Defoliation frequency and season affected radiation use efficiency and dry matter partitioning to roots of lucerne (*Medicago sativa* L.) crops.

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Abstract

Radiation use efficiency (RUE), and subsequent partitioning between shoots and roots were investigated for 'Grasslands Kaituna' lucerne crops grown in the cool temperate climate of Canterbury, New Zealand. Crops were grazed by sheep every 28 or 42 days and yielded 12 and 23 t DM/ha.year, respectively. The RUE for above ground shoots (RUE_{shoot}) was 1.7-2.0 g DM/MJ of intercepted photosynthetically active radiation (PAR_i) in spring but decreased systematically to ≤1.0 g DM/MJ PAR_i in autumn . The RUE for total biomass, (RUE_{total}) ranged from 1.3 to 3.1 g DM/MJ PAR_i in response to air temperature and defoliation treatment. The lowest RUE_{total} in mid summer for the treatment defoliated every 28 days was related to a 20% decline in the leaf photosynthetic capacity measured at 1000 μmol photons/m^2.s (Pn_{1000}) and at saturating light (P_{max}). In turn, the reduction in Pn_{1000} was related to differences in specific leaf nitrogen (SLN), through changes in specific leaf weight (SLW) rather than the leaf N concentration of 4 to 6% DM.

The fractional partitioning of DM to roots (p_{root}) increased from near zero in winter/early-spring to >0.45 in autumn, which explained the observed seasonality of RUE_{shoot}. For the treatment defoliated each 42 days, p_{root} increased linearly from ~0.05 to >0.45 as Pp increased from 10.5 to 16.5 h. In decreasing photoperiods p_{root} averaged 0.45. There was a linear increase (R^2=0.52) in p_{root} with T_{soil}/T_{air} but only in the treatment defoliated each 42 days. Agronomic treatments that result in sub optimal N reserves post grazing can be expected to produce conservative canopy characteristics but reduced photosynthetic capacity of the first 5 main stem leaves. Beyond this development stage, canopy expansion may be reduced with more conservative leaf N.

Key words: Alfalfa; carbon and nitrogen partitioning; light use efficiency, photosynthesis, shoot/root ratio, root reserves, simulation modelling.

Introduction

The productivity and persistence of lucerne (*Medicago sativa* L.) stands is influenced by the frequency of cutting or grazing (Keoghan, 1982). Several studies have suggested a defoliation schedule based on calendar days, thermal-time units or the developmental stage of the crop (e.g. Belanger *et al.*, 1992; Brown *et al.*, 1990; Moot *et al.*, 2003). For example, in the subtropical climate of Queensland (Australia), the annual yield of several lucerne cultivars was optimized through a fixed 35 day cutting interval (Gramshaw *et al.*, 1993). In temperate climates, infrequent defoliations are recommended in autumn to allow the accumulation of root reserves required to support the following spring regrowth (Belanger *et al.*, 1999; Moot *et al.*, 2003). Albeit useful on site, such recommendations are not universally applicable. This

is because the physiological processes that control growth and development of lucerne crops respond to seasonal environmental signals and these responses may be modified by defoliation management (Christian, 1977; Fick *et al.*, 1988). Previous research (Teixeira *et al.*, 2007a; Teixeira *et al.*, 2007b; Teixeira *et al.*, 2007c) has shown that grazing each 28 days reduced annual shoot yield by ~50% compared with the 23 t DM/ha.year produced by crops defoliated each 42 days. This reduction was predominantly explained by the limited interception of photosynthetically active radiation (PAR_i) in the frequently defoliated crops due to reduced rates of expansion of primary and axillary leaves. However, lucerne shoot yield is also affected by the efficiency of conversion of PAR_i into aerial biomass (i.e. radiation use efficiency for shoot DM production, RUE_{shoot}) which can be seasonal (Khaiti and Lemaire, 1992) and sensitive to defoliation frequency (Avice *et al.*, 1997). These authors observed that the RUE_{shoot} of 'Europe' lucerne was 1.45 and 1.87 g DM/MJ PAR_i for crops defoliated at 30 and 45 days respectively. This difference could be caused by the low availability of root N reserves which are observed in frequently defoliated lucerne crops (Teixeira *et al.*, 2007b). Specifically, photosynthetic capacity is dependent on N supply and RUE is strongly associated with net photosynthesis at the canopy level (Sinclair, 1991; Sinclair and Horie, 1989). Thus agronomic or management factors that restrict N supply may affect photosynthetic capacity. Alternatively, RUE_{shoot} could be affected by changes in the partitioning of DM between shoots and roots as speculated by Avice *et al.* (1997).

