CHO, a fitted equation for each treatment was estimated with correspondent R^2 values. Statistical analysis was performed for the parameters obtained from the fitted equation, using a split-plot analysis of variance (ANOVA) with three replicates. Canopy water status (irrigated and non-irrigated) was set as the main plots and light regimes (open, shade cloth and wooden slats) were the sub-plots. Means were separated using the least significant difference at 5% level (LSD 5%).

Statistical analysis for canopy architecture was based in the estimated extinction coefficient and MCA values obtained weekly with the canopy analyser. From the slope of the fitted regression line Ln (I/Io) against GAI, the K estimated value was obtained for each treatment during the whole experiment period. The ANOVA was performed for K values, using a split plot design with three replicates. From the relationship between canopy radiation interception and GAI, an equation was fitted. Then, the critical GAI was estimated at 95% radiation interception based on the fitted equation for each treatment and a statistical analysis was performed, using a split plot design with three replicates. The same statistical analysis was also performed for MCA in both rotations. The main plots and sub plots for these analyses were set as previously described in this chapter.

Results for the canopy-stratified analysis (GAI increment and MCA) were analysed using a split-split-plot ANOVA with three replicates. The main plots and sub plots were set as previously described in this chapter. The sub-sub plots were set as canopy layer (measurements at 0.10 m intervals from 0 to 0.50 m canopy height). To facilitate the statistical analysis, using balanced treatments, GAI increment missing values, for plants shorter than 0.50 m, were set at a minimum value of 0.01. This situation occurred particularly for non-irrigated and shaded treatments. For MCA stratified analysis, statistical analysis was performed from 0 to 0.40 m canopy height as MCA measurements lose precision when associated with low GAI (LAI 2000 Manual, LI-COR Inc., Nebraska). Means were separated using the least significant difference at 5% level (LSD 5%).

6.2.3- Environmental measurements

Quantum sensors were set above the canopy to measure PPFD (μmol photons m^{-2} s^{-1}) in full sunlight, under the shade cloth and under the wooden slats. All quantum sensors were set in replicate 2 and maintained 0.10 m above the canopy and 0.20 m below the artificial shade materials, using a moveable aluminium bar connected to the shade structures. Sensors were lifted weekly as the canopy height increased. Details about the sensors were described in Section 3.2.3.1. To run the canopy Pn model, PPFD data was converted to PAR units (1 W m^{-2} = 4.61 μmol photons m^{-2} s^{-1}) as described in Chapter 3. Ambient temperature in full sunlight was assessed from the Broadfields Meteorological Station (New Zealand Institute for Crop & Food Research Ltd., Lincoln). Figure 6.01 shows the actual PAR measured under the three light regimes and the ambient temperature in full sunlight during the validation periods.

In addition, temperature sensors were set immediately above the canopy in both water status treatments and under the three light regimes in replicate 3. Sensors were maintained 0.10 m above the canopy and 0.20 m below the artificial shade materials and they were raised as the canopy height increased. Temperature sensors were installed inside an aluminium shelter (0.10m diameter) covered externally with white plastic paint and internally with black paint. The aim was to isolate the sensors from direct radiation effects and measure the airflow temperature in all treatments at the canopy height. Other details about the sensors were described in Section 3.2.3.2.

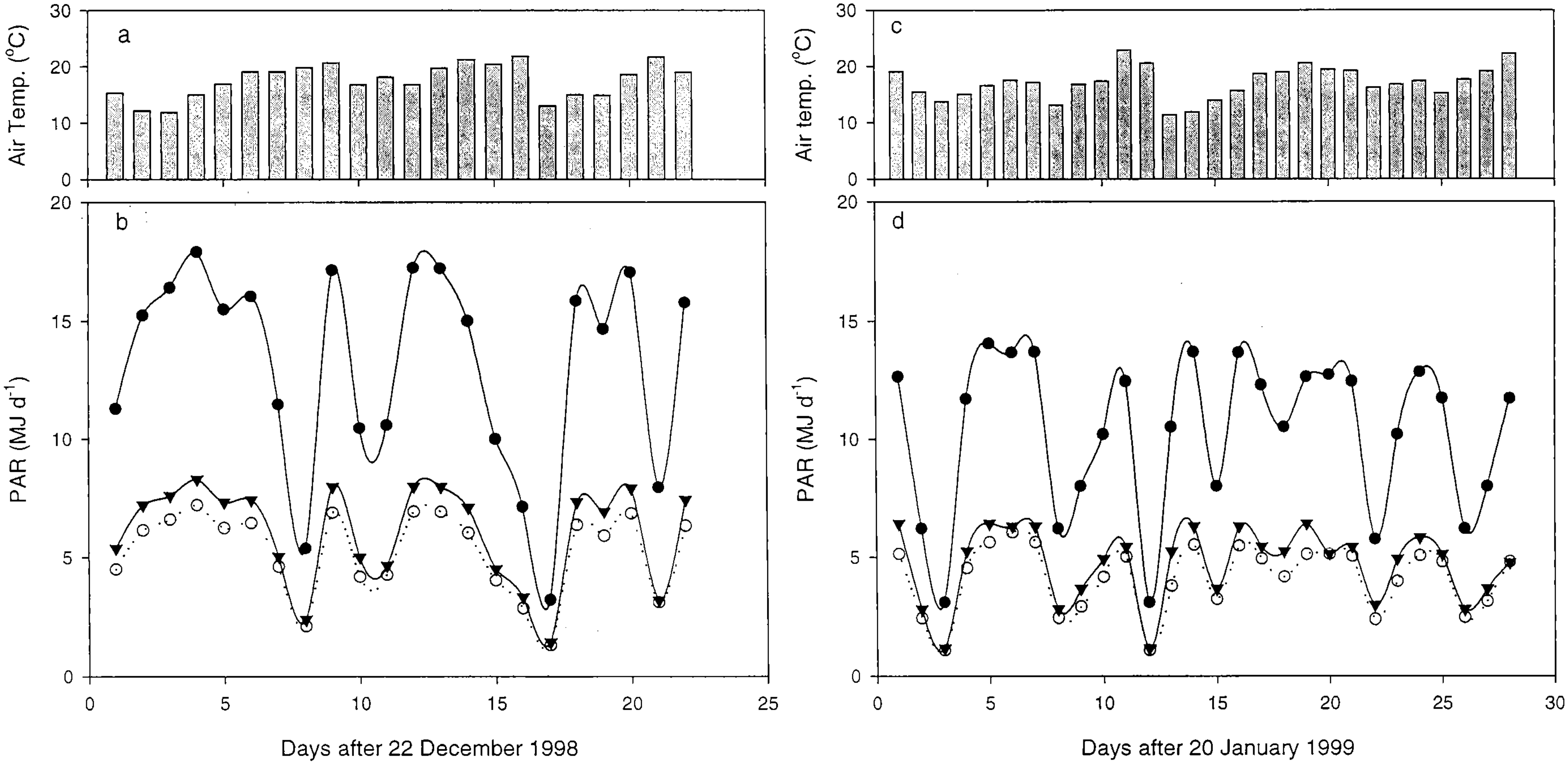

Figure 6.01. Mean daily ambient temperature (°C) and total daily photosynthetically active radiation (PAR) in full sunlight (—●—), under shade cloth (···O···) and wooden slats (—▼—) from 22/12/98 (*a* and *b*) and 20/01/99 (*c* and *d*) in Canterbury, New Zealand.

6.2.4- Physiological measurements

6.2.4.1- Gross photosynthesis rate

Parameters involved in the gross photosynthesis rate (Pg) sub-model (Equation 2.3, Section 5.2.2) were obtained from net photosynthetic light response curves measured in the field at 0, 100 250, 500, 750, 1000 and 2000 μmol photons m^{-2} s^{-1} using the infra-red gas analyser (LI-6400, LI-COR Inc., Nebraska). Air temperature in the equipment's chamber was blocked at 21° C and CO_2 concentration was set at 400 ppm. Pn rates were measured on the youngest fully expanded leaves at the top of the canopy. Samples were only collected in clear skylight conditions between 11.00 AM and 2.00 PM local time. Under the wooden slats regime, Pn rates were measured during the sunny period. For these validations, the negative Pn rate measured at zero PPFD was assumed to be equal to the leaf dark respiration rate. This value was then added to the Pn rates measured at PPFD >0 μmol photons m^{-2} s^{-1} to obtain an approximation of the Pg light curve. A non-rectangular hyperbola was fitted to the Pg light curves in each replicate to estimate the parameters α (photosynthetic efficiency) and θ (curvature of the curve). The maximum photosynthesis rate of the youngest fully expanded leaf (Pm^0) was obtained from the light curves at 2000 μmols photons m^{-2} s^{-1} in each treatment. Pm^0 values were used in Equations 2.4 and 2.5 (Section 5.2.2) and corrected for the amount of light penetration (Iz/Io) and the mean PLWC in each treatment to estimate the final maximum leaf photosynthesis (Pm). In this chapter, Pn rates in μmol CO_2 m^{-2} s^{-1} were converted to mg CO_2 m^{-2} s^{-1} by multiplying by 0.044 because of the canopy Pn model specification. Other details for the Pg parameters and coefficients were previously described in Sections 2.1.5.2 and 5.2.2.

6.2.4.2- Total respiration rate

Coefficients for total respiration (Equation 2.8, Section 5.2.3) were not measured in this experiment. The *a* and *b* coefficients used to run the canopy Pn model were obtained from the literature. A growth respiration coefficient (*a* coefficient) of 0.34 was used as reported for cereals (Weir *et al.*, 1984) which is also within the range cited for lucerne (Shone & Gale, 1983 and Heichel *et al.*, 1988) under non-stressed conditions. For full sunlight and irrigated conditions, coefficient *b* was set at 0.03 d^{-1} as reported for lucerne by Shone & Gale (1983). In this analysis, the assumption was that the maintenance coefficient reduced with increased water stress conditions (Penning de Vries, 1975; Wilson *et al.*, 1980). Therefore, the canopy CHO production was predicted for three different maintenance respiration coefficients obtained from the literature to choose a suitable value for the non-irrigated plots.

Crop dry weight (W) used to estimate the total canopy respiration rate (Rt) was obtained from the relationship between GAI and shoot crop dry matter in each treatment (Table 6.01). A mean value of W for every 0.1 GAI unit was calculated for all treatments in both rotations and then converted to CO_2 equivalents by multiplying DM yield by 1.43 (McCree, 1974). W was applied in Equation 2.8 to calculate maintenance respiration and it resulted from the mean value of the three replicates for each treatment and collected at final harvest. Likewise, maximum and minimum daily ambient temperatures (Tmax and Tmin) were applied to Equation 2.8 to calculate maintenance respiration. The values were obtained from the Broadfields Station. Daily values for Tmax, Tmin and PAR (Figure 6.01) were used as input data during the rotation period to estimate Rt. Ambient temperatures for the simulations were assumed to be equivalent for all light regimes.

Table 6.01- Lucerne crop weight (W) used to simulate total respiration rate (Rt) under the three light regimes and different water status in rotation 1 (Rot.1, from 23 December 1998 to 13 January 1999) and rotation 2 (Rot. 2, from 20 January to 16 February 1999). Values are averages of 3 replicates for final harvest.

Treatments	**Crop weight (W)** mg CO_2 eq.per 0.1 GAI*	
	Rotation 1	Rotation 2
Irrigated:		
Open	7700	7500
Shade cloth	7700	7200
Wooden slats	7400	7000
Non-irrigated:		
Open	7400	7600
Shade cloth	7300	7400
Wooden slats	7400	7000
F probability	*($0.68 \leq P \leq 0.87$**)*	*($0.35 \leq P \leq 0.25$)*

*Dry weight (W) was expressed in CO_2 equivalents (eq.) by multiplying DM yield by 1.43.

**F probability tests resulted from ANOVA for main effects (water status and light regimes) are shown in parenthesis.

6.2.4.3- Net photosynthesis rate

Instant canopy net photosynthesis was simulated as the difference between Pg and Rt for 0.1 unit of GAI intervals. The instant Pn rates were calculated at 5 minute intervals, summed, converted to daily canopy Pn production in g CO_2 m^{-2} d^{-1} and then values were expressed as accumulative Pn production over the GAI range. To facilitate comparisons with field measurements, accumulated Pn production was converted to a CHO base by multiplying by 0.65 (Hay & Walker, 1989).

6.2.4.4- Statistical analysis for physiological responses

From the measured leaf photosynthetic curves, a fitted equation was estimated based on a non-rectangular hyperbola (Equation 2.3, Section 5.2.2) for each treatment with correspondent R^2 values. Statistical analysis was performed for the parameters obtained from the fitted Pg equation (θ, α and Pm), using a split-plot analysis of variance (ANOVA) with three replicates. Canopy water status (irrigated and non-irrigated) were set as the main plots and light regimes (full sunlight, shade cloth and slats) were the sub-plots. In addition, an ANOVA was performed for mean PLWC (Section 6.2.1) measured during the rotation periods. Means were separated using the least significant difference (LSD) at α=0.05.

6.2.5- Simulations procedures

The simulation procedures for a complete lucerne rotation were performed as follows: The starting GAI point was 0.3 as observed for field measurements. The daily canopy Pn production (CHO base) was assessed for a GAI value of 0.3 in the simulation for day 1 after regrowth. The total CHO production predicted on day 1 was then converted into new GAI, using the relationship shown in Section 6.3.1. Then, the canopy Pn production in day 2 was predicted for the newly estimated GAI. The subsequent canopy Pn in days 1 and 2 were summed and the expansion in GAI was used to predict CHO production for day 3. Total CHO production in day 3 was assessed, summed to the production in days 1 and 2 and again converted into a new GAI. These procedures continued iteratively on a daily basis for the duration of the rotation period.

Partitioning of CHO to roots was assumed to start at GAI=1 or about 7 days after regrowth, as reported by Pearce *et al.* (1969) for lucerne. The rate of CHO partitioning to roots during the vegetative stage for summer in this chapter was calculated according to the pattern described by Khaiti & Lemaire (1992) for full sun plants. Because of the lack of data for lucerne under shaded, the same rate of partitioning was applied for all light regimes. That is, it was assumed that 19% of the total daily CHO produced was translocated below ground in the summer regardless of light regimes and water availability. Details of simulation procedures were the same as described previously until the canopy GAI=1. Above this, daily canopy Pn productions were reduced by 19% before CHO production was accumulated for the next GAI estimation. The following simulations of daily canopy Pn production were performed (Table 6.02):

Simulation 1: Daily variation from simulated canopy Pn (accumulative CHO production) and GAI growth for irrigated lucerne in full sunlight, under shade cloth and wooden slats in the first summer rotation (from 23 December 1998 to 13 January 1999). GAI growth was estimated according to the relationship described in Section 6.2.2.

Simulation 2: Accumulated predicted daily canopy Pn (CHO production) for lucerne in full sunlight regime and under non-irrigated conditions during two consecutive summer rotations (from 23 December 1998 to 13 January 1999 and from 20 January to 16 February 1999), using three different maintenance respiration coefficients (*b* coefficient): 0.030, 0.025 and 0.020 d^{-1}.

Simulation 3: Accumulated predicted daily canopy Pn (CHO production) for lucerne in a full sunlight regime under irrigated conditions during two consecutive summer rotations (from 23 December 1998 to 13 January 1999 and from 20 January to 16 February 1999). Parameters and coefficients used for canopy Pn simulations were described in Section 6.2.4.

Simulation 4: Accumulated predicted daily canopy Pn (CHO production) for lucerne grown in full sunlight regime and under non-irrigated conditions during two consecutive summer rotations (from 23 December 1998 to 13 January 1999 and from 20 January to 16 February 1999). Parameters and coefficients used for canopy Pn simulations were described in Section 6.2.4.

Simulation 5: Accumulated predicted canopy Pn (CHO production) for lucerne grown under cloth regime and in irrigated conditions during two consecutive summer rotations (from 23 December 1998 to 13 January 1999 and from 20 January to 16 February 1999). Parameters and coefficients used for canopy Pn simulations were described in Section 6.2.4.

Simulation 6: Accumulated predicted canopy Pn (CHO production) cloth regime and in non-irrigated conditions during two consecutive summer rotations (from 23 December 1998 to 13 January 1999 and from 20 January to 16 February 1999). Parameters and coefficients used for canopy Pn simulations were described in Section 6.2.4.

Simulation 7: Accumulated predicted canopy Pn (CHO production) under slats regime and in irrigated conditions during two consecutive summer rotations (from 23 December 1998 to 13 January 1999 and from 20 January to 16 February 1999). Parameters and coefficients used for canopy Pn simulations were described in Section 6.2.4.

Simulation 8: Accumulated predicted canopy Pn (CHO production) under slats regime and in non-irrigated conditions during two consecutive summer rotations (from 23 December 1998 to 13 January 1999 and from 20 January to 16 February 1999). Parameters and coefficients used for canopy Pn simulations were described in Section 6.2.4.

Simulation 9: Temperature sensitivity analysis (2 and 3 °C mean air temperature decrease) for accumulated predicted canopy Pn (accumulative CHO production) under cloth regime in irrigated and non-irrigated conditions during two consecutive summer rotations (from 23 December 1998 to 13 January 1999 and from 20 January to 16 February 1999). Parameters and coefficients used for canopy Pn simulations were described in Section 6.2.4.

Simulation 10: Temperature sensitivity analysis (2 and 3 °C mean air temperature decrease) for accumulated predicted canopy Pn (accumulative CHO production) under slats regime in irrigated and non-irrigated conditions during two consecutive summer rotations (from 23 December 1998 to 13 January 1999 and from 20 January to 16 February 1999). Parameters and coefficients used for canopy Pn simulations were described in Section 6.2.4.

Table 6.02- Summary of the simulations performed to predict lucerne canopy net photosynthesis (Pn) for the FSC experiment during Rotations 1 (23 December 1998-13 January 1999) and 2 (20 January to 16 February 1999) in Canterbury, New Zealand.

Simulation	Light regime	Water status		Rotation		Respiration coefficient		Canopy Pn	GAI
		Irrigated	Non-irrigated	1	2	*a*	*b* (day^{-1})		
1	Full sunlight	✓	-	✓	-	0.34	0.03	daily	daily
2	Full sunlight	-	✓	✓	✓	0.34	0.02-0.03	Sensitivity analysis for *b*	
3	Full sunlight	✓	-	✓	✓	0.34	0.03	cumulative	cumulative
4	Full sunlight	-	✓ -	✓	✓	0.34	0.02	cumulative	cumulative
5	Shade cloth	✓	-	✓	✓	0.34	0.03	cumulative	cumulative
6	Shade cloth	-	✓	✓	✓	0.34	0.02	cumulative	cumulative
7	Slats	✓	-	✓	✓	0.34	0.03	cumulative	cumulative
8	Slats	-	✓	✓	✓	0.34	0.02	cumulative	cumulative
9	Shade cloth	✓	✓	✓	✓	0.34	0.02-0.03	Temp. sensitivity analysis	
10	Slats	✓	✓	✓	✓	0.34	0.02-0.03	Temp. sensitivity analysis	

6.2.5.1- Statistical analysis for validations

The accuracy of each of the predictions was tested using the root mean square deviation (RMSD) as suggested by Wallach & Goffinet (1989), according to the following equation:

$$\text{RMSD} = \sqrt{\frac{\sum(predicted - observed)^2}{no.\ \text{of}\ observations}} \qquad \text{Equation 6.1}$$

Where *observed* was the DM yield measured in the field (CHO base) and *predicted* was the canopy Pn production (CHO base) simulated by the model described in Section 5.2.

