Temperature responses of lucerne radiation and water use efficiency

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Abstract

Shoot dry matter production (DM), radiation interception and water use were measured from re-growth lucerne crops over two years (2000 – 2002) at Lincoln University. From these data radiation use efficiencies (RUE) and water use efficiencies (WUE) were calculated throughout both years. The WUE values were normalised (WUE*) for seasonal variation in vapour pressure deficit. Dry matter partitioning between shoot and perennial DM (roots and crowns) was measured from lucerne grown in individual columns to give a seasonal pattern of the proportion of total DM partitioned to shoots (P_{shoot}). The RUE and WUE* values calculated from field measurements were then multiplied by the reciprocal of P_{shoot} (from column measurements) to give an estimate of RUE and WUE* for total DM production (RUE_{tot} and WUE^*_{tot}). The RUE_{tot} showed a strong linear increase with temperature from 0.8 kg DM/MJ at 9 °C to 1.6 kg DM/MJ at 17 °C. The WUE^*_{tot} also increased linearly from ~15 kg DM/ha/mm.kPa at 9 °C to ~35 kg DM/ha/mm.kPa at 17 °C. The link between RUE_{tot} and WUE^*_{tot} and their temperature responses are discussed.

Introduction

Radiation use efficiency (RUE) is frequently used to quantify the relationship between shoot dry matter (DM) production and intercepted radiation (Sinclair and Muchow, 1999). This is a simplification of canopy photosynthesis dynamics but accurately quantifies DM production over a long period when other factors are non-limiting (Monteith, 1977). The concept of RUE was developed for annual crops and usually relates above ground (shoot) DM to radiation interception assuming root production is a small and constant proportion of total DM (Sinclair and Muchow, 1999). Thus, RUE can be used in combination with intercepted radiation to predict crop DM production (Jamieson *et al.*, 1998; Keating *et al.*, 2003).

Water use efficiency (WUE) quantifies the relationship between shoot DM production and crop water use (transpiration). Crop WUE is also a simplification of canopy photosynthesis and water loss that quantifies the amount of water a particular crop needs to produce DM (Monteith, 1986). The WUE of a crop decreases as vapour pressure deficit (VPD) increases. It is common to multiply WUE by the daylight averaged VPD for the period of measurement (Tanner and Sinclair, 1983) to give a VPD normalised WUE (WUE*). A WUE* can then be used in combination with a prediction of DM production to predict how much water a crop will use and subsequent soil water extraction (Keating *et al.*, 2003; Meinke *et al.*, 2002).

The concepts of RUE and WUE* have been extended to quantify DM production and water extraction of perennial crops such as lucerne (Robertson *et al.*, 2002). However, some of the inherent assumptions within RUE and WUE* are not relevant to perennial crops. Firstly, root production is not always small nor is it always a constant fraction of total DM production and changes in partitioning between shoots and perennial organs (tap roots and crowns) affect RUE (Chen *et al.*, 2003; Zahid *et al.*, 2003) and WUE (Smeal *et al.*, 1991; Undersander, 1987). The most specific example was given by (Khaiti and Lemaire, 1992) who showed total RUE of lucerne was constant (1.15 g DM/MJ) for an establishing crop, but shoot RUE decreased from 0.9 g DM/MJ in summer to 0.55 g DM/MJ in autumn when lucerne partitioned more DM to perennial organs. There is also evidence that the partitioning of DM to lucerne shoots is higher in spring than in summer (Dhont *et al.*, 2003; Justes *et al.*, 2002). However, there are no functional relationships established for the seasonal pattern of DM partitioning between shoots and perennial organs for lucerne.

It is often assumed that RUE and WUE* are independent of temperature (Sinclair and Muchow, 1999; Tanner and Sinclair, 1983). This assumption is usually made for annual crops that grow through a similar temperature profile each year. However, perennial crops such as lucerne may regrow 3 – 7 times per year and regrowth periods can experience a wide range of temperatures. Lower temperatures experienced in temperate environments are expected to influence canopy photosynthesis they so would also be expected to influence RUE (Sands, 1996) and WUE* (Sadras *et al.*, 1991; Singh and Sri Rama, 1989).