The fractional partitioning of DM to roots (p_{root}) has previously been shown to differ seasonally (Brown *et al.*, 2006). Khaiti and Lemaire (1992) observed that lucerne RUE_{shoot} ranged from 1.1 g DM/MJ PAR_i in autumn to 1.8 g DM/MJ PAR_i in summer in the temperate climate of Northern France. In their study, when RUE was expressed in relation to

total biomass (i.e. shoots plus roots; RUE_{total}) its value was conservative at 2.3 g DM/MJ PAR_i throughout the year (i.e. regardless of environmental conditions). In contrast in New Zealand, Brown *et al.* (2006) showed that RUE_{total} of 'Grassland Kaituna' lucerne was responsive to air temperatures below 18ºC.

These previous observations suggest that the seasonality of RUE_{shoot} may reflect differences in (i) carbon assimilation (e.g. photosynthesis or RUE) and (ii) DM partitioning between shoots and roots, in response to environmental factors (e.g. temperature, photoperiod), but the relationships are insufficiently quantified to be predictive (Brown *et al.*, 2006; Collino *et al.*, 2005; Noquet *et al.*, 2001). Furthermore, any additional impact of defoliation frequency, which changes the demand for carbon and nitrogen in perennial organs (Richards, 1993), has not been investigated. As a result, the lack of explanation about the underlying processes that control RUE_{shoot}, RUE_{total} and p_{root} limits the mechanistic understanding of lucerne growth processes and compromises the accuracy of current simulation models (Confalonieri and Bechini, 2004; Gosse *et al.*, 1984; Robertson *et al.*, 2002). The objective of this research was to quantify the seasonal pattern of lucerne RUE_{shoot} of individual regrowth cycles in response to long (42-day) or short (28-day) frequency of defoliation and describe mechanisms that explain any differences in RUE_{shoot} through the analysis of RUE_{total}, p_{root}, leaf photosynthesis rates, and the N status of leaves.

Materials and Methods

Experimental site and defoliation treatments

A field experiment was conducted from 14 June 2002 to 04 October 2004 at Lincoln University Canterbury, New Zealand (43°38'S, 172°28'E, 11 m a.s.l). The soil is a 'Wakanui' deep silt loam (USDA Soil Taxonomy: Aquic Ustochrept, fine silty, mixed, mesic) classified as 'Pallic' in the New Zealand Soil Classification system (Hewitt, 1993; Watt and Burghan, 1992). An established, fully irrigated, two year old crop of 'Grassland Kaituna' lucerne was subjected to four contrasting defoliation treatments. Treatments were imposed as a complete randomized block design (4 replications) being a combination of (i) two grazing frequencies (28 or 42 days) and (ii) two periods when these grazing frequencies were imposed (before and/or after 4 February). For two treatments, a constant grazing frequency of 42 days (L, long cycle) or 28 days (S, short cycle) was applied throughout the year (LL and SS treatments, respectively). For LS and SL treatments, the 28 or 42-day grazing frequency was applied from early-spring until mid-summer (4 February) and then switched to the alternative treatment for the remainder of the year.

Sheep of mixed age classes grazed the individual 315 m^2 plots and any residual stem left post-grazing was trimmed to a height of ~50 mm to aid measurement of new shoot regrowth but avoid damage to the crown or emerging basal shoots. Crops were irrigated to avoid water stress, fertilized as required for optimal yields and weed ingression was avoided by chemical control. Additional details about the site and crop management were given in Teixeira *et al* (2007b).

Initial research quantified annual shoot yield, rates of canopy development and concentrations of endogenous reserves in crowns and taproots (Teixeira *et al.*, 2007a; Teixeira *et al.*, 2007b). They showed the greatest differences were between LL and SS

treatments so these were subjected to further detailed measurements of RUE, DM partitioning patterns, photosynthesis rates and leaf nitrogen concentration.

Measurements

Accumulated intercepted photosynthetically active radiation ($\sum PAR_i$)

Accumulated intercepted PAR ($\sum PAR_i$) was calculated by summing daily estimates of intercepted PAR (PAR_i) for each regrowth period. Daily PAR_i was obtained by multiplying the daily available above canopy PAR of each day (PAR_o) by the fractional PAR interception (PAR_i/PAR_o). Daily PAR_o was calculated from hourly logs of incoming total solar radiation (R_o) taken with a pyranometer LI-200SA (LI-COR Inc., Lincoln, Nebrasca, USA) on site as 0.5 x R_o (Szeicz, 1974). The PAR_i/PAR_o was estimated from measurements of fractional diffuse non-interceptance (DIFN) taken with a canopy analyser LAI-2000 (LI-COR Inc., Lincoln, Nebraska, USA). Detailed methodology of sampling and calibration of the LAI-2000 were given in Teixeira *et al.* (2007c). Briefly, readings of DIFN were taken in predominantly diffuse light conditions (e.g. twilight) at 7 day intervals, starting 10 days after the last grazing day of each regrowth cycle. Measurements were taken as one reference above canopy and five random below canopy readings per plot.