6.3- Results

6.3.1- Plant measurements

6.3.1.1- GAI versus Carbohydrate yield

The mean lucerne nutritive value (N and minerals) did not show great differences amongst treatments in the final summer harvest (Appendices 5 and 6). In full sunlight regime, N was 3.2% (± 0.06 standard deviation) and 3.4% ± 0.07 in irrigated and non-irrigated plots, respectively. These values slightly increased to 3.6% (± 0.02) and 3.5% (± 0.06) under the shade cloth regime in irrigated and non-irrigated plots, respectively. Likewise, under the slatted regime lucerne N reached 3.6% regardless of the water status treatments (± 0.05 standard deviation in irrigated plots and ± 0.01 under non-irrigated conditions). Lucerne shoot minerals content followed the same pattern as for N. The consequence was that estimated lucerne shoot carbohydrate content (100%DM – % total nitrogen – %minerals) was similar amongst light regimes and plant water status treatments in summer with a mean value of 91%.

DM yields observed in the field were converted to a CHO units based on the results shown in Appendices 5 and 6. Figure 6.02 shows that the relationship between GAI and total shoot CHO yield was estimated by a fitted equation with 3 parameters ($Y = Y_0 + a X^b$). The ANOVA showed no significant difference for both equation coefficients a ($P>0.24$ for light regimes and water status treatments) and b ($0.21 \leq P \leq 0.36$) in full sunlight, under shade cloth and under slats regimes either in irrigated or non-irrigated conditions. Therefore, a single curve was fitted for all data and a single equation was used in these simulations to describe GAI growth against CHO production.

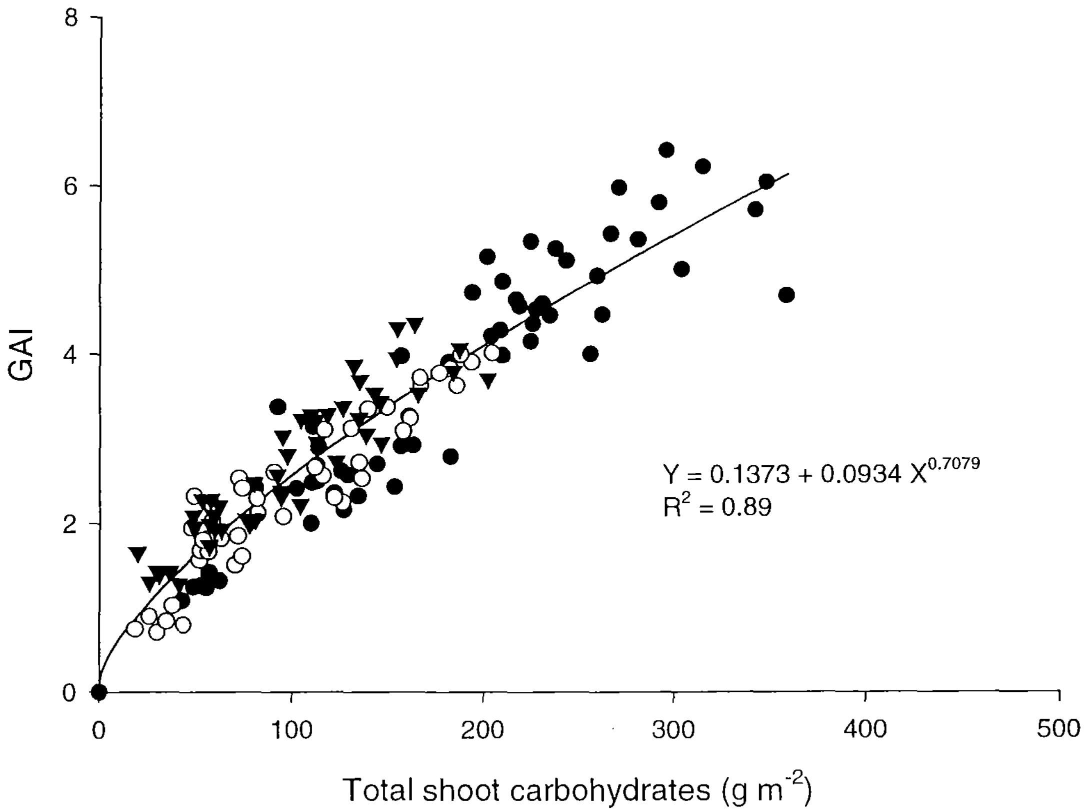

Figure 6.02. Lucerne green area index (GAI) against total shoot carbohydrates for full sunlight (●), shade cloth (○) and wooden slats (▼) regimes. Data for irrigated and non-irrigated plots were combined between December 1998 and June 1999 in Canterbury.

6.3.1.2- Canopy architecture:

Canopy architecture was similar amongst treatments during the two summer rotations with a mean canopy angle of 47° ± 2.5 (standard error) in rotation 1 ($0.68 \leq P \leq 0.86$) and 43° ± 1.1 in rotation 2 ($0.12 \leq P \leq 0.19$). The estimated K value for the whole experiment period, calculated from the slope of the linear regression in Figure 6.03*a*, confirmed that canopy architecture was equivalent for all treatments ($0.16 \leq P \leq 0.73$). The mean K was 0.82 ± 0.013 (standard error) for the full sunlight, shade cloth and wooden slats regimes, regardless of water status treatment. This indicated that radiation penetration within the canopy was equivalent for the three light regimes and the two water status conditions during the experiment period (Figure 6.03*b*). Additionally, it was observed that 95% of the radiation was intercepted at a mean GAI= 3.6 ± 0.04 (critical GAI) for all treatments ($0.64 \leq P \leq 0.82$) and this value was similar to that estimated in the theoretical simulations performed in Chapter 5 (Section 5.3.1).

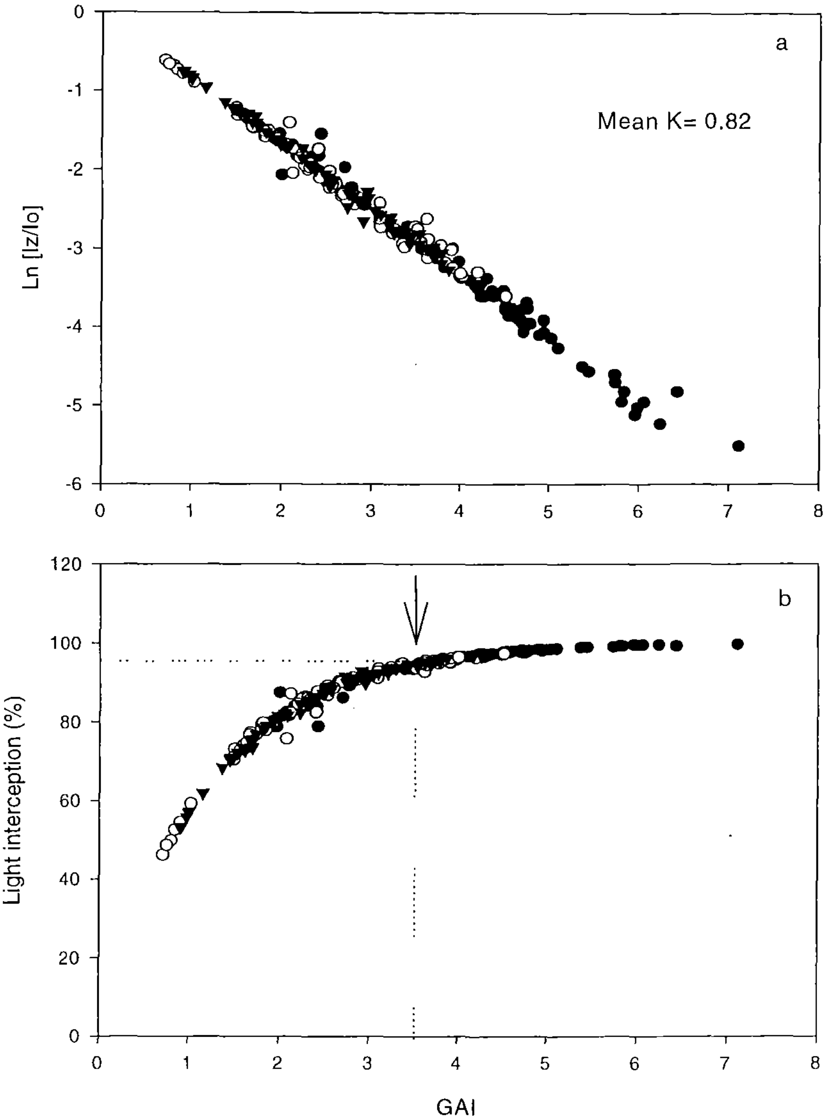

Figure 6.03. Natural log (Ln) of radiation penetration (a) and light interception within the canopy (b) against green area index (GAI) for irrigated and non-irrigated lucerne in full sunlight (●), under shade cloth (O) and wooden slats (▼) during the experiment period in Canterbury. Mean K value is the average slope of the linear regressions in Figure 6.03a.

The stratified analyses using the canopy analyser (Figure 6.04) showed differences in leaf angle for canopy layers ($P<0.001$), but there was no difference for water status condition ($P=0.97$) and light regimes ($P=0.83$). Likewise, significant difference was found for the interactions ($0.42 \leq P \leq 0.86$). Lucerne leaves were more vertical in the top 0.40 m of canopy height (54°) than the layers measured below that value (SEM= 1.6, LSD at 5%= 4.5). Mean MCA at 0.30 m height was 47°, whereas at 0.20 m, it was 43° and at 0.10 m height was 45°. It is important to state that MCA, measured by the canopy analyser, gave a mean canopy angle for the total amount of foliage available above a particular canopy height, but not just for the 0.10 m interval between canopy layers. Therefore, the results indicated that MCA decreased consistently for the foliage below 0.30 m height compared with the top layer (0.40 m height) because leaf inclination became more horizontal for layers close to the ground. However, there was no difference for layers below 0.30 m height, indicating that lucerne foliage angle became nearly constant for middle and bottom canopy layers.

The weighted average of canopy angle (corresponding to the GAI) was 47, 44 and 46° in full sunlight, under shade cloth and slats, respectively, in irrigated plots. In non-irrigated conditions, the weighted average was 45, 46 and 47°in full sunlight, under shade cloth and slats, respectively. Overall, for the simulations proposed in this Chapter, a constant mean canopy angle of 45° for all treatments was assumed.

The stratified analysis (Figure 6.04) also showed significant effects of GAI increment for the triple interaction water*light*height ($P<0.05$). In the full sunlight regime and under irrigated conditions, GAI increment within the canopy profile was greater between 0.20 and 0.30 m height (SEM= 0.18, LSD 5%= 0.52) compared with the other layers. Under the shade cloth and slatted regimes, GAI increment was more evenly distributed within the canopy profile than for the full light regime and the greatest increment in foliage area occurred between 0.10 and 0.30 m height from the top of the canopy. In contrast, under non-irrigated conditions, GAI increment was greatest between 0.10 and 0.20 m height for the full light regime, whereas under both shaded regimes foliage area index was evenly distributed between 0.10 and 0.40 m height. For all light regimes under irrigated conditions, there was a significant difference (SEM= 0.18, LSD 5%= 0.52) in GAI increment between top and mid canopy layers. However, under non-irrigated conditions, the difference in GAI between top and mid part of the canopy was not evident for the shade cloth and slats regimes.

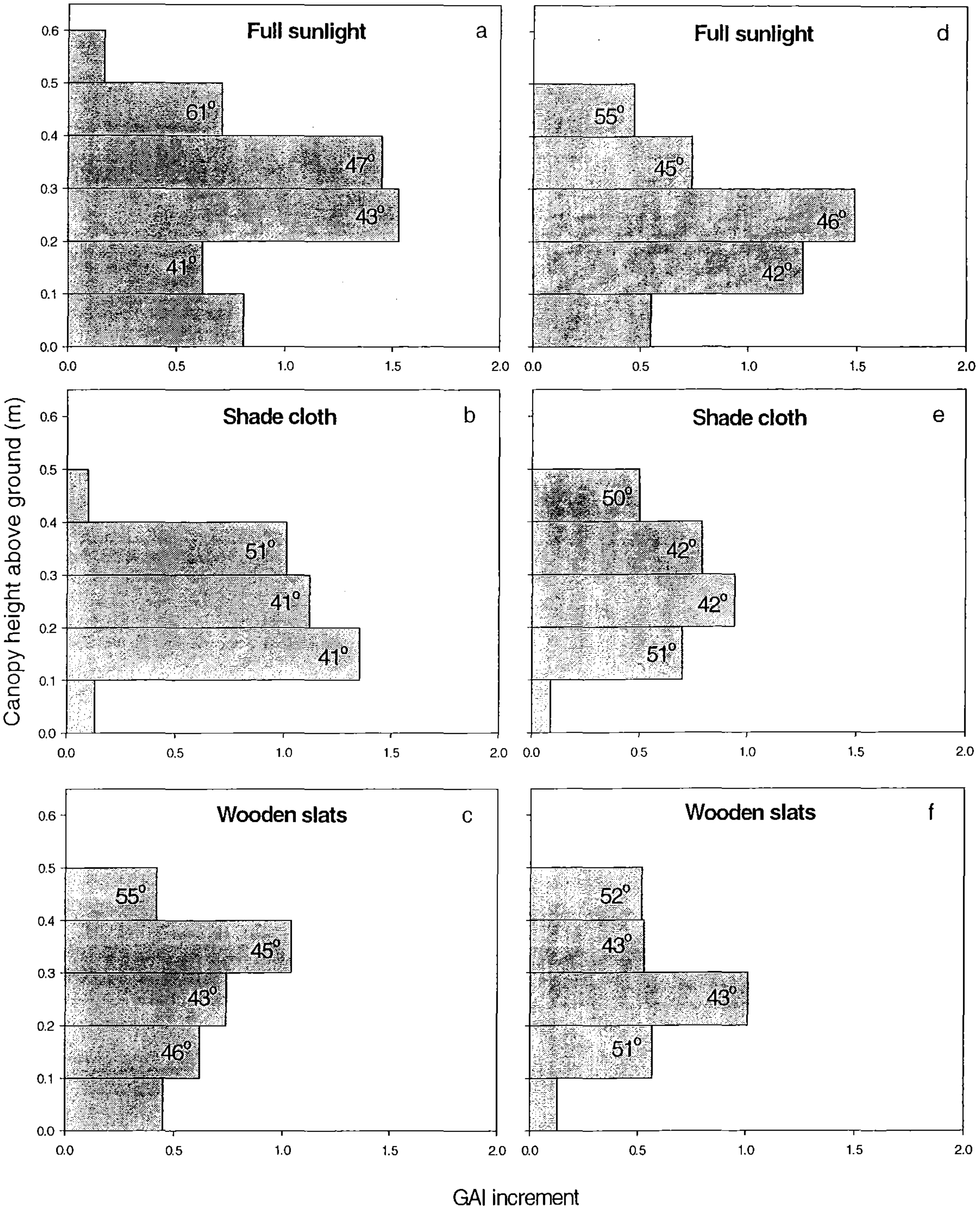

Figure 6.04. Green area index (GAI) increments and mean canopy angle (MCA) at 0.10 m height intervals from the ground to top of the canopy for the three light regimes under irrigated (*abc*) and non-irrigated (*def*) conditions in Canterbury. Standard error of means (SEM) of the interaction *water*light*plant height* for GAI increment was 0.18 and for MCA was 1.6.

6.3.2- Photosynthetic curves

Statistical analysis of the parameters (Tables 6.03 and 6.04), obtained from the fitted non-rectangular equation (Figure 6.05), showed greater effects of water status treatments than for light regimes. There was a difference in α for water status treatments in Rotation 1 ($P<0.006$) and Rotation 2 ($P< 0.008$), but not for light regimes ($P>0.62$). The mean photosynthetic efficiency in irrigated treatment was 0.017 mg CO_2 J^{-1}, whereas in non-irrigated conditions α decreased to 0.015 mg CO_2 J^{-1} (SEM= 0.0001, LSD 5%= 0.0006). For Pm^o values, there was no significant difference among water ($P> 0.39$) and light regime ($P= 0.25$) treatments in the first summer rotation. However, differences occurred in Pm^o for light regimes ($P< 0.004$) in the second summer rotation. The full sunlight regime produced the greatest Pm^o in the second summer rotation (1.78 mg CO_2 m^{-2} s^{-1} in irrigated and 1.70 in non-irrigated plots). The Pm^o values in full light were similar to those measured under the shade cloth regime (SEM= 0.013, LSD 5%= 0.043), but they both were greater than Pm^o observed under the slatted regime (1.65 mg CO_2 m^{-2} s^{-1} in irrigated and non-irrigated plots). In addition, there were no verified significant effects of water status ($P= 0.87$) and light regimes ($P> 0.40$) for θ values in both lucerne rotations.