The aim of this study was to quantify seasonal variations in DM partitioning so that RUE and WUE* can be calculated for total DM production (RUE_{tot} and $WUE*_{tot}$) with explicit account for changes in DM partitioning. Then RUE_{tot} and $WUE*_{tot}$ will be calculated for different times of the year and assessed to determine any temperature response of these parameters.

Materials and Methods

Field experiments (RUE and WUE)

Measurements were taken from lucerne crops in two adjacent paddocks (I8 and I9) at Lincoln University, Canterbury, New Zealand (43 °38 'S, 172 °28 'E, 11 m a.m.s.l.). The soils are classified as a Wakanui silt loam (Udic Ustochrept, USDA Soil Taxonomy) with 1.8–3.5 m of fine textured material overlying gravels (Cox, 1978). Meteorological data were recorded at Broadfields station 2 km north of the site. Mean daily temperature ranged from 6 °C in June/July to 17 °C in January/February and mean total daily radiation receipts increased from 5–23 MJ m^{-2} over the same period.

Measurements were made from regrowth lucerne over two growth seasons from 1 July 2000–30 June 2002. There were 6 or 7 regrowth cycles within each growth season except I9 in 2000/01 (establishment season) where treatments had 2–3 regrowth cycles. Regrowth cycles were defined as the time from the finish of grazing until the start of the subsequent grazing. Lucerne was defoliated by grazing with sheep of mixed classes for 3–7 days. Post grazing residual stem was trimmed to ~70 mm above ground level on the day grazing finished.

Soil tests were conducted annually and fertiliser applied to maintain nutrient levels within optimal ranges. Herbicide was applied during winter to remove annual grass weeds from lucerne plots. Irrigation was applied as necessary to maintain a soil water deficit <200 mm in the top 2 m of soil and avoid water stress (Brown, 2004). Additional details of the design and management of field experiments were reported by Brown (2004).

Dry matter measurement

Dry matter (DM) measurements were taken from each plot by cutting a single 0.2 m^2 quadrat 70 mm above crown height (to avoid damaging the plants). To avoid re-cutting previously sampled areas in any year samples were taken from different sections of the plot in each regrowth cycle. All DM samples were dried in a forced air oven (70 ºC) to constant weight.

Radiation interception

Fractional radiation interception (I/I_o) was measured with a LI-COR LAI-2000 canopy analyser (Lincoln, Nebraska, USA; Welles and Cohen, 1996). One above canopy reference and five below canopy measurements were taken per replicate during stable overcast or twilight conditions. Measurement positions were selected at random and the LAI-2000 was used without a lens cap so measurements considered all surrounding foliage.

Transpiration

Soil water content (SWC) was measured from 0 – 0.2 m depth using a Time Domain Reflectometer (TDR) and at 0.1 m intervals from 0.2 to 2.3 m depth using a neutron probe (Brown *et al.*, 2003). Transpiration was calculated using a water balance where total WU for each measurement period was calculated from measured ΔSWC, rainfall, irrigation and estimates of soil evaporation. Soil evaporation was estimated using a modified form of the Ritchie soil evaporation calculation (Brown, 2004).

Column experiment (dry matter partitioning)

This experiment measured total DM production of lucerne to determine the seasonal pattern of DM partitioning between shoot (leaf and stem) and perennial DM (roots, crowns and crown stems). Lucerne plants were established and grown in plastic PVC columns (0.8 m long, 0.15 m diameter), located in three separate (replicate) pits (1 m deep, 0.7 m wide, 1.4 m long) in the South West corner of Iversen 9. Each pit contained 32 columns that were used for repeated destructive sampling. Columns were arranged touching and pits were dug within an existing lucerne crop to provide a continuous crop canopy for column grown plants. Eight rows of four columns were arranged inside each pit in December 2000 and filled with a 30 % perlite, 70 % sand mixture. Twenty 'Grasslands Kaituna' lucerne seeds were sown per column on 2 January 2001. These were thinned to eight plants per column following emergence (in February 2001). Plants were finally thinned in March 2001 to leave the three largest plants per column at a population of 100 plants/m^2, which was equivalent to field conditions. This experiment focused on the perennial re-growth of lucerne so the establishment period from sowing (2 January 2001) to 30 June 2001 was not analysed.