Sampling of shoot dry matter (DM_{shoot}) and calculation of total dry matter (DM_{total})

Shoots were cut with a set of hand shears above the crown and harvested from the area of a single 0.2 m^2 quadrat placed randomly in each plot. These shoot dry matter (DM_{shoot}) samples

were taken each 7-10 days within cycles starting ~10 days after the previous grazing. The material was dried in a forced air draft oven at 65°C for at least 48 hours to a constant weight.

Total plant DM (DM_{total}) was calculated as the sum of DM_{shoot} and crown plus taproot DM taken to a depth of 300 mm (DM_{root}). Crown plus taproot DM were excavated on the same dates and from the same 0.2 m^2 quadrat area where shoots were previously harvested. Samples were immediately kept on ice, freeze dried and weighed. The full data set for seasonal shoot and crown plus taproot DM was reported in Teixeira *et al.* (2007b).

RUE calculation

Radiation use efficiency for shoot DM (RUE_{shoot}) was calculated from linear regression (y=a+bx) of DM_{shoot} against $\sum PAR_i$ for each regrowth cycle where the coefficient (b) represents RUE. The intercept (a) of regressions was not forced through the origin because, unlike annual crops, there may be an allocation of DM from perennial organs to shoots during the early stages of lucerne regrowth (Avice *et al.*, 2001). Similarly, the radiation use efficiency for total DM (RUE_{total}) was calculated as the linear slope between accumulated PAR_i and total crop DM (DM_{total}= DM_{shoot} + 1.25 x DM_{root}). In this calculation the sample of DM_{root} taken at 300 mm was assumed to represent 80% of the total underground biomass (Lemaire *et al.*, 1992). The calculation of RUE_{total} was only carried out in regrowth cycles when there was a measurable increase in DM_{root}. This resulted in 16 estimates of RUE_{total} from 36 available regrowth cycles.

Due to the response of lucerne RUE to temperature (Brown *et al.*, 2006; Collino *et al.*, 2005), the estimated values of RUE_{total} were reported as a function of mean air temperature (T_{air}) and

compared with the temperature framework developed by Brown *et al.* (2006) for 'Grassland Kaituna' in Canterbury conditions. In this temperature response, RUE_{total} is nil at 0°C but increases linearly to an optimum RUE (RUE_{opt}) of 3.2 g DM/MJ PAR_i at a mean daily T_{air} of 18°C.

Calculation of DM partitioning to crown plus taproot

The estimates of fractional dry matter partitioning to crown plus taproot (p_{root}) were calculated as the slope (*b*) of the linear regression $DM_{root} = a + bDM_{total}$ for each regrowth cycle. The p_{root} was estimated for the same 16 regrowth cycles, from which RUE_{total} was calculated.

To test photoperiod and temperature as predictors of p_{root}, an alternative rationale was used to indirectly derive p_{root} for all regrowth cycles. To do this, p_{root} was calculated from the quotient of 'measured' RUE_{shoot} and 'estimated' RUE_{total} (RUE'_{total}) from the temperature response by Brown *et al.* (2006) as $p_{root} = 1 - (RUE_{shoot} / RUE'_{total})$.

Leaf net photosynthesis rate

Spot readings at 1000 µmols photons/m^2.s (Pn_{1000})

Approximately 740 individual readings of leaf net photosynthesis rates (Pn_{1000}, µmol CO_2/m^2.s) were taken during 42 dates from 29 August 2002 to 02 May 2004. Readings were taken on 3-4 of the youngest fully expanded leaves per plot, at artificial light fluxes (photosynthetic photon flux density, PPFD) of 1000 µmol photons/m^2.s using a portable

photosynthesis system LI-6400 (LI-COR Inc, Lincoln, Nebraska, USA). The Pn_{1000} measurements were taken between 1100 and 1400 h in clear sky conditions. The temperature in the leaf chamber was set to 21°C and the CO_2 concentration at 400 μmol/mol.