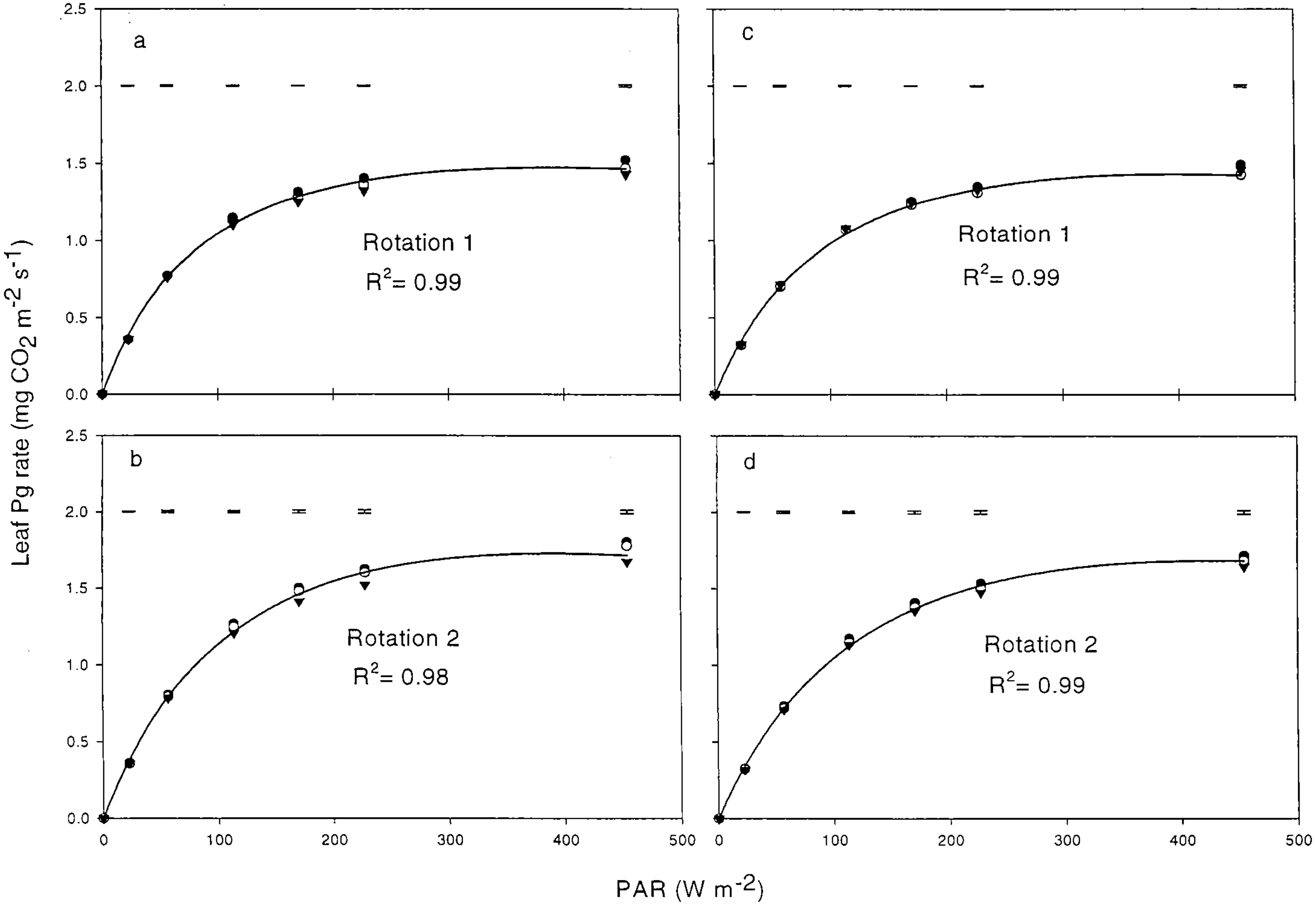

Figure 6.05. Lucerne leaf gross photosynthesis (Pg) rate against light intensity (PAR) measured on fully expanded leaves in full sunlight (●), under shade cloth (O) and wooden slats (▼) in irrigated (*a* and *b*) and non-irrigated (*c* and *d*) plots in Rotations 1 (ac) and 2 (bd) Canterbury. Values are averages of 3 replicates measured before final harvest and bars represent standard errors for reps in each of the light intensity levels.

Table 6.03- Mean gross photosynthesis parameters estimated from measured light curves (α, θ and Pm^0) and plant water content (PLWC) of lucerne grown in three light environments for the first summer rotation (from 23 December 1998 to 13 January 1999). Values of α, θ, Pm^0 and PLWC are averages of 3 replicates. Standard errors of means for PLWC and standard errors for Pm^0, α and θ are shown in parenthesis. Values of PLWC are averages of the rotation and standard deviations are shown in parenthesis.

Treatments	**PLWC** %	α mg CO_2 J^{-1}	θ dimensionless	**Pm^0 *** mg CO_2 m^{-2} s^{-1}
Irrigated:	(0.005)	(0.00032)	(0.005)	(0.012)
Open	0.87	0.0171	0.71	1.50
Shade cloth	0.86	0.0170	0.73	1.46
Wooden slats	0.86	0.0170	0.71	1.42
Non-irrigated:				
Open	0.83	0.0154	0.69	1.47
Shade cloth	0.82	0.0152	0.74	1.42
Wooden slats	0.83	0.0152	0.72	1.44

* To convert mg CO_2 m^{-2} s^{-1} to μmol CO_2 m^{-2} s^{-1}, it is necessary to divide by 0.044

Table 6.04- Mean gross photosynthesis parameters estimated from measured light curves (α, θ and Pm^0) and plant water content (PLWC) of lucerne grown in three light environments for the second summer rotation (from 20 January to 16 February 1999). Values of α, θ, Pm^0 and PLWC are averages of 3 replicates. Standard errors of means for PLWC, α and Pm^0 are shown in parenthesis. Standard error for θ is shown in parenthesis. Values of PLWC are averages of the rotation and standard deviations are shown in parenthesis.

Treatments	**PLWC** %	α mg CO_2 J^{-1}	θ dimensionless	**Pm^0 *** mg CO_2 m^{-2} s^{-1}
Irrigated:	(0.006)	(0.00012)	(0.011)	(0.038)
Open	0.85	0.0169	0.72	1.78
Shade cloth	0.85	0.0166	0.71	1.76
Wooden slats	0.84	0.0168	0.73	1.65
Non-irrigated:				
Open	0.78	0.0152	0.72	1.70
Shade cloth	0.78	0.0149	0.72	1.67
Wooden slats	0.79	0.0147	0.71	1.65

* To convert mg CO_2 m^{-2} s^{-1} to μmol CO_2 m^{-2} s^{-1}, it is necessary to divide by 0.044

6.3.3- Simulation 1: daily variation in canopy photosyntheis

Daily net photosynthetic production (expressed in carbohydrates) changed with light and temperature regimes. Figure 6.06 shows the daily variation of canopy Pn in the three light regimes during the first summer rotation. The simulated canopy Pn production in full sunlight (Figure 6.06*a*) ranged from about 2 g CHO m^{-2} d^{-1} on an overcast day (7 MJ d^{-1}

PAR) and high mean air temperature condition (22 °C) on day 16 to nearly 20 g m^{-2} d^{-1} on the best environment condition observed in the field (16 MJ d^{-1} PAR and 15 °C on day 18). Canopy GAI growth resulted from the accumulative predicted daily Pn production and was calculated according to the Equation from Figure 6.02. There was little GAI growth in days with limiting light or temperature conditions (days 16 and 21 after grazing).

Variations in daily canopy Pn under the shade cloth followed nearly the same pattern as in the full sunlight regime, but the magnitude of the results decreased. In optimum environmental conditions (day 18, 6.4 MJ d^{-1} PAR and 15 °C) under the shade cloth, canopy Pn production reached about 10 g CHO m^{-2} d^{-1} (Figure 6.06*b*), i.e. 50% of full sun. In contrast, under overcast conditions (day 16, 2.9 MJ d^{-1} PAR and 22 °C) daily Pn production under the shade cloth reached –1.7 g m^{-2} d^{-1}, much less than full sun. Similarly, canopy Pn production followed the same daily variations under the slatted treatment, but the magnitude of the Pn rate was even lower than under the shade cloth regime (Figure 6.06*c*). Under the intermittent light, maximum CHO production was 5.2 g m^{-2} d^{-1} in maximum environmental conditions (day 18, 7.3 MJ d^{-1} PAR and 15 °C), about 25% of full sun, but decreased to –0.6 g m^{-2} d^{-1} on a cloudy day (day 16, 3.3 MJ d^{-1} PAR and 22 °C), less than cloth shade. The GAI growth was always simulated to be slower under the wooden slats treatment compared with the shade cloth regime.

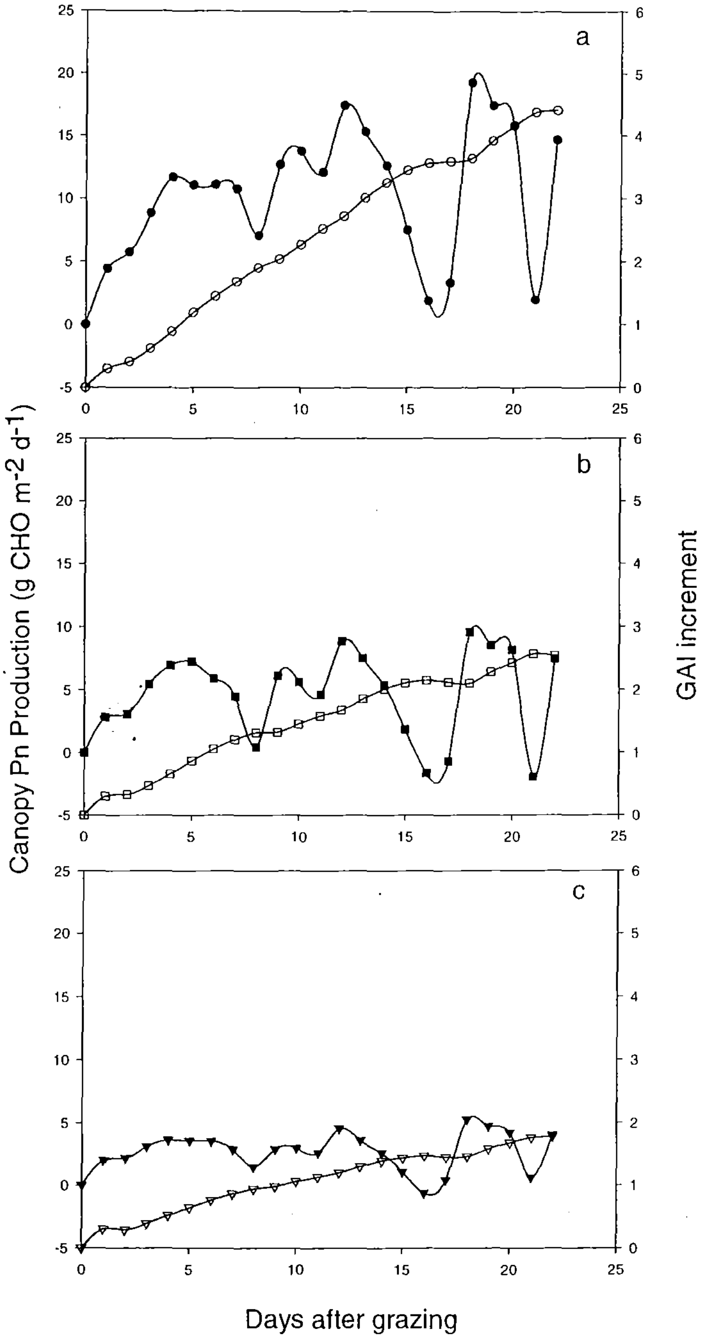

Figure 6.06. Simulated daily canopy Pn production (closed symbols) and GAI increment (open symbols) in irrigated lucerne against days after grazing (from 23 December 1998 to 13 January 1999) in full sunlight (*a*), under shade cloth (*b*) and under wooden slat regimes (*c*) in Canterbury, New Zealand.

6.3.4- Simulation 2: maintenance respiration coefficients

Simulated canopy Pn production was inversely related to the maintenance respiration coefficient (Figure 6.07). For the first summer rotation (Figure 6.07 *abc*), a *b* coefficient between 0.030 and 0.025 day^{-1} reduced the difference between predicted and actual lucerne Pn production. However, for the second rotation (Figure 6.07 *def*), when water limitation increased compared with the previous growth period (Section 6.2.1), a *b* coefficient of 0.030 day^{-1} caused an underestimation of predicted lucerne production compared with the actual data. For this rotation, a *b* value of 0.025 day^{-1} was found to be appropriate in non-irrigated plots.

Therefore, a maintenance respiration coefficient (*b* coefficient) was set at 0.030 d^{-1} for irrigated plots and 0.025 d^{-1} for non-irrigated plots in further analysis, regardless of the light regimes. These values were consistent with Shone & Gale (1983) for lucerne under similar mild water stress conditions (0.6 MPa of osmotic potential). Wilson *et al.* (1980) found for sorghum that the *b* coefficient was reduced by a factor of about two as night leaf water potential decreased from 0.3 to 1.1 MPa. Althought leaf water potential was not measured in this experiment, it was found to be appropriate and consistent with the literature under non-irrigated condition to reduce the *b* coefficient by 20% relative to that used in irrigated conditions (0.030 d^{-1}). No evidence was found in the literature to support changes in respiration coefficients under shaded environments, except when starvation of carbohydrates, induced by prolonged shade, forces the cell to degrade protein (Penning de Vries, 1975), which was unlikely to occur in the treatments used in this experiment. On the other side, the growth respiration coefficient (*a* coefficient) was set at 0.34 for all treatments in this analysis and it was found to be quite independent on the water stress levels applied by Wilson *et al.* (1980) and Shone & Gale (1983).

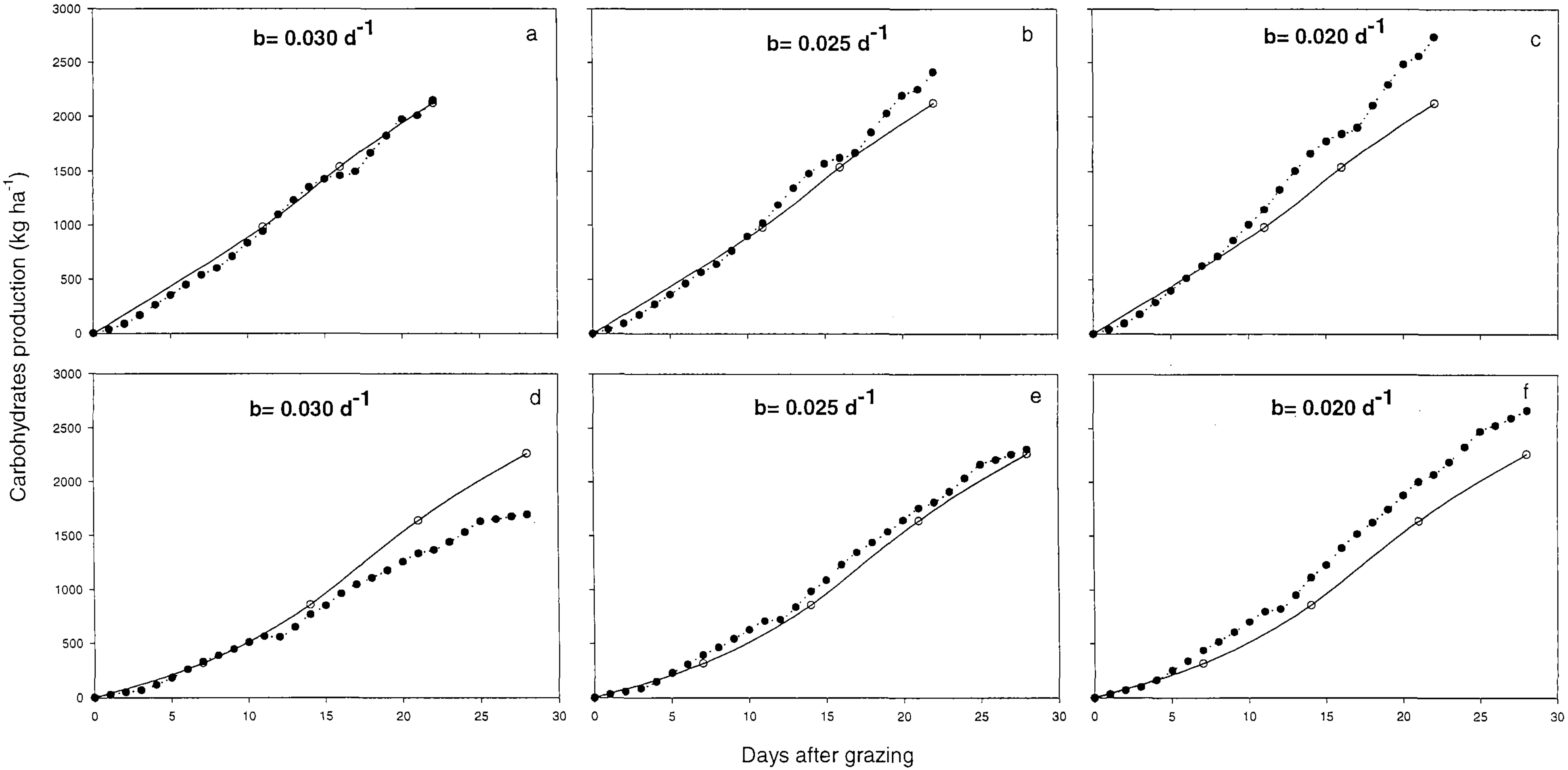

Figure 6.07. Predicted (closed symbol) and actual (open symbol) lucerne Pn production (kg CHO ha^{-1}) against date for three different maintenance respiration coefficients (b= 0.030, 0.025 and 0.020 day^{-1}) in non-irrigated conditions for the first (*abc*) and second (*def*) summer rotations in Canterbury, New Zealand.

6.3.5- Simulations 3 and 4: full sunlight

Simulations in full sunlight under either irrigated or non-irrigated conditions frequently overestimated the actual carbohydrate production in both summer rotations (Figure 6.08). The RMSD for rotation 1 was 134 kg CHO ha^{-1} or 8% of the mean observed data (Appendix 7). In the first rotation under irrigation conditions (Figure 6.08*a*), predicted values overestimated CHO production in open lucerne by 11% in the first harvest, but this difference became close to zero in the second and final harvests. Otherwise, CHO predictions in non-irrigated treatments (Figure 6.08*b*) were similar to the observed yields in the first and second harvests, but in the final harvest predicted production was 13% greater than the actual value.

For the second summer rotation, CHO production predictions equally overestimated actual yields in irrigated conditions (Figure 6.08), but the difference between predicted and actual values were greater than in the first rotation, especially in irrigated plots. The RMSD was 220 kg CHO ha^{-1} or 15% of the mean observed data (Appendix 7). In the full sunlight and under irrigation conditions, simulations were 29% greater than the actual CHO production in the first harvest. This difference increased to 41% in the second cut, but finished only at 5% overestimation in the final harvest. In non-irrigated plots (Figure 6.08*d*), where soil moisture deficit reached a peak of 360 mm, predicted CHO yield overestimated the actual production by 24 and 15% in the first and second harvest, respectively. However, the difference decreased in the last two harvests and predictions overestimated by only 7 and 2% the actual production.