Plants were defoliated when 50 % of stems had initiated flower buds. In the first spring regrowth plants did not flower but were defoliated at the same time as the field experiment (25 September 2001). Columns were defoliated with a set of hand shears to ~70 mm height and the lucerne crop surrounding each pit was defoliated with a lawnmower. Full experimental and DM sampling procedures are given by (Brown, 2004).

Dry matter sampling from column experiment

Destructive samples were taken from each replicate pit on each defoliation date and 2–3 occasions between defoliations. Sample columns were removed in the evening and stored in a chiller (<4 °C) overnight for dissection the following day. Sampled columns were replaced with buffer columns to maintain the continuous canopy of the remaining columns. The contents of columns were tipped out and whole plants were removed from the sand/perlite mixture and gently washed clean with cold water. All three plants from each sample column were separated into shoot and perennial fractions. Shoots consisted of leaves, stems (above defoliation height) and basal buds. Perennial material was defined as crown stem (below defoliation height), crowns, taproots and thick lateral roots. Fine roots were not considered as perennial material, because they may be shed during the season, and were removed from the root-system by pulling roots between thumb and forefinger. Any roots that could be gently stripped off in this manner were excluded from perennial material. Perennial material was cut into 10–20 mm pieces with a set of hand pruners and samples were dried in a forced air oven at 70 °C until constant weight (24–48 h).

Analysis

The seasonal pattern of DM partitioning was calculated as the proportion of total DM production that was partitioned to shoots (P_{shoot}). The P_{shoot} was calculated with DM production from the first (7–10 d after defoliation) to the final (at defoliation) DM measurement date within each regrowth cycle.

A RUE for above ground DM production (g DM/MJ total radiation) was calculated from shoot DM production within each of 15 individual regrowth cycles by regressing shoot DM against accumulated radiation interception (slope = RUE). The WUE was also calculated for shoot DM production from the same regrowth periods by regressing shoot DM against accumulated transpiration (slope = WUE). The WUE from each regrowth cycle was then multiplied by the mean daylight averaged VPD over that period to give a normalised WUE (WUE*).

Estimates of RUE and WUE* for total DM production (RUE_{tot} and WUE^*_{tot}) were calculated by multiplying these values by the reciprocal of P_{shoot} ($1/P_{shoot}$). This explicitly accounts for seasonal variation in DM partitioning. Total RUE and WUE* were then regressed against the mean daily temperature for each regrowth cycle to detect any temperature responses.

Results

Shoot DM accumulation

Shoot DM showed a strong linear relationship ($R^2 = 0.97 \pm 0.07$) with accumulated intercepted radiation and accumulated transpiration within each regrowth cycle for field grown crops. An example of these relationships is given in Figure 1. Of note, the fifth regrowth cycle, which occurred during March/April, had a lower slope than other regrowth cycles. This difference was apparent in all paddock/season combinations.

Seasonal DM partitioning

The measurements from column grown lucerne showed a distinct seasonal pattern in the proportion of total DM production that was partitioned to shoots (Figure 2). Specifically, P_{shoot} was 0.9 in the first regrowth cycle, decreased 0.6–0.7 from November to January and decreased abruptly to 0.4 in March.