Readings were taken after a coefficient of variation (CV) ≤ 3% was obtained for the Pn_{1000} logs. Readings were adjusted according to the actual area of the leaf contained in the equipment chamber. Individual leaf area was quantified after photosynthesis measurements by opening each leaf flat onto white A4 paper and then digitally photographing it. Leaf surface area was then estimated by image analysis using the software QUANT (Vale *et al.*, 2003) which was calibrated to the number of pixels contained in a 200 mm reference scale. To standardize Pn_{1000} for specific environmental (e.g. temperature) and management conditions on the sampling day (Peri *et al.*, 2004), Pn_{1000} values for each plot were normalized by the mean maximum Pn_{1000} observed on the sampling day ($Pn_{1000max}$) and multiplied by an optimum Pn_{1000} of 31.5 μmols $CO_2/m^2.s$ measured for 'Grasslands Kaituna' in Canterbury from previous long-term measurements (Teixeira, 2006; Varella, 2002). Normalized values of Pn_{1000} (Pn'_{1000}) were then compared by ANOVA as pooled means during the initial (≤150ºCd, basis 5ºC) and final (>150ºCd) stages of each individual regrowth cycle (Equation 1).

Equation 1

$$Pn'_{1000} = (Pn_{1000}/Pn_{1000max}) \times 31.5$$

Photosynthetic light response curves

In addition to the Pn_{1000} readings, photosynthetic light response curves were measured with the portable photosynthesis system in 102 individual leaves during 14 dates from 28 September 2002 to 28 April 2003. Readings were taken at seven PPFD intensities: 0, 100, 250, 500, 750, 1000, 2000 µmol photons/m^2.s on 3 or 4 of the youngest fully expanded leaves of each plot from LL and SS treatments. The criteria for taking measurements were a minimum waiting time of 60 seconds and a CV ≤ 3% for each measurement. The photosynthesis system configurations and criteria used to perform the light response curves were the same as for the Pn_{1000} readings.

A non-rectangular hyperbola (Equation 2) was fitted to the data to obtain the main parameters from the light-response curves (Thornley and Johnson, 2000):

(Equation 2)

$$Pn = \frac{(P_{max} + \alpha \times PPFD) - [(P_{max} + \alpha \times PPFD)^2 - (4 \times \theta \times \alpha \times PPFD \times P_{max})]}{2 \times \theta} - R_d$$

Where Pn is the leaf net photosynthesis rate (µmol CO_2/m^2.s), R_d is the rate of dark respiration (µmol CO_2/m^2.s). The parameters α, θ and P_{max} represent the initial slope (µmol CO_2/µmol photons), the convexity (dimensionless) and the upper asymptote (µmol CO_2/m^2.s) of the light-response curve. Curves were fitted with Sigmaplot v.8 (SPSS, Inc.) using the following constraints: $\alpha>0$; $0.3<\theta<1.0$; $2.0< P_{max}<70.0$; $R_d <5.0$.

Based on the observation that the effects of the defoliation treatment on crop yield and endogenous root reserves occurred mainly after the first spring of 2002/03 (Teixeira *et al.*,

2007b), the parameters of the light-response curves were analysed as pooled averages for separate spring and summer-autumn periods.

Data analyses

When years or regrowth cycles were compared, the experiment was analysed as a split-plot design with as period the main plot and defoliation frequency as the subplot. Seasonal trends were shown graphically by displaying the average and the standard error of the mean (SEM) of each measured variable. Linear and non-linear functions were fitted between explanatory and dependent variables using SIGMAPLOT version 8.02 (SPSS Inc.). The variables and the regression coefficients of equations were compared using analysis of variance (ANOVA). In all cases, means were compared whenever treatment effects in the ANOVA presented $P<0.05$. Then, a Fisher's protected least significant difference (LSD) was used to separate means at the 5% level ($\alpha=0.05$). The software used for statistical analysis was GENSTAT 7th edition (Lawes Agricultural Trust, IACR, Rothamsted, UK).

Results

Shoot radiation use efficiency (RUE_{shoot})

Shoot radiation use efficiency (RUE_{shoot}) followed a consistent seasonal pattern being higher ($P<0.05$) in early-spring/summer than autumn (Figure 1). For example, the RUE_{shoot} of the LL treatment decreased ($P<0.01$) from ~1.7 g DM/MJ PAR_i in October 2002 (early-spring) to ~1.0 g DM/MJ PAR_i in late May (autumn). The exception to this pattern was the last autumn cycle of LL in 2002/03 which had RUE_{shoot} of ~2.5 g DM/MJ PAR_i. However, this result was

inflated by the low shoot yield of <400 kg DM/ha. Overall, RUE_{shoot} for both treatments was higher ($P<0.05$) in the second (2003/04) than the first year, particularly during summer.

The effect of grazing treatments on RUE_{shoot} was characterized by a strong interaction ($P<0.01$) with season. The SS treatment had the highest RUE_{shoot} in late-winter/early-spring (>2.0 g DM/MJ PAR_i; Figure 1) when yield ranged from 1.0 to 2.0 t DM/ha in the second and first year, respectively. During spring/summer, the periods of greatest DM accumulation, there were no differences between treatments with an average RUE_{shoot} of 1.5 g DM/MJ PAR_i.