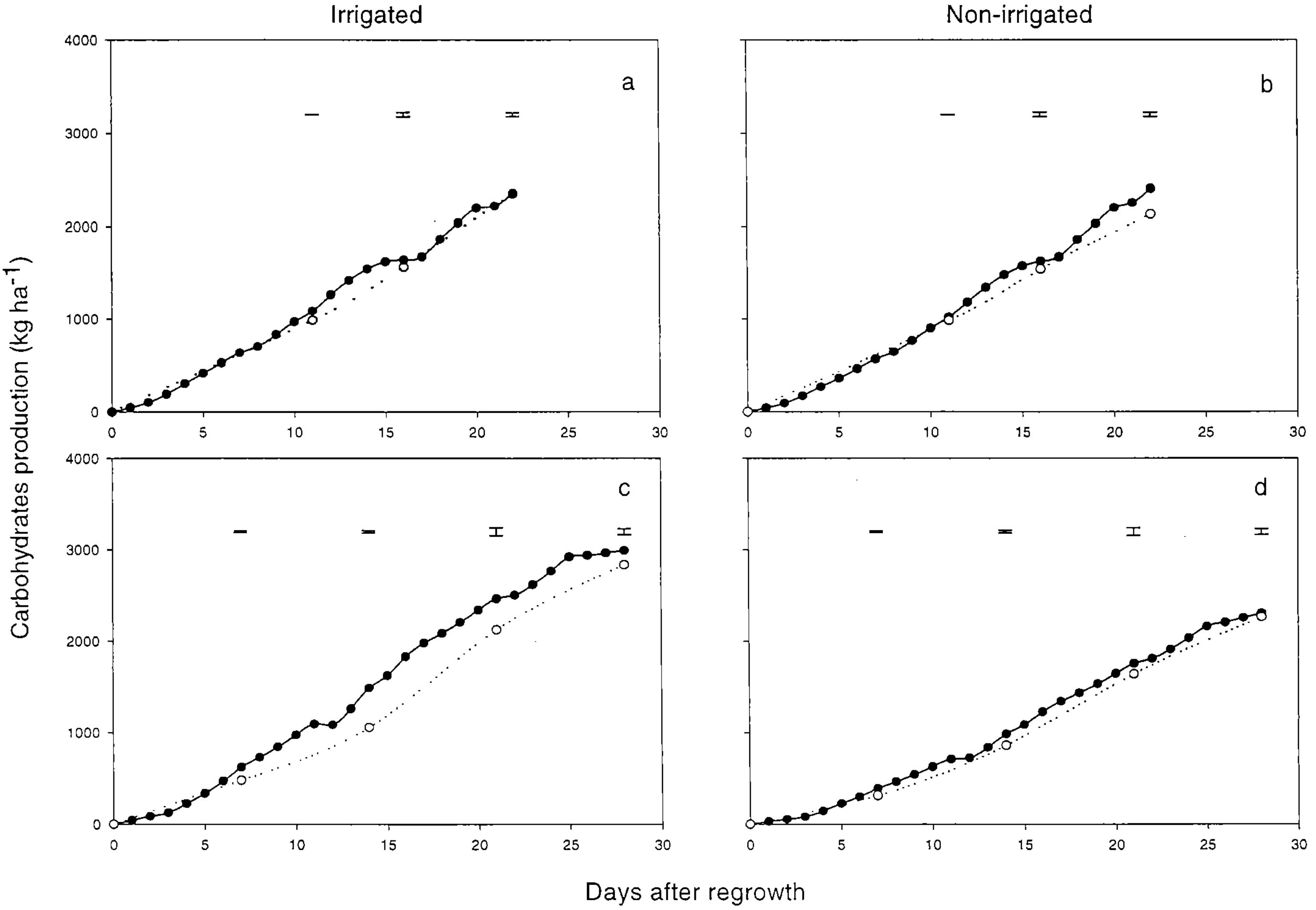

Figure 6.08. Accumulated daily predicted (closed symbols) and actual (open symbols) carbohydrate yields for lucerne in full sunlight regime under irrigated (ac) and non-irrigated (bd) conditions against days after grazing during the first (ab) and second (cd) summer rotations in Canterbury, New Zealand. Coefficient *b* was set at 0.03 d^{-1} for irrigated and 0.023 d^{-1} for non-irrigated condition. Bars on the top show the standard error of reps for actual data at each harvest.

6.3.6- Simulations 5 and 6: shade cloth

Simulations under the shade cloth greatly underestimated actual CHO yields in both summer rotations, particularly for the final harvests (Figure 6.09). The RMSD was 465 kg CHO ha^{-1} or 40% of the mean observed data in the first rotation and this decreased to 314 kg CHO ha^{-1} or 34% of the mean observed data in the following rotation (Appendix 8). In the summer rotation 1, predictions in irrigated plots were 2, 32 and 43% lower than the actual CHO production in the first, second and final harvests, respectively (Figure 6.09*a*). Under non-irrigation conditions, the first harvest simulation was 18% lower than the actual yield in the first cut and to 31 and 32% in the second and final harvests, respectively (Figure 6.09*b*). In the field, lucerne under shade cloth produced on average 80% of the CHO yield observed in full sunlight by the end of the first rotation, whereas shade cloth simulation was on average 67% of that predicted in full sunlight by the end of the first rotation.

Simulated CHO production underestimated by 16 and 32% the actual yield for the two final harvests in irrigated plots (Figure 6.09*c*) and by 29 and 32% in non-irrigated conditions (Figure 6.09*d*) for the second rotation. The difference between predicted and actual CHO yield for the second summer rotation decreased compared with the first rotation. In irrigated field conditions, lucerne under shade cloth produced on average 63% of that in full sun for the last two harvests, whereas simulated values under shade cloth were 43% of that predicted in full sunlight. Likewise, actual lucerne CHO yield under cloth in dry conditions was on average 68% of that in the full sunlight regime, but predicted values under shade cloth was 46% of those simulated in the open treatment.

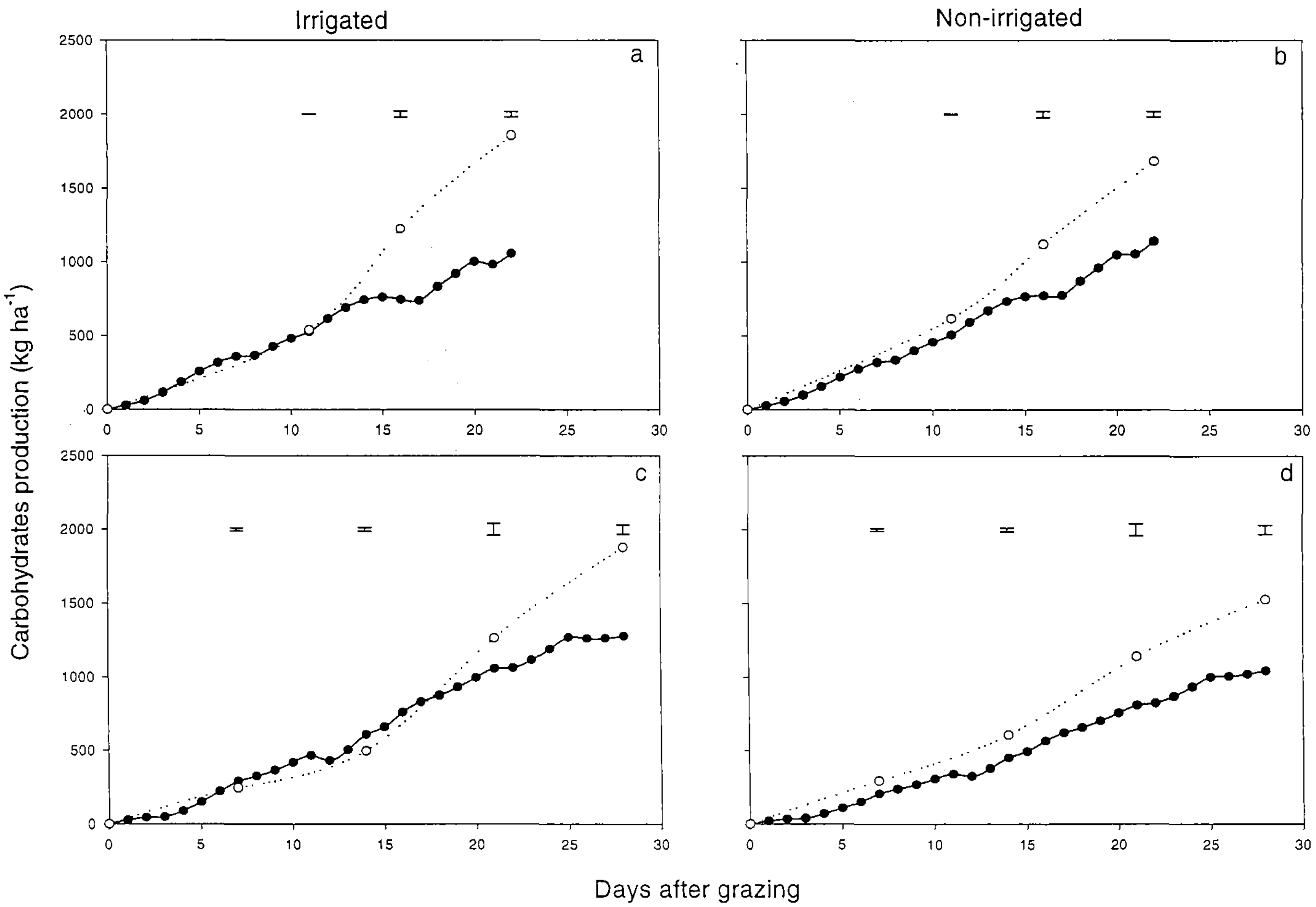

Figure 6.09. Accumulated daily predicted (closed symbols) and actual (open symbols) carbohydrate yields for lucerne grown under the shade cloth regime under irrigated (ac) and non-irrigated (bd) conditions against days after grazing during the first (ab) and second (cd) summer rotations in Canterbury, New Zealand. Coefficient *b* was set at 0.03 d^{-1} for irrigated and 0.023 d^{-1} for non-irrigated condition. Bars on the top show the standard error of reps for actual data at each harvest.

6.3.7- Simulations 7 and 8: wooden slats

Predictions for crop growth under the slatted regime also greatly underestimated the actual values (Figure 6.10). As found for the shade cloth regime, difference between predicted and actual CHO yields was greater for the first summer rotation than for the subsequent growth period. In the end of first Rotation, RMSD for lucerne grown under the intermittent regime was 710 kg CHO ha^{-1} or 64% of the mean observed data, but RMSD reduced to 30% of the observed production in the second Rotation (Appendix 9). In this Rotation (Figure 6.10 *ab*), simulated value was underestimated by 62% of that observed in irrigated full sunlight condition for the last two harvests. Similarly, for lucerne grown under the slats and in non-irrigated treatment, final predicted value was underestimated by 58% of that measured in full light.

In the second Rotation, canopy CHO yield under irrigated slatted condition was underestimated by 29% of that in full sunlight (Figure 6.10*c*) and RMSD decreased to 286 kg CHO ha^{-1}. In the non-irrigated treatment, the lucerne production was underestimated by 34% of that observed in full sun (Figure 6.10*d*). These results were consistent with those found for the shade cloth regime. Overall, field lucerne CHO production under slats was on average 76% of that in full sunlight at the end of the first rotation and 58% in the second summer rotation. In contrast, lucerne simulated values under the slatted treatment were on average only 28% of those predicted in the full sunlight for the first summer period and 38% for the second rotation.

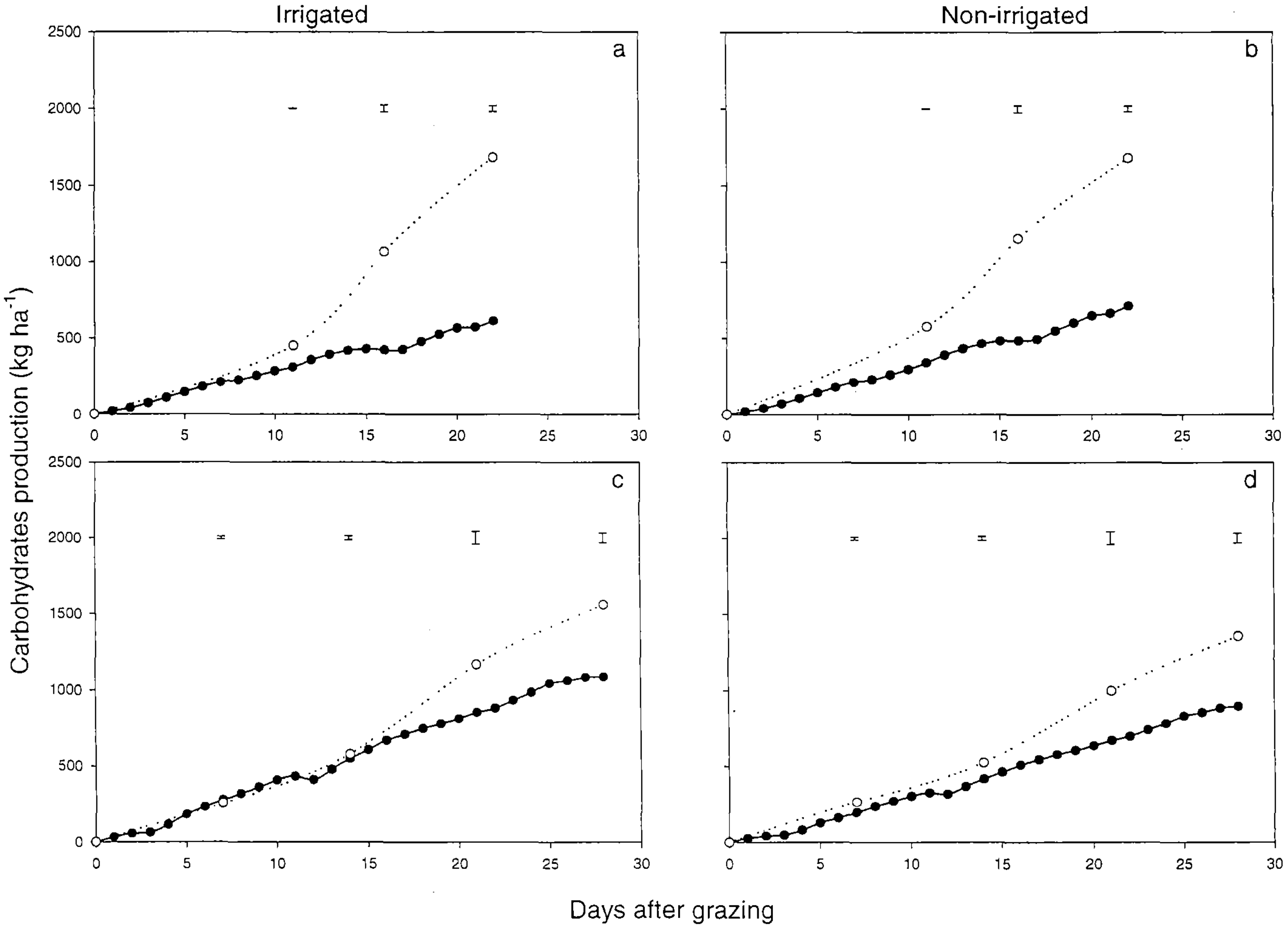

Figure 6.10. Accumulated daily predicted (closed symbols) and actual (open symbols) carbohydrate yields for lucerne grown under the wooden slats regime under irrigated (ac) and non-irrigated (bd) conditions against days after grazing during the first (ab) and second (cd) summer rotations in Canterbury, New Zealand. Coefficient *b* was set at 0.03 d^{-1} for irrigated and 0.023 d^{-1} for non-irrigated condition. Bars on the top show the standard error of reps for actual data at each harvest.

6.4- Discussion

6.4.1- GAI versus carbohydrates yield

The relationship between GAI and shoot CHO production was similar among treatments in this experiment (Figure 6.02). In lucerne, shading reduced both GAI and DM yield (Sections 3.3.2.1 and 3.3.2.2), but the relationship between GAI and DM was similar to that observed in the full sunlight regime. In addition, little change was observed in shoot nitrogen and mineral content for lucerne submitted to different water and light regimes in this experiment (Appendix 6). Smith (1970) found similar weighted averages of shoot N and mineral content for lucerne grown in full sunlight and cool temperature (17 ^{o}C) to those measured in this experiment. The consequence was that mean carbohydrate content did not change among treatments and a single relationship for all treatments was appropriate to predict GAI growth from shoot CHO production in this analysis.

6.4.2- Canopy architecture

Light and water status treatments did not affect lucerne canopy architecture substantially during the experimental period (Figures 6.03 and 6.04). The results indicated that light and water regimes did not modify the lucerne K value. The mean extinction coefficient was K=0.82 for all treatments and this was close to the typical range cited for lucerne by Khaiti & Lemaire (1992), Sheehy *et al.* (1979) and Wilfong *et al.* (1967). Most of the radiation (95%) was intercepted at a mean GAI=3.6, regardless of the light regimes and water status treatments. The mean observed critical GAI was exactly the same as found in the theoretical simulations of Chapter 5. Likewise, the mean foliage angle (45^{o}) measured for all treatments during the two summer rotations was equivalent to that simulated in Section 5.3.1. These foliage inclination values agreed with those measured for non-water stressed (0.5 MPa leaf water potential) and full cover lucerne by Moran *et al.* (1989) who reported a mean leaf inclination of 42^{o} at noontime in late spring. However, the same authors reported a decrease in the leaf inclination to 24^{o} for water stressed lucerne (1.5 MPa leaf water potential).

The level of water stress experienced by plants in the non-irrigated plots was minimal and did not affect canopy architecture during summer rotations. Based on the mean soil moisture deficit measured in non-irrigated plots (Section 6.2.1), it was unlikely that lucerne plants in this experiment were exposed to the levels of water stress that altered leaf angles as reported by Moran *et al.* (1989). At the same experimental site used in this analysis, Brown (1998) reported, for the same lucerne stand aged three years, that DM production and radiation use efficiency started decreasing when the maximum soil moisture deficit reached 290 mm within the 2250 mm soil depth.

The stratified analysis of the canopy (Figure 6.04) showed a weighted average of 46° for canopy foliage angle, similar to data collected over the experimental period, and no statistical differences between light and water status treatments. From this analysis, it was observed that leaves on top layers were more vertically arranged than mid and bottom parts in all treatments. However, the greatest GAI increment was measured in the middle parts of the canopy for all treatments. The combination of higher GAI with the leaves horizontally dispersed in the middle part of the canopy resulted in most of the radiation being intercepted by GAI= 3.6 for all treatments. The advantage of this foliage arrangement was observed in non-limiting conditions (full sunlight and irrigated plots) where the greatest GAI increment of all treatments was measured. Increments of GAI were more evenly distributed within the canopy profile under slats than under shade cloth, particularly in irrigated conditions, although canopy foliage angle distribution was similar between the two shaded regimes. This result was probably associated with the morphological modifications observed in plants under slats compared with those under the cloth. Stem class analysis (Section 3.3.2.4) showed that plants under slats had virtually similar proportions of long stems (> 20 cm) compared with plants grown under the shade cloth. However, a variation within the long stem class was noted between slats and cloth treatments. Some of the long stems grown under slats reached lengths as long as 50 cm, approaching the sizes observed in full sunlight. On the other hand, under shade cloth long stems were uniformly distributed within the 20-30 cm range. This difference in stem sizes can explain the difference in increments of GAI in the top canopy part between the two light regimes.

6.4.3- Plant physiological responses

Leaf maximum photosynthesis measured at 2000 μmol photons m^{-2} s^{-1} or about 500 W m^{-2} PAR (Pm^o) was the most affected parameter of the Pg curve under the experimental conditions (Figure 6.05, Tables 6.03 and 6.04). Pm^o values for irrigated plots were slightly greater than non-irrigated plots for all light regime treatments. The small differences observed between water status treatments was probably a result of the low levels of maximum soil moisture deficit measured in this experiment (Section 6.2.1) and the high ability of lucerne crop to uptake water from deep soil layers. The greatest difference in Pm^o was observed between full sunlight and wooden slats especially in the second summer rotation. It probably took a while for lucerne to adjust to the new source and sink relationships experienced under the shaded regimes and this had a direct influence on the measured Pg curves.