[Figure 1, suggested place]

Radiation use efficiency for total dry matter (RUE_{total})

The pooled treatment average RUE_{total} was 2.2±0.4 g DM/MJ PAR_i, with individual values ranging from 1.3 to 3.1 g DM/MJ PAR_i (Figure 2). To account for temperature effects, estimated values of RUE_{total} were compared with the temperature framework proposed by Brown *et al.* (2006). The RUE_{total} values of the LL treatment were consistent with the temperature framework (RMSD of 0.4 g DM/MJ PAR_i) and increased ($P<0.06$) at 0.10 g DM/MJ.ºC as T_{air} ranged from 8 to 18ºC. In contrast, there was no systematic influence ($P=0.88$) of T_{air} on RUE_{total} in the SS treatment. This was mainly because in four of the eight analysed regrowth cycles of the SS treatment, RUE_{total} was 0.7-1.0 g DM/MJ PAR_i less than predicted. This increased the RMSD in relation to the model to 0.9 g DM/MJ PAR_i for the SS treatment.

[Figure 2, suggested place]

Fractional partitioning of DM to crown plus taproots (p_{root})

The fractional partitioning of DM to crown plus taproots (p_{root}) increased ($P<0.01$) from <0.05 in late-winter/early-spring to 0.33 in summer and >0.45 in mid-autumn in the LL treatment (Figure 3). During spring and autumn, the p_{root} in the SS crops followed a similar pattern to LL treatment. By contrast, during summer p_{root} was on average 0.13 in the SS treatment compared with 0.33 in LL treatment.

[Figure 3, suggested place]

Net photosynthesis of leaves

The impact of treatments on Pn_{1000} depended on the stage of crop regrowth. Pn_{1000} readings taken in the first half of regrowth cycles (<150°Cd) were ~20% greater ($P<0.05$) in the LL treatment (24.9 μmol $CO_2/m^2.s$) than the SS treatment (20.4 μmol $CO_2/m^2.s$) (Table 1). In contrast, after 150°Cd, both treatments had a similar ($P=0.34$) Pn_{1000} of ~24 μmol $CO_2/m^2.s$.

[Table 1, suggested place]

Specific leaf nitrogen and leaf photosynthesis

The specific leaf nitrogen (SLN) explained 68% of the differences in normalized Pn_{1000} (Pn'_{1000}) that increased ($P<0.01$) from 15 µmol $CO_2/m^2.s$ at a SLN of 1.5 g/m^2 to ~30 µmol $CO_2/m^2.s$ at a SLN of 3.4 g/m^2 (Figure 4 a).

[Figure 4, suggested place]

The response of leaf photosynthesis to SLN followed a saturation curve with a projected null Pn'_{1000} at an SLN of 0.92 g/m^2. While $N\%_{leaf}$ ranged from 4 to 6% DM, without any systematic effect on leaf Pn'_{1000} ($0.29<P<0.70$, Figure 4 b), SLW ranged from 35 to 70 g/m^2 and explained 81% of the variation in leaf Pn'_{1000} (Figure 4 c).

Discussion

Overall, results showed that the conversion efficiency of PAR_i into DM (i.e. RUE_{shoot} and RUE_{total}) and the partitioning of DM to roots (p_{root}) of lucerne crops differed seasonally and were affected by defoliation frequency.

The seasonality of RUE_{shoot}, RUE_{total} and p_{root}

There was a consistent seasonal pattern of change in lucerne RUE_{shoot}, regardless of defoliation frequency and the amounts of root endogenous reserves (Figure 1). The range and pattern of RUE_{shoot}, that declined from ~1.7 g DM/MJ PAR_i in spring to <1.0 g DM/MJ PAR_i in autumn, was in accordance with previous observations for the temperate climates of France and New Zealand (Brown *et al.*, 2006; Duru and Langlet, 1988; Khaiti and Lemaire, 1992). This regular seasonality suggests that environmental factors exerted a stronger control of RUE_{shoot} than the availability of C and N, created by the defoliation treatments. Nevertheless, air temperature (T_{air}) was a poor predictor ($P=0.41$, $R^2=0.11$) of RUE_{shoot} (data not shown) which differs from the observations made by Collino *et al.* (2005) for lucerne crops grown in the temperate Argentinean pampas. This contrast may be explained by the fact that, in the current experiment, RUE_{total} and p_{root} (the two components that influence RUE_{shoot}) responded separately to temperature. The RUE_{total} increased linearly ($P<0.06$) with air temperature (T_{air}) in LL treatment (Figure 2), but the p_{root} was poorly associated with T_{air} ($P=0.26$, data not shown). The response of RUE_{total} to T_{air} (Figure 2) is consistent with the increase in leaf net photosynthetic rates of the lucerne leaves with air temperature, observed under controlled environments (Al Hamdani and Todd, 1990; Murata and Honma, 1968).