Figure 6.05 shows that plant leaves on the top of the canopy operated with similar efficiency once exposed to the same radiation level, regardless of light treatment. This result was consistent with the discussion by Thornley & Johnson (2000) for a tropical legume and grass pasture growing in different irradiance levels. The basis for this assumption was that leaves grown in a low irradiance have virtually the same rate of gross photosynthesis as leaves grown at much greater light level, indicating that leaves can maintain sufficient photosynthetic machinery to operate efficiently in their growth environment. However, if instant photosynthetic rates were compared at the actual irradiance levels (454 W m^{-2} of PAR in full sunlight, 182 under shade cloth and 210 under slats), then differences between light regimes would be more evident.

The timing at which lucerne leaves under the slats regime were exposed to full light appeared to be critical in this analysis of photosynthetic rate. Top leaves under the intermittent regime were exposed to a switch sun/shade regime in this experiment (Section 5.2.1), but photosynthetic curves were measured at an unknown time after the leaf left the slatted shade. Using the same slatted structure, Peri *et al* (2002b) stated that the time required for cocksfoot leaves (*Dactylis glomerata*) to reach the same maximum photosynthesis as observed in full sunlight (full induction), were 15, 20 and 37 minutes after being 30, 60 and 180 minutes under the shade period, respectively. The same authors reported that maximum photosynthesis rate of cocksfoot leaves decreased asymptotically after 1 minute under shade, reaching a minimal value of 40% of that observed in full sunlight at 140 minutes of severe shading. In contrast, it was found in this work that cocksfoot leaf photosynthesis declined slower under cloth shade (50% transmissivity) than the slatted light regime, reaching a Pm value 76% of that in full continuous light after 120 minutes under shading. These figures have not yet been determined for lucerne leaves. In this experiment, maximum sun period under the slats was about 120 minutes at noontime (Section 3.3.1.1).

Based on the great difference between actual and predicted lucerne CHO yield found in this experiment, there is an indication that lucerne Pg would operate at a higher part of the light curve during the shade period under the slats than that simulated by the canopy Pn model. Therefore, there might have been an underestimation of Pm^0 values under the slatted regime and this would be associated with either the time required by leaves to fully complete photosynthetic activation after leaving shade or the time required to achieve the complete photosynthetic deactivation under the severe shade regime. To avoid this discrepancy, leaf Pg curves need to be measured at regular and short intervals of time during the activation (after leaving the shade) and deactivation (after leaving the full sunlight) periods. The wooden slat structure easily permits modifications of the timing under shade and full sun, simply by changing either the wood slat dimensions or distance between slats and top of the canopy.

Growth irradiance slightly changed α, but θ remained unaffected by the treatments (Figure 6.05; Tables 6.03 and 6.04). Lucerne top leaves showed the same photosynthetic efficiency for all light treatments within the light transmissivities used, although total CHO yield decreased markedly under the shade compared with the full sunlight regime (Figures 6.08, 6.09 and 6.10). The reason for that was probably associated with the rapid decrease in radiation penetration at layers below the top, which led leaves to operate in a lower part of the photosynthetic curve than those performing above the 50% full light transmissivity. Also lower leaves quickly changed to light levels below compensation point and then an increase in respiration drain on whole canopy occurred. Philippot *et al.* (1991) assumed the same α value for different daily radiations applied on lucerne in his photosynthesis predictions. In this work, a mean θ value of 0.72 was calculated for all treatments, although a value of 0.90 was found by Sheehy *et al.* (1979) for seedling lucerne in full sunlight regime for a fitted rectangular hyperbola. Low values of θ are more likely to be found in curves for non-stressed C_4 plants compared with C_3 crops, because complete photosynthetic saturation usually does not occur at the maximum PPFD rate found in nature (approximately 2000 μmol m^{-2} s^{-1} in New Zealand). Following the discussions in Chapter 5, the physiological meaning of low θ values is related to increasing carboxylation resistance to CO_2 transfer at chloroplast level (Marshall & Biscoe, 1980).

6.4.4- Daily variations in the canopy Pn model

Daily canopy Pn simulations were sensitive to variance measured in daily radiation and mean air temperatures (Figure 6.06). Low canopy CHO production was observed on cold and fully overcast days. Variation in daily CHO production was less evident for plants under the slats regime than in full sunlight and under shade cloth. The main differences in canopy CHO production between shade cloth (Figure 6.06b) and slats (Figure 6.06c) occurred particularly on clear days. This was possibly a consequence of the underestimation in the photosynthetic activity simulated during the heavy shaded period under the slatted regime.

A detailed analysis of the canopy Pn model outputs showed no differences in Pm values, calculated from Equations 2.4 and 2.5 (Section 5.2.2), between the sun and shade periods under slats, because the ratio Iz/Io was constant for the two periods and the same Pm^{0} value (Equation 2.4. Section 5.2.2) was applied for both cases. However, the major problem for the intermittent light regime simulation actually occurred in the Pg rate calculations (Equation 2.3, Section 5.2.2) because of the very low Iz value applied during the shade phase. For instance, simulated Pg rate for top leaves (GAI<1) during the shade period under slats was only about 20% of that calculated during the sun phase and this proportion consistently decreased to only 7% at GAI=3.

Knowing that the final actual CHO yield for lucerne grown under the slatted light regime (Figure 6.10) was about 60% of that observed in the full sunlight conditions at the second summer rotation, it is valid to presume that the actual photosynthesis rate during the shade period under slats would be greater than that predicted by the proposed canopy Pn model. Thornley (1976) stated that the factors involved with the discrepancy between measurements and estimates of photosynthesis under fluctuating light were the response time of the photosynthetic system in the leaf and the steady-state light response curve with the degree of non-linearity and the value of the light flux for Pmax. The current work has limited data to correct such a discrepancy produced by the slatted regime. To avoid this problem in the future, it would be necessary to make measurements with greater precision at low PPFD levels as would be found under the slatted treatment. Then, the induction response of photosynthesis after leaving the shade period and the deactivation pattern after leaving the sun period could be accurately simulated for this light regime. Overall, it was clear that the canopy Pn model underestimated Pg for plants grown under the slatted regime, particularly during the shade period.

6.4.5- Full sunlight simulations

Simulations for canopy Pn production in the full sunlight regime were reasonably accurate at different stages of lucerne regrowth (Figure 6.08 and Appendix 7). The critical part of these simulations was the shoot to root partitioning, which applied a fixed coefficient after the canopy reached GAI=1 based on literature data. Although the constant shoot to root partitioning value of 19% appeared to work well, it did not consider the exponential decrease of shoot carbon substrate after defoliation as discussed by Johnson & Thornley (2000) and shown by Sheehy *et al.* (1979) data. This meant that the partitioning rate for the first days after reaching GAI=1 was possibly overestimated, but became adequate afterwards. The consequence was that early CHO prediction was underestimated for the first days after grazing. The partitioning rate was maintained the same for non-irrigated plots, because the level of water stress was considered mild. It has been reported that, under severe water stress, plants could enhance carbohydrate translocation rate into roots (Johnson & Thornley, 2000). However, in response to drought similar to that in this experiment, plants first reduce leaf growth (Bradford & Hsiao, 1982) and architecture (Moran *et al.*, 1989), while continuing to partition carbohydrate to root growth. A detailed study of lucerne carbon shoot and root translocation, with different levels of water stress during the growing period, would be necessary to correctly estimate the partitioning rate.

One of the most used techniques to estimate carbon partitioning in lucerne is the shoot and root DM ratio measured at different stages of maturity as used by Luo (1991) and Philippot *et al.* (1991). Khaiti & Lemaire (1992) also suggested that the relationship between RUE calculated for lucerne shoot biomass and for total biomass (shoot and root) gave a reasonable estimate of partitioning rate.

6.4.6- Shaded regimes simulations

Predicted lucerne CHO production under the shade cloth and under the slatted regimes was underestimated especially at the end of the two summer rotations, regardless of the water status treatments (Figures 6.09 and 6.10). For both shaded regimes, the difference between simulated and actual CHO production in the first rotation was greater than the second rotation and this was evident particularly for the final harvests. This result was likely to be a consequence of field lucerne adjusting partitioning to the newly fixed carbon among sources and sinks in the first Rotation. There was also a greater underestimation in the slatted treatment compared with the actual CHO production than in the shade cloth regime at the end of the first Rotation (Appendices 8 and 9). For the subsequent rotation, predicted values for both shaded regimes equally underestimated the production observed in the field.

There were two main values in the model that could be involved with the underestimation of actual CHO yields for shaded regimes using the proposed canopy Pn model: (i) high partitioning rate and (ii) high total respiration rates. Partitioning between shoot and roots after defoliation can be highly variable and depends on the environmental conditions (Johnson & Thornley, 2000). When photosynthesis decreases due to shading, plants become short of carbon but have a relative surplus of mineral nutrients and water. Such plants tend to transfer less photosynthates to roots and produce proportionately less root and more shoot material than full sunlight plants to achieve the functional equilibrium between plant parts (Loomis *et al.*, 1971, Brouwer, 1983). As a result, carbon shortage is relieved over time through the compensatory increase in leaf area and photosynthesis (Pearce & Lee, 1969). However, Luo (1991) found that functional equilibrium between lucerne fine roots and leaves was not achieved with light treatments in autumn. The author found that both leaf and fine root growth were substantially reduced when full sunlight was reduced by 33% and 67% in an autumn rotation, but the ratio of fine root to leaf biomass was lower than the control when radiation was reduced in a late summer rotation. If lucerne shoot to root partitioning rate really decreased under both shade treatments in summer, then comparison curves for above ground biomass in this analysis would certainly overestimate simulations of CHO production. However, the reduced translocation of CHO's to the roots would likely manifest itself in later growing periods by decreasing recovery rate after grazing.

It was also possible that maintenance respiration rates were overestimated under both shaded conditions in this model. The effects of high maintenance respiration would be especially noted for the shaded canopy parts (high GAI) as discussed in Section 5.3.2, which would coincide with the CHO yield underestimation by the end of both rotations. The reasons could be associated with air temperature changes under both the shade cloth and wooden slats. There is no evidence in the literature that the maintenance respiration coefficient (*b* coefficient) changes under low radiation levels such as those reported for this experiment, except when plants are submitted to carbohydrate starvation under low light conditions (Penning de Vries, 1975). Additionally, canopy maintenance respiration could be overestimated under shade because the canopy Pn model did not accounted for actual loss of biomass as it was shown in some species under shade conditions by Schwenke (1996).

Initially, it was assumed in these simulations that air temperature did not change under shade conditions. Air temperature was measured with a partially covered sensor to avoid direct incidence of sun flecks. However, it has been reported that air temperature can be reduced in agroforestry areas, which also produce an intermittent light regime. Wilson & Ludlow (1991) reported mean daily values of 2-3 ^{o}C higher in full sunlight compared with a tree-pasture system in the subtropical areas. Wong & Wilson (1980) observed a difference between 1 and 2 ^{o}C in both maximum and minimum air temperature as well as in leaf temperature of C_4 grasses under shade cloth compared with the full sun. In this experiment, canopy temperatures were also on average 1-2 ^{o}C lower under both shaded regimes than in open during daytime in summer rotations (Chapter 3, Section 3.3.1.2). It was possible that air temperatures were overestimated in the simulations performed for both shaded treatments in this analysis and this would overestimate particularly maintenance respiration rates and decrease canopy Pn productions. Accurate air temperature measurement was not possible under the shade cloth and wooden slats because of the short distance (0.30 m) between the top of canopy and shade structures. So, it is necessary to perform a temperature sensitivity analysis for both shaded regimes with daily mean temperatures lower than those measured in the full sunlight and evaluate the magnitude of the canopy Pn increase in summer conditions.

6.4.7- Temperature sensitivity analysis

As shown in Figure 6.11, lucerne under the shaded structures was submitted to a different temperature above the canopy than in full sunlight and this could influence canopy respiration rates and development. A theoretical comparison of the energy environment between the shade cloth and wooden slat structures may indicate the reasons for temperature modifications under the low radiation regimes.

The incoming energy was equivalent for full sunlight and above both shaded structures and it consisted of two main components: (i) solar radiation (direct and diffuse radiation) and (ii) terrestrial radiation (long-wave radiation). Theoretically, when total radiation reached the black plastic shade cloth, a considerable amount of energy was absorbed and re-emitted as thermal re-irradiation upwards and downwards, according to the Stefan-Boltzmann law. The cloth reflected a small amount of solar radiation because of the low reflectance (albedo) value of the material. The radiation in which plants were exposed under the shade cloth structure was predominantly diffuse light. As described in Section 3.2.3.1, the shade cloth structure had an overhang material at both east and west sides to prevent direct radiation on plants at low solar inclination angles. These overhangs might have partially blocked the horizontal wind speed and turbulence under the cloth and reduced the convective transfers from the leaf surfaces. Likewise, two main components of the energy environment would likely be altered under the slatted structure namely: thermal re-irradiation and light reflection. Because the wooden slats were white painted on the top, less radiation absorption and more reflection would be expected compared with the black shade cloth material. Besides, the white wooden slat was a poorer heat conductor than the black plastic cloth. Therefore, the wooden slat material would heat at slower rates and produce less thermal re-irradiation downward and upward than the cloth. Under the slatted structure, horizontal wind flows were similar to the full sun. Under this treatment, lucerne plants were submitted to an alternating regime of direct and diffuse light.

This theoretical analysis led to the assumption that plants could be exposed to a lower ambient temperature environment under both shaded regimes compared with the full sunlight especially at daytime. Having a clear sky condition in the open field, the amount of emitted long-wave radiation would be greater than the amount absorbed by soil and vegetation (Monteith & Unsworth, 1990). So, ambient temperature above the canopy usually increases at daytime and cool down at nighttime. Under the shaded regimes, however, downward long-wave radiation fluxes would be similar to upward long-wave fluxes from soil and crop, thus rate of atmosphere cooling would be considerably slower than in full sunlight (Brenner, 1996). As a consequence, night temperatures above the canopy could be warmer under the shade cloth and wooden slat regimes and daytime temperatures cooler than in the full sunlight. Figure 6.11 shows exactly this daily pattern of temperature modification at canopy height under the cloth and slats regimes relative to that observed in full sunlight in a clear and sunny day. Temperatures were on average 10% warmer under the shade cloth and 3% under the slatted structure than the full sunlight at night-time in irrigated plots. At daytime, temperatures under the shade cloth was 3% cooler and under slats 5% cooler than the full sun. Relative differences for temperature at canopy height between light regimes disappeared in non-irrigated treatments. Temperatures under both shaded regimes were 6% greater at night-time and 8% lower at daytime than in full sunlight conditions. Therefore, it was possible that respiration rates were overestimated in the simulations performed for the shaded regimes as Tmax and Tmin were set as measured in full sunlight.

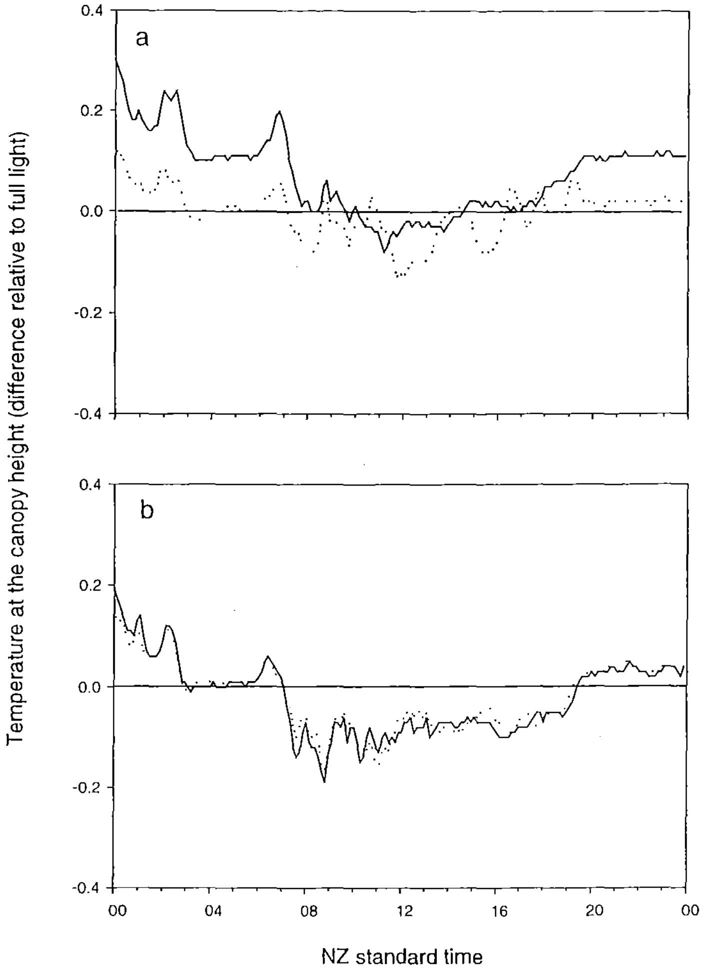

Figure 6.11. Relative air temperature at canopy height (5 cm above canopy top) under the shade cloth (—) and wooden slat (---) regimes compared with the full sunlight against time during a clear sunny day in irrigated (*a*) and non-irrigated (*b*) conditions. A relative temperature of zero means same temperature as measured in full sun. Data were collected in repetition 3 on February 13th 1999 in Canterbury, New Zealand.

Therefore, a temperature sensitivity analysis was performed to verify possible overestimation of canopy maintenance respiration rate and consequently excessive reduction in Pn production. The current daily maximum and minimum air temperatures measured in the full sunlight regime were decreased by 2 and 3 °C under both shaded regimes.

Figures 6.12 and 6.13 showed that differences between predicted and actual values under the shade cloth and wooden slats light regimes reduced especially in the second summer rotation, but both continued to underestimate the final CHO productions observed in the field. The differences between predicted and actual values were again smaller in the second rotation than the first growth period. The RMSD under the cloth regime decreased to 327 kg CHO ha^{-1} in rotation 1 and 209 kg CHO ha^{-1} for a 2° C increase in the daily mean temperatures. For a 3° C increase, the RMSD was 273 and 169 kg CHO ha^{-1} in rotations 1 and 2, respectively. Under the slatted regime, predicted values were still excessively underestimated in the first summer rotation. The RMSD under the intermittent light regime was 623 kg CHO ha^{-1} in rotation 1 and 184 kg CHO ha^{-}1 for a 2° C increase in the daily mean temperatures. On the other side, the RMSD was 575 and 129 kg CHO ha^{-1} in rotations 1 and 2, respectively, for a 3° C increase in the daily mean temperatures.

The accuracy of the proposed canopy Pn model for lucerne under the shade cloth and wooden slat regimes was enhanced with reductions in mean daily temperatures. The criteria to establish partitioning rate under shaded environments for modelling purposes requires further work. These modifications can improve the accuracy of the canopy Pn model especially under continuous radiation. However, the adjustments made in the canopy Pn model to accommodate switches of high/low radiation with intermediate frequencies (1-2 hours) seemed to be insufficient to accurately predict canopy production under intermittent regimes. Further work must be done to adjust other mathematical relationships with particular emphasis on Pm and Pg Equations, including functions to predict correctly the activation and deactivation photosynthetic phases. Finally, leaf Pm functions should be corrected for low temperatures if the proposed canopy Pn model is used for spring and autumn seasons, particularly in temperate areas. These functions have already been successfully tested Weir *et. al.* (1984) and Thornley & Johnson (2000).

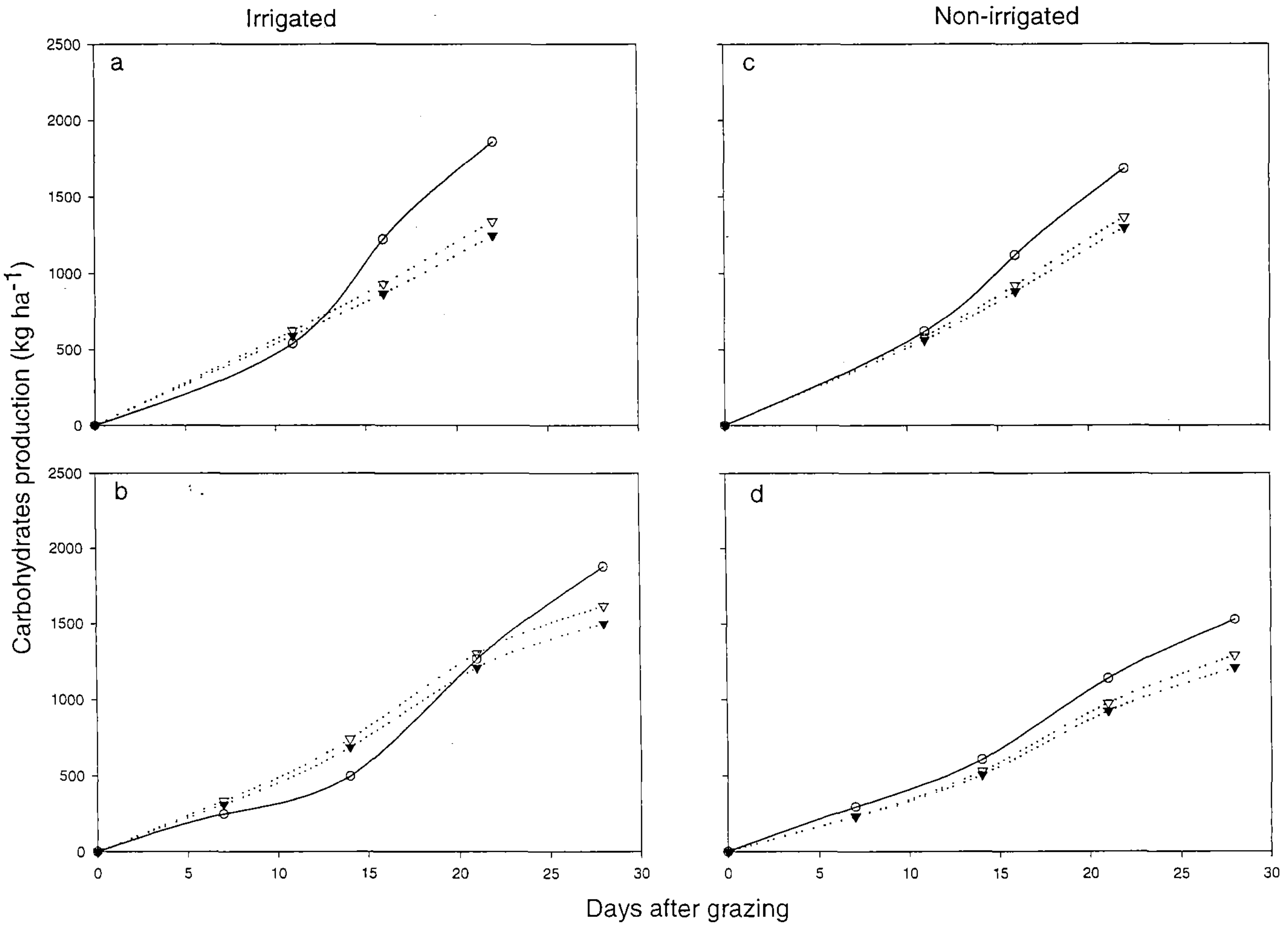

Figure 6.12. Actual (——) and predicted (······) carbohydrate yields for lucerne under the shade cloth regime in irrigated (a and b) and non-irrigated (c and d) conditions during first (ac) and second (bd) summer rotations in Canterbury. Daily mean air temperatures in simulations were reduced by 2 (▼) and 3 °C (∇).

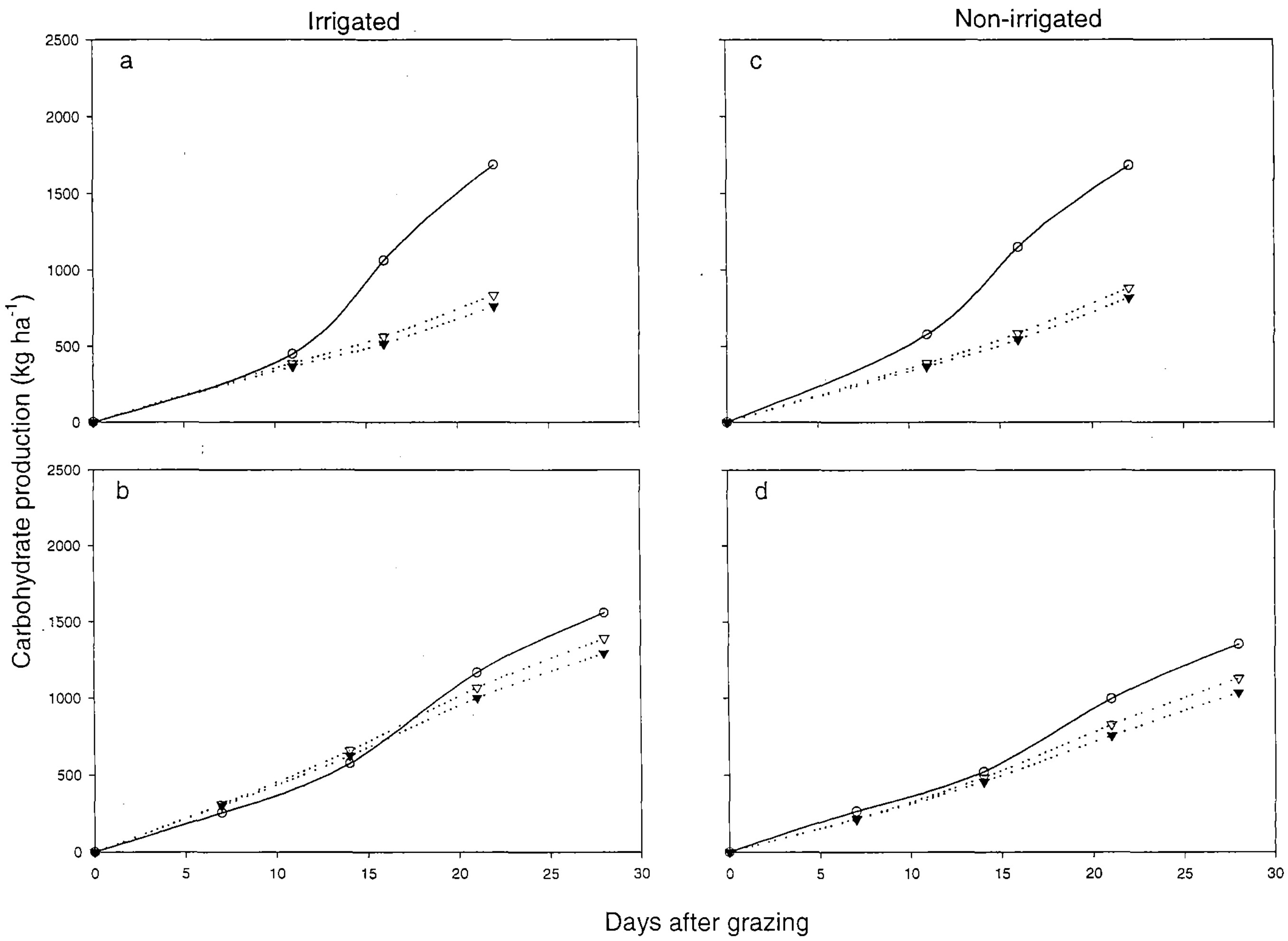

Figure 6.13. Actual (——) and predicted (······) carbohydrate yields for lucerne under the wooden slats regime in irrigated (a and b) and non-irrigated (c and d) conditions during first (a and c) and second (b and d) summer rotations in Canterbury. Air temperatures in simulations were reduced by 2 (▼) and 3 °C (∇).

6.5- Conclusions

The validation performed for lucerne in summer rotations suggested that:

1- Lucerne canopy architecture was not affected by the light regimes proposed in this study. Overall, the adjustments proposed for the canopy Pn model allow applications of different randomised leaf angles. Therefore, the model can be used for different crops and environmental situations.

2- Top leaf photosynthetic capacity was similar between the full sunlight and shade cloth regimes, but both were greater than the slatted treatment (sunny phase). The Pm was affected by the light regimes and α was particular sensitive to plant water status. The photosynthetic curvature (θ) was not affected by either the light or water status regime.

3- The canopy Pn model was accurate in predicting field lucerne CHO yield in full sunlight, for irrigated and non-irrigated conditions in summer rotations.

4- The canopy Pn model greatly underestimated field lucerne CHO production under the shade cloth regime. The reasons for the inaccuracy of the simulations were probably associated with no allowance being made for the decrease in partitioning rate from shoot to root and canopy maintenance respiration rate under the continuous shade conditions.

5- The canopy Pn model also greatly underestimated field lucerne CHO production under the wooden slats regime. The reasons were associated with an underestimation of photosynthesis rates at the shade phase, an overestimation of the rate of partitioning to roots and an overestimation of the maintenance respiration under the intermittent regime.

CHAPTER 7

General Discussion

7.1- Lucerne as a potential crop for temperate agroforestry systems

Light competition from the tree canopy and soil water competition between the understorey and overstorey species are the main factors that can affect the integration of a lucerne crop with trees. This research has shown that the mean annual DM yield observed for lucerne plants growing under trees, slats and cloth shade regimes of about 50% PPFD was 10 t ha^{-1} yr^{-1} compared with 18 t ha^{-1} yr^{-1} in full sunlight in the agroforestry area (Chapter 4, Section 4.3.2.1). This showed a decrease of approximately 40% in DM yield under the shade compared with about 50% reduction in daily PPFD under these treatments. At this same agroforestry site, Peri (2002) reported an annual cocksfoot (*Dactilys glomerata*) yield of 7 t DM ha^{-1} yr^{-1} under the wooden slats structure and 6 t DM ha^{-1} yr^{-1} under trees compared with 8 t DM ha^{-1} yr^{-1} in the open field. The author also found the same annual DM yield under intense shade (23% PPFD) of 4 t ha^{-1} yr^{-1} for cocksfoot as that observed for lucerne in this study. The implication was that lucerne yield was more sensitive than cocksfoot to intermediate shading levels, but the perennial legume always produced more total biomass than the grass. The yield advantage of lucerne over cocksfoot at this site was probably related to its higher leaf photosynthetic activity at 50% light transmissivity, its deeper root system (drought tolerance) and the ability to fix nitrogen.

Worldwide, cocksfoot or orchardgrass has been referred to as one of the most shade tolerant temperate pasture species (Sheehy & Peacock, 1975; Christie & McElroy, 1995; Devkota *et al.*, 1998, Chang *et al.*, unpublished data, Joshi *et al.*, 1999). However, lucerne actually showed greater yield under trees in the current study. In addition, data collected from the site since 1990 (Mead *et al.*, 1993; Pollock *et al.*, 1994; Yunusa *et al.*, 1995b; Chang & Mead,

2002) has confirmed that the lucerne was more persistent and had a higher DM yield growing under radiata pine trees than any of the other temperate pasture species initially used (ryegrass, phalaris, white clover and red clover). Results from the present study indicated that even a newly established lucerne crop had the potential to grow under mature trees at intermediate levels of shade. Forage nutritive value and sheep performance were also higher with the lucerne understorey compared with cocksfoot (Peri *et al.*, 2001a and 2001b). This suggests that the conventional concept of shade tolerance, defined by Wong (1991) as the higher relative growth performance of plants in shade compared with full sun is inappropriate. It should be reviewed to include the concept of potential yield or the maximum yield that can be reached by a crop in a given environment (Evans & Fischer, 1999), particularly when screening pasture species for grazing in an agroforestry system.

Over the two experimental periods, lucerne biomass accumulation responded to the amount of incident PPFD, but there was little effect of radiation periodicity. One indication of this was that plants increased mean RUE of shoot biomass by 64% under FS+CL and 45% under FS+SL compared with FS over the first experiment period (Chapter 3, Section 3.3.2.6) and by 62% under FS+CL, 50% under FS+SL and T over the second experiment period (Chapter 4, Section 4.3.2.5). Indeed, the lucerne crop under shade seemed to operate efficiently at intermediate levels of radiation. However, these results require careful analysis because RUE estimated from aerial DM, as performed for the present study, is strongly affected by the partitioning of assimilates between shoots and roots (Khaiti & Lemaire, 1992). The same authors reported that estimations of RUE based on the total biomass yield (shoot and root) were constant over the seasons, but they also observed that environmental stress conditions could modify the crop RUE. In this study, the apparent overestimation of canopy RUE is acknowledged since no shoot/root ratio measurements were taken. Nevertheless, the analysis of RUE based on shoot DM is still useful to indicate the potential of crops growing under low radiation environment compared with full illumination conditions. There are two theoretical hypotheses to explain the increase of RUE under shade compared with full sun. These are either (i) preferential partition of assimilates to shoot rather than root growth or (ii) similar leaf photosynthetic activity in lucerne for a wide range of radiation flux levels.

The small effect of radiation periodicity on lucerne RUE was probably an indirect consequence of the changes in spectral composition (Table 4.07) that altered plant morphology. The initial theory was that lucerne plants should alter its canopy architecture under the distinct light regimes, but this did not occur for the light treatments in both experiments (Chapter 3, Section 3.3.2.3 and Chapter 4, Section 4.3.2.4). One morphological change observed was an increased stem height and internode elongation under the intermittent compared with continuous shade (Chapter 4, Section 4.4.1.5). This was consistent with the decrease of R/FR ratio observed during the shade period under slats and trees compared with full sunlight, but was not observed under shade cloth. In fact, results of both experiments indicated a slight decrease in RUE under the intermittent compared with continuous shade. This apparently rejects Rabinowitch's hypothesis (Chapter 2, Section 2.1.5.3) that plant production could be expected to be higher in alternating compared with continuous light regime if the periods of shade and light are very long or very short. However, the definitions of short and long fluctuating light were not given by Rabinowitch (1956). It appeared that lucerne under the FS+SL and T was submitted to temporal patterns that would be classified between intermediate and long light fluctuations. Besides, Rabinowitch's hypothesis was based mainly on studies of photosynthetic production and not on the efficiency use of radiation.

Given that canopy architecture was unchanged by light regimes in both field experiments, the increased RUE of shaded compared with full sun plants could not be explained by an improvement in the pattern of radiation interception. In addition, it has been cited an increase of L/S ratio for grasses, but not for legumes in the literature (Wong, 1991). Indeed, in the present study plants under the intermittent regimes seemed to prioritize remobilization of assimilates to above ground herbage by elongating stems in an attempt to intercept more light as has commonly been observed under the dynamics of stem competition for light (Gosse *et al.*, 1988; Lemaire, 2001). In contrast, plants under shade cloth did not follow this pattern despite the increase in RUE. This was possibly because the spectral composition under cloth was unchanged from the full sun conditions. Thus, the morphological responses of lucerne under the intermittent regimes were typical from sun-adapted plants grown under low light quality conditions (Ballare *et al.*, 1995).

It also seems likely that the higher RUE under shade compared with full sun from both field studies was enhanced by lucerne leaves continuing to operate at efficient parts of the photosynthetic curves. This was supported by the photosynthetic light curves (Figures 4.12 and 4.13, Section 4.3.2.6; Figure 6.05, Section 6.3.2), which showed a relatively slow increase in leaf Pn rates for PPFD levels between 500 and 2000 μmol photons m^{-2} s^{-1} (~115 and 450 Watts m^{-2}, respectively) n all treatments. Therefore, leaf photosyntheis at the top of the canopy, where most of the radiation was intercepted (Sections 3.3.2.3 and 4.3.2.4), was potentially similar for all 6 light regimes. These responses were consistent with the lower decrease in DM yield and leaf Pn than the decline measured in PPFD under all shaded regimes and probably explains some of the increase of RUE under shade compared with full sun.

Overall, a potential understorey crop for agroforestry systems must show persistence and a balanced interaction with trees over time. Lucerne has been shown to perform well under this agroforestry area over time (Mead *et al.*, 1993; Pollock *et al.*, 1994; Yunusa *et al.*, 1995b; Chang *et al.*, unpublished data), but its deep root system occupies a niche similar to that of the pine roots (Kemp *et al.*, 1999; Chang & Mead, 2002). Although this was not the focus of this study, it is appropriate to consider lucerne competitiveness with trees. Results from previous investigations (Peri *et al.*, 2002) showed that radiata pine trees growing with no understorey had 34% and 29% higher volume than trees growing with lucerne and cocksfoot understoreys, respectively, at age 10. This study also found that understorey competition effects on growth became more evident during summer and early autumn months when soil water deficits are common in Canterbury dryland areas. In this study, the newly established lucerne replaced phalaris plots in 1999 and thus tree growth results (Table 4.02, Section 4.2.1.2) were greatly influenced by the past 10 years grass growth. However, Peri *et al.* (2002) concluded that the 10 year old lucerne understorey was more competitive with radiata pine growth (diameter at breast height, height, basal area and total volume) than cocksfoot and ryegrass (Section 2.1.2). These authors highlighted that lucerne had a deep root system, whereas the bulk roots of grasses occurred in the top layers of soil. A premature analysis about the best tree-pasture combination cannot be performed without balancing all outputs from individual components over the years. Indeed, it seems that the greatest competitiveness of only 5% of lucerne on radiata pine growth compared with the perennial grasses would be compensated for by an increase in animal performance observed in the legume pasture under trees (Appendix 3).