The largest seasonal differences in RUE_{shoot} were caused by changes in the fractional partitioning of DM to roots (p_{root}). As the growth season advanced from spring to autumn, the retention of DM in shoots diminished (i.e. p_{root} increased from <0.05 to ~0.45; Figure 3). These results indicate that the increase in the partitioning of DM to roots was not abrupt, but occurred gradually from spring to summer, suggesting a systematic response to environmental signals. Both photoperiod (Pp) and temperature (T_{soil}/T_{air}) were tested as predictors of $p_{root,}$ as these environmental factors are associated with nitrogen and carbon partitioning between shoots and roots of lucerne crops (Brown *et al.*, 2006; Gosse *et al.*, 1984; Hargreaves, 2003; Noquet *et al.*, 2001). The strong linear increase (R^2=0.97) and the range of response of p_{root} to "increasing" photoperiod (IPp) in the LL treatment (Figure 5 a) was consistent with the observations of Morot Gaudry *et al.* (1987) in the temperate climate of France. These authors measured marked carbon (^{14}C) allocation to lucerne roots to be 20% in spring but increase to 50% in autumn. Although the relative allocation of DM to roots (i.e. p_{root}) was greatest in autumn at ~0.45 (Figure 3), the maximum absolute flux of DM to lucerne roots occurs slightly earlier in the season, during mid-summer (Teixeira *et al.*, 2007b). At this time, when p_{root} was ~0.30, total amounts of assimilation of C (photosynthesis) and N (mineral uptake and N_2 fixation) are greater than in autumn due to more favourable temperatures and incoming radiation.

The test of T_{soil}/T_{air} as an empirical predictor of p_{root} (Figure 5 b,d) eliminated the hysteresis in the LL treatment, but the low coefficient of determination suggests that other factors may influence the partitioning patterns of lucerne crops. This contrasts with annual crops such as wheat (*Triticum aestivum*) and maize (*Zea mays*) in which the temperatures experienced by shoots and roots were the main driver of DM partitioning, regardless of the concentration of nitrogen or carbohydrates in these organs (Engels, 1994).

[Figure 5, suggested place]

The effect of defoliation treatments on RUE_{shoot}, RUE_{total} and p_{root}

The lack of response of RUE_{shoot} to defoliation treatments during the periods of greatest DM accumulation (spring/summer) was caused by the compensatory changes that occurred between RUE_{total} and p_{root}. These maintained the overall seasonal pattern as unchanged. Specifically, RUE_{shoot} was unaffected by the low RUE_{total} of the SS treatment during summer (Figure 2) because this was counterbalanced by the greater retention of DM into shoots in this treatment (i.e. lower p_{root} in summer, Figure 3). This reduced partitioning of DM to roots in the SS treatment could be an artefact of the short duration of the 28 day treatment. This interrupted the regrowth when the proportion of DM allocated to storage organs was increasing through the grazing cycle.

During the late-winter/early-spring period, RUE_{shoot} was consistently higher in the SS treatment (2.0-2.4 g DM/MJ PAR_i) than the LL treatment (1.5-1.8 g DM/MJ PAR_i). The first harvest of SS treatment was taken 15 days earlier than LL treatment and this could overweight the initial period of spring regrowth in the RUE calculation. During early spring, the retention of DM in shoots was the highest (Figure 3) with additional remobilization of DM from roots to shoots (Avice *et al.*, 1996) producing a consequent increase in the value of RUE_{shoot}.

The evidence from four summer regrowth cycles of the SS treatment indicated that frequent defoliations reduced RUE_{total} to half the values observed in the LL treatment (Figure 2).

Although it is unclear why this response was not common for all regrowth cycles in SS treatment, these results were consistent with the decline of ~20% in Pn_{1000} in the early stages of regrowth of these crops (Table 1). In addition, a 20% lower ($P<0.05$) average net leaf photosynthesis rate (P_{max}) was also observed in the SS treatment during summer/autumn (Figure 6), but the number of measurements of light response curves was insufficient to allow an ANOVA for comparison of stages of regrowth.

[Figure 6, suggested place]

Under field conditions, the factors that are most likely to impact on leaf photosynthesis rates are N supply, water availability and temperature (Lawlor, 2001). Of these only the availability of endogenous root N were manipulated through the frequent defoliation treatments.

Endogenous root N was reduced by up to 65% in the SS treatment (Teixeira *et al.*, 2007b). This suggests that the limited supply of nitrogen to shoots could be the reason for the limited photosynthetic capacity and reduced RUE_{total} (Avice *et al.*, 1997; Lawlor, 1995). A shortage of N supply to shoots may occur immediately after defoliations, when 65-75% of the N mobilized from roots is translocated to growing leaves (Kim *et al.*, 1991). This hypothesis was consistent with the positive observed response of leaf net photosynthesis to specific leaf nitrogen (SLN, Figure 4 a). In the leaves of C3 species, such as lucerne, ~55% of the nitrogen is associated with the photosynthetic system (Calvin-cycle, Rubisco or the light harvest compounds) and photosynthesis can be affected by changes in both chemical and anatomical traits of leaves (Heichel *et al.*, 1988; Lawlor *et al.*, 2001). In this sense, the SLN can be conceptually analysed through its structural (specific leaf weight, SLW) and metabolic

(nitrogen concentration, $N\%_{leaf}$) components (Reich *et al.*, 1998). In the current experiment, lucerne plants adapted to a limited supply of N by producing thinner leaves as indicated by the strong relationship between Pn'_{1000} and SLW (Figure 4 b). Under environmentally controlled conditions such a relationship was previously observed by Pearse et al. (1969) and Okubo et al. (1975) who measured increases of 2.5 to 4.0 fold in P_{max} as SLW augmented from ~19 to 55 g/m^2. This large plasticity of lucerne SLW (Hodgkinson, 1974) may be mediated by changes in the number of palisade mesophyll cell layers (Evans, 1993). For example, nitrogen deficiency during the early stages of regrowth could reduce the number of cells in the leaf primordia (Gastal and Lemaire, 2002; Gastal and Nelson, 1994) when cell division, DNA replication and protein synthesis are intense (Lemaire and Millard, 1999) affecting structural protein formation (Lawlor et al., 2001). On the other hand, at later stages of regrowth (e.g. >150ºCd) a recovery of the photosynthetic capacity of upper leaves would be expected due to the diminishing dependency of shoots on nitrogen reserves (Kim *et al.*, 1991) and the increasing translocation of N from basal senescing leaves to the upper canopy (Lotscher *et al.*, 2003).

Physiological and modelling implications

Overall, results indicate that the responses of lucerne crops to frequent defoliations were mediated though the optimization of nitrogen use for growth. Interestingly, the strategy to adjust to limited N resources, in response to frequent defoliations, differed according to the development stage of the crop. During the early stages of regrowth (e.g. <150ºCd) there was a reduction in photosynthetic capacity of the first five primary leaves (Table 1). The expansion of these same first five leaves was previously shown to be unaffected by defoliation treatments or the amounts of endogenous reserves (Teixeira *et al.*, 2007c). If the

scarcity of N or C from reserves persists at later stages of regrowth (e.g. >150ºCd), the photosynthetic capacity is recovered (Table 1) but at the expense of leaf area expansion (Teixeira *et al.*, 2007c). Assuming that carbon is the most limiting resource after complete defoliation, maximizing the photosynthetic area (i.e. LAI) at the expense of photosynthetic efficiency (i.e. RUE_{total}) seems a logical adaptation strategy for lucerne in the early stages of regrowth. The subsequent recover of photosynthetic capacity can be explained by the translocation of nitrogen from shaded senesced leaves (at the base of the canopy) to photosynthesizing leaves in the upper canopy (Lemaire and Gastal, 1997; Lemaire *et al.*, 1991) at the same time when the absolute N uptake is increasing (Kim *et al.*, 1991). These patterns support the rationale of a functional equilibrium between shoots and roots in which the balance between supply and demand for assimilates (C and N) within the whole plant determine growth of each organ (Lemaire and Millard, 1999).

Together, these results indicate that attempts to mechanistically simulate growth and development of lucerne crops in response to contrasting defoliation frequencies must consider pools and fluxes of carbon and nitrogen in both shoots and roots. Important model parameters such as canopy expansion rates (e.g. LAER) and the conversion efficiency of radiant energy to crop DM (e.g. RUE_{total}) could then be modulated by the availability of C and N.

In current lucerne simulation modelling, RUE_{shoot} is often treated as a parameter (Confalonieri and Bechini, 2004; Robertson *et al.*, 2002). Our results show that the differences in RUE_{shoot} can be modelled from the responses of p_{root} and RUE_{total} to environmental and management factors. Therefore, the explicit use of RUE_{total} and p_{root} to

simulate shoot yield (DM_{shoot}; Equation 3) may improve the connection to the underlying physiological mechanisms that explain the seasonal RUE_{shoot} (Equation 4).

$$DM_{shoot}=PAR_i \times RUE_{total} \times (1-p_{root}) \quad \text{(Equation 3)}$$

$$RUE_{shoot}=RUE_{total} \times (1-p_{root}) \quad \text{(Equation 4)}$$

In this sense, the responses of RUE_{total} and p_{root} to temperature, nitrogen and water supply could be derived from empirical experiments as frequently done for arable crops (Hammer, 1998; Sinclair and Muchow, 1999).