7.2- Optimized strategies of a lucerne crop under different light regimes

Having observed that lucerne canopy architecture was largely unchanged under continuous and intermittent shade and the morphological adjustments were related to spectral composition, the canopy Pn model was used to hypothesise the theoretically optimum response for lucerne plants to maximize yield under the 3 light regimes. The results from the theoretical simulation analyses (Chapter 5) showed that different strategies would be required under the 3 light treatments. For example, the predicted optimum foliage angle was 75° in full sunlight and 45-60° under both continuous and intermittent shade to maximize light penetration within the canopy and net photosynthesis rates (Section 5.4.5). However, this was not observed in the field with a foliage angle of between 40-50° for all light regimes in both field experiments (Sections 3.3.2.3 and 4.3.2.4). The stratified canopy analysis also showed that top strata leaves had more vertical dispersal than intermediate and lower layers mainly for the fully illuminated treatment (Figure 6.04, Section 6.3.1.2). In theory, this is appropriate for full sun condition to minimize the inefficiency of having saturated leaves operating at the top strata and allow maximum photosynthesis to layers below. For shaded environments, this foliage angle distribution may make no difference because of the increase in the proportion of diffuse radiation.

Despite theoretical simulations showing that maximum canopy Pn rates was unchanged with different foliage angles under shade (Figure 5.10), light penetration down to LAI of about 3 (with a foliage angle dispersal of about 60°) was consistent with the canopy leaf area expansions observed in the field (Figures 3.08 and 4.07). The overall analysis indicated that lucerne was not a perfectly responsive crop in the field compared with that predicted from the theoretical simulations. In full sunlight, saturation of photosynthesis (Pmax) was possibly overestimated in the top parts of canopy in full sunlight conditions and this would explain the reasons for an optimum canopy strategy with a foliage angle more vertically disposed, whereas in the field plants showed an intermediate angle dispersal. On the other hand, it is possible that the canopy Pn model also underestimated the effect of the increased proportion of diffuse radiation in the simulations. Plants in shade would take advantage of this predominant diffuse condition to arrange their leaves more horizontally and maximize light interception (Healey *et al.*, 1998). Despite the discrepancies between the theoretical simulations and the field data, the lucerne crop still had a high yield potential under the shaded environments.

7.3- Use of artificial shade materials for agroforestry research

As expected, the black plastic cloth, frequently used in agroforestry research, did not mimic the temporal patterns of shading nor the spectral composition observed in the agroforestry area (Sections 3.3.1.1 and 4.3.1.1). Healey *et al.* (1998) also observed that the filtering of radiation by an overstorey plant community was qualitatively different from the filtering by a number of artificial shade materials. These authors found a dramatic increase in the proportion of diffuse radiation under *Leucaena leucocephala* shade and under a wooden latticed structure for a sunny day. These results do not invalidate previous studies, using plastic shade cloth to screen plants for shade tolerance or to observe crop/pastures responses under shade, but do indicate the need for careful analysis when they are extrapolated to an agroforestry environment. In contrast, the slatted structure used in this study did closely reproduce the temporal and spectral radiation environment of the agroforestry area. In addition, radiation flux and periodicity are easily adjusted by altering the slats height above the crop and by changing the slat/gap ratio (Chapter 3, Section 3.2.3.1). Caution is still necessary, because soil water extraction by plants under the artificial shade may not be as fast as that observed under trees, especially during drought periods. In this study, soil water competition in the agroforestry area was evident when lucerne RUE under trees was similar to that calculated for plants in full sun and below that of the two artificial shade treatments (Section 4.3.2.5).

Despite the differences in radiation environment produced by the slat and cloth structures, most of the crop response data indicated similarities under both artificial shade materials. The plant morphological responses under the cloth and slatted structure were driven by shade and spectral composition changes (Sections 3.3.2.4 and 4.3.2.6) and results suggest that they may continue to occur in a long-term period. If this is true, further morphological responses can lead to modifications in canopy structure and nutritive value, which affect the herbage intake of grazing animals (Hodgson & Brookes, 1999). In addition, previous research has indicated that differences in plant physiological responses between continuous and intermittent light regimes could be expected to happen with very long or very short sun/shade fluctuations (Rabinowitch, 1956). This radiation condition is likely to occur in agroforestry areas with high tree populations or as tree canopy closure occurs (Percival & Knowles, 1988; Hawke & Knowles, 1997). The current research compared only the different light regimes at about 50% full sunlight PPFD and for maximum intermittent shade periods of 1.30 h. Overall, the evidence from this investigation suggests that the wooden slats structure would be more appropriate than shade cloth to artificially simulate the temporal radiation environment in an agroforestry system.

7.4- Canopy growth prediction in agroforestry systems

Adjustments to a canopy photosynthesis model (Thornley, 1976; Marshal & Biscoe,1980; Weir *et al.*, 1984) were functionally appropriate to perform simulations under shaded environments. The complexity of the physiological responses in those plants led to an underestimation of final crop yield under both continuous and intermittent shade. The 5 minute intervals of radiation flux for the canopy light interception sub-model were adequate to resemble the time course of the sun/shade fluctuations under the intermittent regimes and it is probably a sufficiently short period to be appropriate for most agroforestry radiation environments (Section 5.2.1). These changes had immediate effects on the other two linked sub-models (Pg and Rt sub-models). From the three likely reasons used to explain the underestimation of crop yield under the shade treatments (Section 6.4.6), two were due to inadequate fixed parameters applied to the sub-models (partitioning rate from shoot to root and maintenance respiration) and the other suggested a mechanistic adjustment for the gross photosynthesis model due to the intermittence effects.

7.4.1- Predicting maintenance respiration under shade

The hypothesis that maintenance respiration was overestimated under the two shaded regimes was supported by Figures 5.04b and 5.05b (Sections 5.3.2 and 5.3.3, respectively), which indicated that the effects of the changes in either mean daily air temperature or maintenance respiration coefficient typically occurred at the high cumulative GAI (most shaded parts of the leaves). The graphs of predicted and simulated crop yields (Figures 6.09 and 6.10, Sections 6.3.6 and 6.3.7, respectively) showed that underestimation occurred for the last two harvests (after mid-rotation) under the shade cloth and slats regimes, when actual plants GAI were between 3 and 4 units (Figure 3.08, Section 3.3.2.2). Calculations of the critical GAI indicated that most of the radiation intercepted by shaded canopies was at this same cumulative GAI interval (Figures 3.09ab, Section 3.3.2.3).

According to Equation 5 (Section 5.2.3), the mean air temperature, crop dry weight and maintenance respiration coefficient (*b*) determine the total maintenance respiration rate. In the first experiment, air temperature at the top of canopy (Figure 3.03, Section 3.3.1.2) appeared to decrease under shade relative to full sunlight in the daytime, but increase at night. Overall, simulations were performed with equivalent mean air temperatures for the 3 light regimes in this study. The proximity of the temperature sensor to the top of the canopy might have resulted in overestimation of temperatures under cloth and slats. In the literature, there is no evidence of shading effects on *b* coefficient, but there have been reports showing that it increases exponentially with temperature and leaf water potential (Amthor, 1986). In addition, King & Evans (1967) showed an exponential decrease of dark respiration in the lower and shaded leaves of lucerne canopy and Penning de Vries (1975) observed that starvation of carbohydrates induced by prolonged shade reduce the levels of enzymes (Rubisco) and presumably the protein turnover rate, declining maintenance respirations costs (Amthor, 1986). Despite the theoretical evidence that maintenance respiration was overestimated in the simulations performed in Chapter 6, new research is necessary to measure the costs of maintenance respiration in plants exposed to different radiation flux and periods of shade, following the methodology suggested by McCree (1970) and used previously by Wilson *et al.* (1980).

Given that maintenance respiration costs in shaded plants might be overestimated, a temperature sensitivity analysis was performed for lucerne grown under the shade cloth and slats by decreasing daily air temperatures by 2 and 3 °C (Figures 6.12 and 6.13, Section 6.4.7). This was based on indications that daytime temperature above the canopy was lower under shade than in full sun from this experiment (Section 6.4.7, Figure 6.11) and from literature (Wong & Wilson, 1980; Wilson & Ludlow, 1991). These results improved the prediction of final crop yield compared with the actual data, particularly in the second summer rotation. However, there was still an underestimation of about 17% under the irrigated continuous and 18% under non-irrigated continuous shade, 14% under the irrigated intermittent and 21% under non-irrigated intermittent shade regimes at the second summer rotation. The remaining difference between actual and predicted data might possibly be corrected by accounting for a decline in root biomass under shade (Schwenke, 1996) i.e. a decrease in W for the canopy maintenance respiration (Equation 2.8, Section 5.2.3).

7.4.2- Predicting carbohydrates remobilisation under shade

The remaining difference between the predicted and actual crop yields under the two artificial shade regimes was presumably caused by making too high an allowance for partitioning rates of CHO from shoots to roots. In these simulations, partitioning from shoots to roots was assumed to occur after reaching canopy GAI=1 or about 7 days regrowth, as reported by Pearce *et al.* (1969). The validation graphs (Figures 6.12 and 6.13) confirmed that underestimation of actual crop yield increased with the regrowth duration. Partitioning between shoots and roots for lucerne in different light regimes was not the focus of this work and is still not completely understood in lucerne crop agronomy (Brown *et al.*, 2000). A similar difficulty to predict partitioning rates under low light was observed in simulations using the ALFALFA 1.4 model (Denison & Loomis, 1989). Using this model, Luo (1991) observed an unexpected increase of fine-root to leaf ratios in lucerne exposed to 33 and 67% shade cloth. The author concluded that functional equilibrium between fine roots and leaves was achieved with water treatments, defoliation and fine root pruning, but not with light treatments. The carbohydrate translocations between the crown and fine root pools were complex and underestimated by this model under low light intensity. Further investigation is necessary to elucidate lucerne canopy strategy to translocate carbohydrates between shoots and roots under low light regimes and over different seasons.

7.4.3- The intermittency effect on canopy photosynthesis

Finally, the third hypothesis for the underestimation of crop yields was discussed in terms of the intermittent effect of radiation on the photosynthesis sub-model (Section 6.4.7). This sub-model worked as a switch on/off photosynthetic response with the radiation flux in which the canopy was exposed as discussed in Section 5.4.3. The radiation flux measurements under slats indicated that plants were exposed to alternating periods of about 94% (sun period) and 6% (shade period) full sunlight flux (Sections 3.3.1.1). Because the Pg sub-model estimated photosynthetic responses based on the light curves parameters measured in the field (Section 6.3.2), those responses decreased and increased instantaneously with changes in radiation flux absorbed by canopy leaves. This was particularly evident for the Pmax function (Equation 3, Section 5.2.2) where maximum photosynthesis rate was corrected based on the growth irradiance within the canopy profile. Thornley (1976) stated that the photosynthesis of a leaf, plant or canopy is often estimated by combining measurements of light flux with the appropriate light response curve, and the estimated value is then compared with a value derived from gas exchange rates from field experiments. However, this estimated value and the derived value may not be in agreement because of the temporal changes in the incident radiation.

Peri *et al.* (2002) has recently reported an exponential decrease of cocksfoot Pmax leaves with time under heavy shade. The authors observed a decrease of Pmax rates from 1 to 140 minutes of heavy shade and then stabilised until 180 minutes. Under 50% shade cloth, cocksfoot Pmax rates decreased slower than under the heavy shade and stabilised after 120 minutes under moderate light. In this same work, Peri *et al.* (2002) observed that the time required to reach full induction on return to full sun was dependent on the duration of the previous shade phase. For instance, the authors found 15 minutes to reach full induction after 30 minutes under severe shade and 37 minutes after 180 minutes of shade. Those photosynthetic responses were probably closely linked to stomatal (physical resistances) and non-stomatal (biochemical resistances) responses of leaves under intermittent light regimes. The rates of photosynthetic induction and deactivation processes, however, can vary with the shade tolerance ability of plants. In this case, it is speculated that lucerne leaves would present somewhat different photosynthetic responses to shade duration. Such physiological relationships are important and should be considered in any future mathematical model aiming to accurately predict canopy photosynthesis under natural or artificial intermittent regimes.

7.5- Recommendations for future research

There is no doubt of the practical importance of artificial shade materials for agroforestry research. First, the proposed wooden slats structure needs to be tested with different overstorey and understorey species and under different radiation flux regimes. Further study should compare plant agronomic and physiological responses at least under 4 PPFD transmissivity levels: 100, 75, 50 and 25%. A suitable crop/pasture growing under an agroforestry area with distinct tree populations should be compared with those growing under shade cloth and wooden slat structures at identical PPFD levels. The results of this investigation would conclusively identify the advantages/disadvantages of using cloth or slats in a range of radiation conditions where most of the agroforestry areas are grown.

Second, with particular interest in using lucerne as a suitable crop for agroforestry systems, grazing experiments should be performed to assess the long-term persistence and feeding value of this legume under shading conditions and compare these results with an open field crop. The potential lucerne production and nutritive value should be compared with the estimated requirements of livestock (cattle or sheep) to determine the carrying capacity of agroforestry areas with distinct light transmissions (Wilson & Ludlow, 1991) and therefore assess the potential viability of an animal enterprise. To assess the system sustainability, tree growth measurements should continue until the final harvest to identify the long-term effects of lucerne understorey competition on final wood production and log quality.

The adjustments performed for the canopy photosynthesis model indicated the importance of obtaining realistic field canopy parameters, such as the maintenance respiration coefficient and partitioning rates, to accurately predict crop yield under shade regimes. The partitioning rate between shoots and roots is especially important for perennial species with reserves storage organs. A field or glasshouse experiment, using artificial shade materials with various light transmissivities, could elucidate how perennial crops/pastures translocate assimilates from shoots to roots in distinct radiation environments and over seasons. Among the most common plant measurements used to study partitioning rate are shoot to root ratio, RUE of shoot material and of total herbage (shoot+roots) and starch and carbohydrates content of above and below ground organs. Modifications of maintenance respiration rates should be measured in field and glasshouse conditions, using the methodology suggested by McCree (1970) and McCree & Silsbury (1978) and exposing plants to different levels of PPFD. The aim would to be to measure the index of plant carbon loss in maintaining its dry weight over a 24-hour cycle of light and shade. Finally, the time course response of photosynthesis under intermittent light regimes with different periods of shade and sun can be assessed using the wooden slat structure by changing slat dimensions or their distance from the top of the canopy. Such an investigation should be performed with frequent photosynthetic responses measured during the illuminated and shade phases to correctly describe the processes of induction and deactivation through simple mathematical equations. It is necessary to measure Pn rate changes under natural light conditions, rather than the artificial light device of the photosynthesis equipment, to maintain leaf readings in similar light conditions to the rest of the plant. Functions obtained from this investigation could be included to correct abnormalities of the Pg sub-model under intermittent light regimes.

In the meantime a simple model using PAR interception and herbage RUE would be practical to predict maximum potential rates of understorey plants in shade, such as that suggested by Schwanke (1996) and Wilson and Ludlow (1991). The RUE model integrates changes in partitioning rate, root mass changes, maintenance respiration changes and Pn delays. It is also more practical than the canopy Pn model, because it requires less instrumentation and less knowledge of the environment conditions. However, the RUE model does not allow for changes in plant morphology and physiology. The canopy Pn model is a valuable tool for suggesting selection traits to optimise production of various pasture/crops types under shade.

An accurate model to predict understorey yield in agroforestry would be useful to assist farmers and scientists to screen 'shade tolerant' crops and to guide forestry management practices over time. Furthermore, by combining research results from appropriate artificial shade methodology with such a model, it would be easy and inexpensive to simulate different agroforestry scenarios, perform risk analyses and choose the most sustainable agroforestry system for each situation.

7.6- Summary and conclusions

Lucerne is a high potential crop for agroforestry in dryland areas. Its performance under 50% shade (10 t DM ha^{-1} yr^{-1}) was better than most of the other temperate pastures referred to in the literature without any fertilizer inputs. This was mainly because lucerne showed high leaf photosynthetic activity for PPFD levels greater than 1000 μmol photons m^{-2} s^{-1} and because of its canopy architecture, which allowed light penetration deep within the canopy. Lucerne persistence under shade was shown in this and previous research, provided careful management practices; although there was an apparent remobilisation of carbohydrates to shoots under shade from the young crop that may diminish over time, lucerne has survived at this site for over 10 years.

The use of artificial shade structures was appropriate to simulate trees shade effects on plants. The wooden slatted structure more closely resembled the complete physical radiation environment (radiation flux, spectral composition and temporal patterns) of the agroforestry system than shade cloth. However, the advantage of slats over cloth was only expressed in morphological plant responses for lucerne. This legume, when grown under the intermittent treatments had a potential yield equivalent to those under the continuous shade regime. Plant response differences under cloth and slatted structures may occur at different PPFD transmissivities. Nevertheless, the crop responses might be different for other species with more asymptotic light response curves or lower saturation points and with a distinct frequency of sun/shade fluctuations. The ideal canopy grown under intermittent regimes of 50% shade would be morphologically like plants in full sunlight in order to maximize photosynthesis during the illuminated period. In addition, this crop would require biochemical adaptations to slow the deactivation of photosynthesis during the shade phase and accelerate the recovery (induction) during the illuminated period under trees or slats.

It is possible to predict crop yield under continuous and intermittent shade regimes, such as that found in agroforestry systems, using the classical canopy photosynthesis model published in the literature for full sunlight conditions. The adjustments performed in this model allowed solving the time-scale problem of the intermittent light regimes. Further attention must be addressed to the overestimations in maintenance respiration and partitioning rate between shoots and roots under shade and the intermittency light effect on leaf photosynthetic activity, before the canopy photosynthesis model is used to predict accurately the understorey yield in agroforestry areas.

The following conclusions resulted from this research:

- The wooden slats structure artificially mimic better the agroforestry radiation environment than the shade cloth.

- Radiation periodicity had little influence on lucerne crop responses at intermediate shade levels. The amount of PPFD and the spectral composition had the most important effect on crop growth and morphology.

- Canopy architecture in lucerne was unchanged by radiation flux, periodicity and spectral composition.

- Lucerne has a high yield potential to grow in agroforestry areas if well managed for long persistence.

- The canopy photosynthesis model require further adjustment in canopy respiration, partitioning of carbohydrates and light intermittency effect on leaf photosynthesis to accurately predict the yield of understorey plants in agroforestry systems.