In the current experiment, no simple relationship was found to derive p_{root} from photoperiod or temperature (Figure 5) and an interaction between environmental signals or the impact of management deserves further consideration. At this stage, the uncertainties about the underlying mechanisms controlling DM partitioning still justify empirical attempts for modelling p_{root} (Sinclair and Seligman, 1996). Nevertheless, these approaches are expected to be site and cultivar specificity, i.e. must be limited by the known genetic variability among lucerne cultivars and the interactions with the wide environmental conditions in which lucerne crops are grown worldwide (Irwin *et al.*, 2001).

In conclusion, frequent defoliations reduced root nitrogen reserves of lucerne crops. Limited supply of endogenous nitrogen to shoots explained the reduction in RUE_{total} of frequently defoliated crops. This impact was carried through a decrease in photosynthetic capacity of the earliest initiated leaves post-grazing, which together with subsequent reductions in canopy

expansion rates, diminished total yields. When coupled with the seasonal response in RUE_{shoot}, due to changes in DM partitioning to roots, these results support recommendations for differential grazing times based on the seasonality of lucerne production, with emphasis on rebuilding underground nitrogen reserves in late-summer/autumn (Moot *et al.*, 2003).

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Tables

Table 1. Leaf photosynthesis at 1000 µmol photon/m^2.s of lucerne crops subjected to 28-day (SS) or 42-day (LL) regrowth cycles.

Stage of regrowth	LL	SS
	µmol CO_2/m^2.s	
Early regrowth (0-150°Cd)	24.9_a	20.4_b
Late regrowth (151-350°Cd)	23.5_a	24.2_a

Note: Values with the same letter within rows are not significantly different (α=0.05). SEM is 0.702.

Figure captions

Figure 1. Seasonal shoot radiation use efficiency (RUE_{shoot}) of lucerne crops subjected to a long (LL, 42 days) or a short (SS, 28 days) regrowth cycle during the 2002/03 and 2003/04 growth seasons at Lincoln University, Canterbury, New Zealand.

Figure 2. Total radiation use efficiency (RUE_{total}) against mean air temperature of lucerne crops subjected to a long (LL, 42 days) or a short (SS, 28 days) regrowth cycle during 2002/03 and 2003/04 growth seasons at Lincoln University, Canterbury, New Zealand. Note: Dashed line represents model developed by Brown et al. (2006) for lucerne grown in columns under near-field conditions. Projection to zero in dotted line.

Figure 3. Fractional partitioning of DM to crown plus taproot biomass in lucerne crops subjected to a long (42-day, LL) or short (28-day, SS) defoliation frequency at Lincoln University, Canterbury, New Zealand during the 2002/03 and 2003/04 regrowth seasons. Dashed line indicates the overall pattern observed in LL treatment.

Figure 4. Response of the normalized rate of net leaf photosynthesis (Pn'_{1000}) to specific leaf nitrogen (a), specific leaf weight (b) and leaf nitrogen concentration (c). Data-points represent average of 3 to 4 leaves per plot.

Figure 5. Estimated fractional partitioning of DM to crown plus taproot in lucerne crops defoliated with a long (a, b) or a short (c, d) regrowth cycle against increasing (IPp) and decreasing (DPp) photoperiod (a, c) and the relationship between 100 mm depth soil and air temperature (b, d). Note: The quotient between measured RUE_{shoot} and estimated RUE_{total} (RUE'_{total}) was used to calculate p_{root} values for each regrowth cycle (assuming no effect of defoliation frequency in RUE_{total}). For decreasing photoperiod, slopes were not significantly different from zero (α=0.05) and the average p_{root} was 0.45 (dotted lines) for LL and SS treatment.

Figure 6. Reconstruction of light-response curves pooled for LL and SS treatments during the summer-autumn period of 2002/03. Note: The parameters α, θ and P_{max} represent the initial slope, the convexity and the upper asymptote of the light-response curve. R_d is the rate of dark respiration and PPFD is the photosynthetic photon flux density. Mean parameter values are followed by one standard error of the mean (SEM) for *n*=4. Different subscript letters after P_{max} values indicate difference at the 0.05 significance level; all other parameters were similar between treatments and average values are presented. The average stage of crop development was ~6 leaves (mean ∑Tt of 194ºCd). During early-spring (data not plotted) all parameters were similar between treatments: P_{max} was 36 µmol $CO_2/m^2.s$; alpha (α) was 0.07 µmol CO_2/µmol photons, theta (θ) was 0.61 and dark respiration (R_d) was 1.82 µmol $CO_2/m^2.s$.