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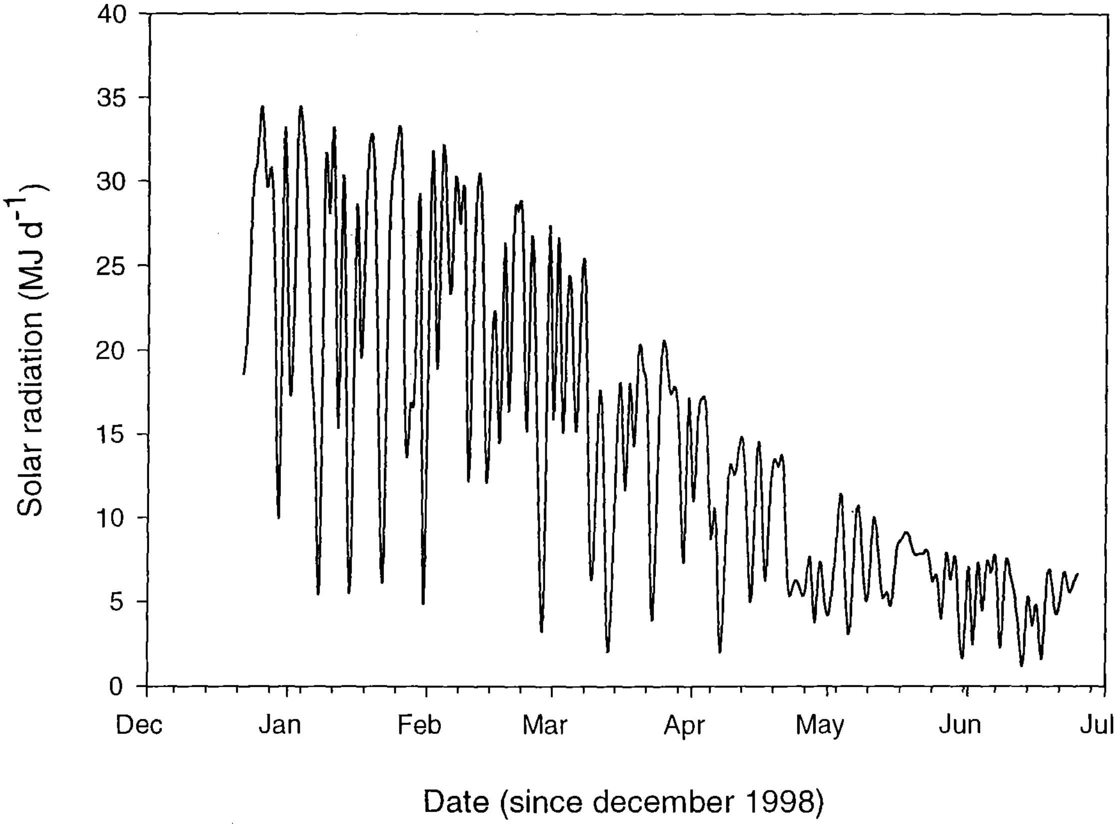
Appendices

Appendix 1- Daily course of global solar radiation (MJ d^{-1}) in full sunlight conditions for the FSC experiment at Canterbury, New Zealand. Data were collected between December 1998 and June 1999.



Appendix 2- Mean coefficient of the slope (RUE) calculated from the linear equation plotted in Figure 3.12 for irrigated and dryland conditions. The slope of the linear regression is an estimation of the radiation use efficiency (RUE). The coefficient of determination (R^2) and standard errors (SE) for each coefficient is also indicated. Regression lines are forced through the origin.

Treatment-Rotation†	R^2	Slope (RUE)	SE (RUE)	
		---g shoot DM MJ (PAR)$^{-1}$---		
Open irrigated- 1	0.97	0.965	0.1356	
Open irrigated- 2	0.99	1.050	0.0548	
Open irrigated- 3	0.99	1.290	0.0689	
Open irrigated- 4	0.97	1.130	0.1029	
Cloth irrigated- 1	0.95	1.833	0.3254	
Cloth irrigated- 2	0.98	1.707	0.1564	
Cloth irrigated- 3	0.99	1.550	0.0867	
Cloth irrigated- 4	0.99	1.407	0.0362	
Slats irrigated- 1	0.96	1.547	0.2465	
Slats irrigated- 2	0.99	1.360	0.0556	
Slats irrigated- 3	0.96	1.520	0.1682	
Slats irrigated- 4	0.98	1.523	0.1057	
Open dry- 1	0.99	0.917	0.0367	
Open dry- 2	0.99	0.857	0.0362	
Open dry- 3	0.97	1.062	0.1029	
Open dry- 4	0.98	1.113	0.0783	
Cloth dry- 1	0.98	1.750	0.2053	
Cloth dry- 2	0.99	1.523	0.0489	
Cloth dry- 3	0.96	1.647	0.1718	
Cloth dry- 4	0.99	1.463	0.0839	
Slats dry- 1	0.97	1.597	0.2049	
Slats dry- 2	0.99	1.250	0.0391	
Slats dry- 3	0.92	1.362	0.2058	
Slats dry- 4	0.98	1.487	0.0981	
	Rot. 1	**Rot. 2**	**Rot. 3**	**Rot. 4**
*SEM**	*0.0448*	*0.0469*	*0.0453*	*0.0214*
F probability				
Water	*0.780*	*0.0964*	*0.615*	*0.988*
Light	*<0.001*	*<0.001*	*<0.001*	*<0.001*
*Water*light*	*0.587*	*0.796*	*0.063*	*0.319*

† Rotation lengths (1-4) are indicated in Table 3.4;* SEM= standard error of means for light effect.

Appendix 3- Lucerne grazing parameters and sheep performance in open field and under trees over the experimental period at the Lincoln University agroforestry area. Plant data are averages of 3 replicates and sheep performance data are means of the flock.

Treatment	Date*	Plant Stage	Pre-grazing	Post grazing	Stocking rate	Grazing days	Plant height	Bulk density	Growth rate	Sheep Liveweight gain		Pasture allowance
			kg DM ha^{-1} d^{-1}		hd ha^{-1}		cm	mg cm^{-3}	kg DM ha^{-1} d^{-1}	kg hd^{-1} d^{-1}	kg ha^{-1} d^{-1}	kg DM hd^{-1} d^{-1}
Tree lucerne	27Nov 99	Bud	2955.33	1279.25	16.67	128.33	61.67	0.48	68.73	0.162	2.70	4.12
Open lucerne	27Nov 99	Bud	3426.33	1371.50	21.67	166.83	45.45	0.75	79.68	0.234	5.07	3.68
Tree lucerne	15Feb 00	Bud	1836.17	1420.96	18.33	128.33	53.60	0.34	44.78	0.162	2.97	2.44
Open lucerne	15Feb 00	Flower	2982.33	1676.50	21.67	151.67	52.13	0.57	72.74	0.262	5.68	3.36
Tree lucerne	27Apr 00	Veg.	1001.17	410.42	10.83	67.17	27.93	0.36	19.63	0.112	1.21	1.81
Open lucerne	27Apr 00	Veg.	1509.58	857.49	16.67	103.33	35.12	0.43	29.60	0.160	2.67	1.78
Tree lucerne	27Nov 00	Bud	2525.17	868.33	16.39	122.91	61.82	0.41	60.12	0.186	3.05	3.67
Open lucerne	27Nov 00	Bud	5088.00	1735.00	27.78	208.38	52.42	0.97	121.14	0.211	5.86	4.36
Tree lucerne	10Jan 01	Bud	1898.33	365.50	15.83	114.00	70.00	0.27	54.24	0.261	4.14	3.43
Open lucerne	10Jan 01	Flower	4176.67	2282.67	23.33	168.00	65.00	0.64	119.33	0.269	6.27	5.11
Tree lucerne	27Mar 01	Flower	1288.92	314.90	10.83	32.50	41.11	0.31	18.15	0.140	1.52	1.68
Open lucerne	27Mar 01	Flower	3204.58	1715.00	26.67	133.33	65.67	0.49	45.13	0.239	6.37	1.69
Tree lucerne	***Averages***		*1917.51*	*776.56*	*14.81*	*98.87*	*52.69*	*0.36*	*44.28*	*0.171*	*2.60*	*2.86*
Open lucerne			*3397.92*	*1606.36*	*22.96*	*155.26*	*52.63*	*0.64*	*77.94*	*0.229*	*5.32*	*3.33*
Tree lucerne	***Stdev***		*733.229*	*488.370*	*3.195*	*39.883*	*15.565*	*0.073*	*21.158*	*0.0510*	*1.078*	*1.024*
Open lucerne			*1203.290*	*470.453*	*4.002*	*35.518*	*11.675*	*0.197*	*37.478*	*0.0397*	*1.381*	*1.376*

* Date of liveweight measurement

Appendix 4- Zenith angle formula according to *PAR Ceptometer Operator's Manual* (Decagon, Pullman, Washington). The Equation was used to calculate solar angle elevation (90 – zenith angle) in Lincoln, New Zealand (43° 30' S and 172° 28' E).

$\theta z = \arcos * [\sin L * \sin D + \cos L * \cos D * \cos 0.2618 * (t-t_o)]$

Where L is the latitude (in the Southern hemisphere, L is negative), D is the solar declination, t is the time and t_o is the time of solar noon. The factor 0.2618 converts hours to radians. Time t is used in hours (standard local time). Solar declination is calculated from:

$D = \arcsin * [0.39785 * \sin * [4.869 + 0.0172 * J + 0.03345 * \sin * (6.224 + 0.0172 * J)]$

Where J is the day of the year in Julian calendar. The time of solar noon is calculated from:

$t_o = 12 - LC - ET$

Where LC is the longitude correction and ET is the equation of time. LC is +4 minutes or +1/15 hour for each degree east of the standard meridian and –1/15 hour for each degree west of the standard meridian. New Zealand is about 7.7 degrees west of the closest standard meridian of 180 degrees. The equation of time is a 15 to 20 minute correction which depends on the day of the year and it can be calculated from:

$ET = [-104.7 * \sin\gamma + 596.2 * \sin2\gamma + 4.3 * \sin3\gamma - 12.7 * \sin4\gamma -429.3 * \cos\gamma -2.0 * \cos2\gamma + 19.3 * \cos3\gamma]/3600$

Where $\gamma = (279.575 + 0.986 * J) * \pi/180$.

Appendix 5- Nitrogen and minerals (P, Mg, Ca and K) content in lucerne leaves and stems collected at bud stage in 16th February 1999 in Canterbury, New Zealand. Samples were harvest from replicates 1 and 3. Values are expressedas % of dry matter.

Treatment	**Water**	**Rep.**	**Sample**	N	P	Mg	Ca	K
Full sun	Irrigated	1	Leaf	5.49	0.36	0.29	2.16	4.03
			Stem	1.69	0.25	0.12	0.64	4.24
Shade cloth	Irrigated	1	Leaf	5.95	0.41	0.28	2.22	4.12
			Stem	2.01	0.21	0.10	0.68	4.34
Wood-slats	Irrigated	1	Leaf	5.74	0.37	0.28	2.31	4.65
			Stem	2.00	0.25	0.12	0.71	4.34
Full sun	Non-Irr.	1	Leaf	5.14	0.31	0.35	1.92	4.41
			Stem	1.88	0.19	0.15	0.70	3.06
Shade cloth	Non-Irr.	1	Leaf	5.53	0.36	0.39	2.22	3.35
			Stem	1.78	0.21	0.13	0.70	3.46
Wood-slats	Non-Irr.	1	Leaf	5.76	0.37	0.37	2.00	4.10
			Stem	1.86	0.20	0.14	0.69	3.71
Full sun	Irrigated	2	Leaf	5.45	0.40	0.34	2.09	4.20
			Stem	1.72	0.25	0.12	0.62	3.67
Shade cloth	Irrigated	2	Leaf	5.73	0.39	0.34	2.08	4.43
			Stem	2.06	0.23	0.11	0.68	4.69
Wood-slats	Irrigated	2	Leaf	5.59	0.41	0.36	2.08	4.45
			Stem	2.12	0.25	0.13	0.64	4.39
Full sun	Non-Irr.	2	Leaf	5.09	0.32	0.30	1.78	5.01
			Stem	1.83	0.20	0.12	0.66	3.58
Shade cloth	Non-Irr.	2	Leaf	5.33	0.33	0.36	1.86	3.96
			Stem	1.96	0.25	0.15	0.71	4.13
Wood-slats	Non-Irr.	2	Leaf	5.62	0.37	0.36	2.04	4.01
			Stem	1.84	0.25	0.15	0.72	4.67

Appendix 6- Proportion of leaves and stems in lucerne shoots and weighted average of nitrogen, total minerals (P, Mg, Ca and K) and total shoot carbohydrates (CHO) content for replicates 1 and 3 collected at bud stage in 16th February 1999 in Canterbury, New Zealand. Values are expressed as % of dry matter.

Treatment	**Rep.**	**Water**	**Leaf**	**Stem**	**Total nitrogen**	**Total minerals**	**Total CHO***
			--------%-------		------Weighted average (% of DM)------		
Full sun	1	Irrigated	38.74	61.26	3.16	5.86	90.98
Shade cloth	1	Irrigated	41.41	58.59	3.64	6.04	90.32
Wood-slats	1	Irrigated	41.35	58.65	3.54	6.32	90.13
Full sun	1	Non-Irr.	47.81	52.19	3.44	5.47	91.08
Shade cloth	1	Non-Irr.	44.94	55.06	3.46	5.32	91.22
Wood-slats	1	Non-Irr.	44.91	55.09	3.61	5.69	90.71
Full sun	3	Irrigated	40.96	59.04	3.25	5.62	91.13
Shade cloth	3	Irrigated	43.84	56.16	3.67	6.38	89.95
Wood-slats	3	Irrigated	43.08	56.92	3.61	6.23	90.16
Full sun	3	Non-Irr.	46.27	53.73	3.34	5.88	90.78
Shade cloth	3	Non-Irr.	47.23	52.77	3.55	5.84	90.61
Wood-slats	3	Non-Irr.	47.09	52.91	3.62	6.25	90.13

Treatment	**Water**	**Total CHO (%)**	
		Mean	**St. Dev.**
Full sun	Irrigated	91.05	0.11
Shade cloth	Irrigated	90.14	0.26
Wood-slats	Irrigated	90.14	0.02
Full sun	Non-Irr.	90.93	0.21
Shade cloth	Non-Irr.	90.91	0.43
Wood-slats	Non-Irr.	90.42	0.41

* Total shoot CHO was estimated by 100% DM - % total nitrogen - %total minerals

Appendix 7- Observed and predicted carbohydrate yields (kg ha^{-1}) of lucerne in the full sunlight regime for two successive summer rotations and at different regrowth periods in Canterbury, New Zealand. Root mean square deviation (RMSD) was calculated for both rotations to test the accuracy of the model.

Light regime	Water status	Rotation	Days after grazing	Carbohydrate yield (kg ha^{-1})		
				Observed	Predicted	(Predicted-Observed)^2
Full sunlight	Irrigated	I	11	981.27	1090.47	11924.64
		I	16	1563.15	1637.85	5580.09
		I	22	2349.68	2362.63	167.70
Full sunlight	Non-irrigated	I	11	981.27	1020.83	1564.99
		I	16	1538.74	1621.64	6872.41
		I	22	2126.43	2411.22	81105.34
					RMSD	**133.68**
Full sunlight	Irrigated	II	7	480.24	619.21	19312.66
		II	14	1056.47	1489.54	187549.62
		II	21	2124.81	2470.88	119764.44
		II	28	2838.51	2994.04	24189.58
Full sunlight	Non-irrigated	II	7	315.12	392.28	5953.67
		II	14	860.20	986.00	15825.64
		II	21	1644.00	1759.34	13303.32
		II	28	2265.35	2307.85	1806.25
					RMSD	**220.14**

Appendix 8- Observed and predicted carbohydrate yields (kg ha^{-1}) of lucerne in the shade cloth regime for two successive summer rotations and at different regrowth periods in Canterbury, New Zealand. Root mean square deviation (RMSD) was calculated for both rotations to test the accuracy of the model.

Light regime	Water status	Rotation	Days after grazing	Carbohydrate yield (kg ha^{-1})		
				Observed	Predicted	(Predicted-Observed)^2
Shade cloth	Irrigated	I	11	540.19	527.46	162.05
		I	16	1222.23	746.54	226280.98
		I	22	1856.87	1056.63	640384.06
Shade cloth	Non-irrigated	I	11	616.25	506.69	12003.39
		I	16	1117.22	772.45	118866.35
		I	22	1681.30	1135.61	297777.58
					RMSD	**464.66**
Shade cloth	Irrigated	II	7	246.87	290.89	1937.76
		II	14	496.80	608.00	12365.44
		II	21	1265.55	1059.33	42526.69
		II	28	1878.49	1279.19	359160.49
Shade cloth	Non-irrigated	II	7	294.71	207.09	7677.26
		II	14	605.67	450.37	24118.09
		II	21	1140.01	810.96	108273.90
		II	28	1527.97	1044.78	233472.58
					RMSD	**314.15**

Appendix 9- Observed and predicted carbohydrate yields (kg ha^{-1}) of lucerne in the wooden slats regime for two successive summer rotations and at different regrowth periods in Canterbury, New Zealand. Root mean square deviation (RMSD) was calculated for both rotations to test the accuracy of the model.

Light regime	Water status	Rotation	Days after grazing	Carbohydrate yield (kg ha^{-1})		
				Observed	Predicted	(Predicted-Observed)^2
Wooden slats	Irrigated	I	11	448.65	308.43	19661.65
		I	16	1062.07	420.12	412099.80
		I	22	1684.98	612.25	1150749.65
Wooden slats	Non-irrigated	I	11	574.54	339.85	55079.40
		I	16	1150.36	484.39	443516.04
		I	22	1680.23	710.14	941074.61
					RMSD	**709.72**
Wooden slats	Irrigated	II	7	254.53	274.91	415.34
		II	14	576.53	547.77	827.14
		II	21	1167.31	853.85	98257.17
		II	28	1559.55	1086.99	223312.95
Wooden slats	Non-irrigated	II	7	264.35	196.75	4569.76
		II	14	522.87	416.12	11395.56
		II	21	996.25	667.63	107991.10
		II	28	1355.93	896.23	211324.09
					RMSD	**286.81**

List of publications

1. Varella, A.C., Moot, D.J., Lucas, R.J., McNeil, D.L., Peri, P.L and Pollock, K.M. 2001. Different methods of artificial shade for agro-silvipastoral research. In JA Gomide, WRS Mattos, & SC da Silva, SC (eds.). *Proceedings of the XIX International Grassland Congress. Grassland Ecosystems: an Outlook into 21st Century, Sao Pedro, 11-21 February 2001.* Sao Paulo, Brazil: Brazilian Society of Animal Husbandry, 659-660.

2. Varella, AC., Peri, PL., Lucas, RJ., Moot, DJ., & McNeil, DL. (2001). Dry matter production and nutritive value of alfalfa (*Medicago sativa* L.) and orchardgrass (*Dactylis glomerata* L.) under different light regimes. In JA Gomide, WRS Mattos, & SC da Silva, SC (eds.). *Proceedings of the XIX International Grassland Congress. Grassland Ecosystems: an Outlook into 21st Century, Sao Pedro, 11-21 February 2001.* Sao Paulo, Brazil: Brazilian Society of Animal Husbandry, 660-661.

3. Peri, Pl., Varella, Ac., Lucas, Rj., Moot, Dj., & McNeil, Dl. (2001). Cocksfoot and lucerne productivity in a Pinus radiata silvopastoral system: a grazed comparison. In *New Zealand Grassland Association Sixty third Conference:Proceedings of the New Zealand Grassland Association, v. 63, Waikato, New Zealand, 30 October-1 November 2001.* Palmerston North: New Zealand Grassland Association, 139-147.

4. Peri, P.L., Mason, E.G., Pollock, K.M., Varella, A.C., Mead, D.J. (2002). Early growth and quality of radiata pine stand in a silvopastoral system in New Zealand. *Agroforestry Systems*, 55, 207-219.