Temperature response of RUE_{tot} and WUE^*_{tot}

The RUE_{tot}, estimated using partitioning patterns from column lucerne data, showed a linear increase from ~0.9 g DM/MJ with a mean air temperature of 9 °C to ~1.6 g DM/MJ at 17 °C (Figure 3a). The y-intercept of a linear regression fitted to the data was not significantly different to zero so was fixed (a = 0). The subsequent regression showed RUE_{tot} increased 0.095 g DM/MJ per 1 °C increase in temperature with a R^2 of 0.67. The WUE^*_{tot} also showed a linear increase from ~15 kg DM/ha/mm.kPa with a mean temperature of 9 °C to ~35 kg DM/ha/mm.kPa at 18 °C (Figure 3b). The y axis intercept was not different to zero and the regression with a fixed (a = 0) y-intercept showed WUE^*_{tot} increased 1.98 kg DM/ha/mm.kPa.

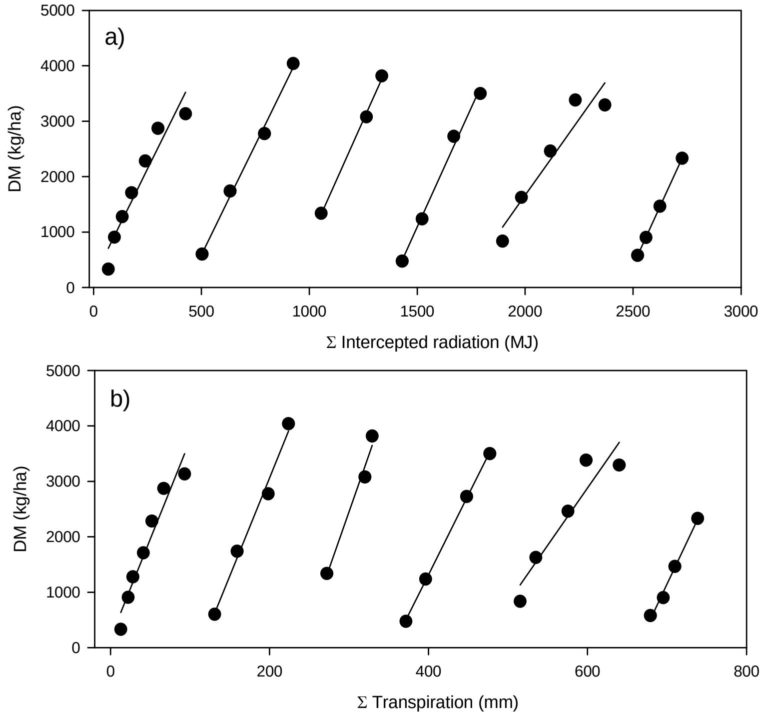

Figure 1. Dry matter accumulation against accumulated intercepted radiation (a) and transpiration (b) of fully irrigated lucerne grown in six regrowth cycles (1 July 2001 – 30 June 2002) in Iversen 9 at Lincoln University. The slopes of fitted regressions give radiation use efficiency and water use efficiency respectively.

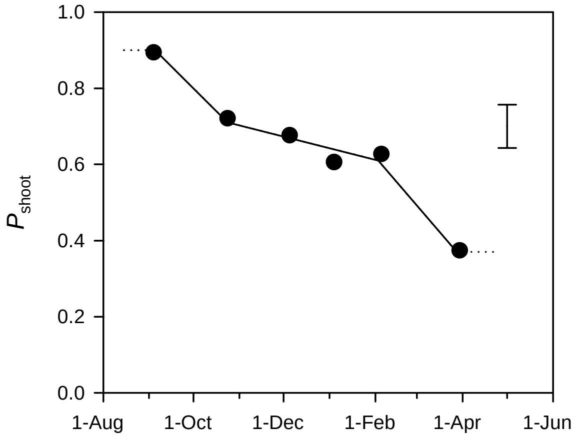

Figure 2. The proportion of total DM partitioned to shoots (P_{shoot}) of fully irrigated column grown lucerne at Lincoln University, Canterbury, New Zealand. Bar represents the pooled standard error. Data from Brown *et al.* (2005).

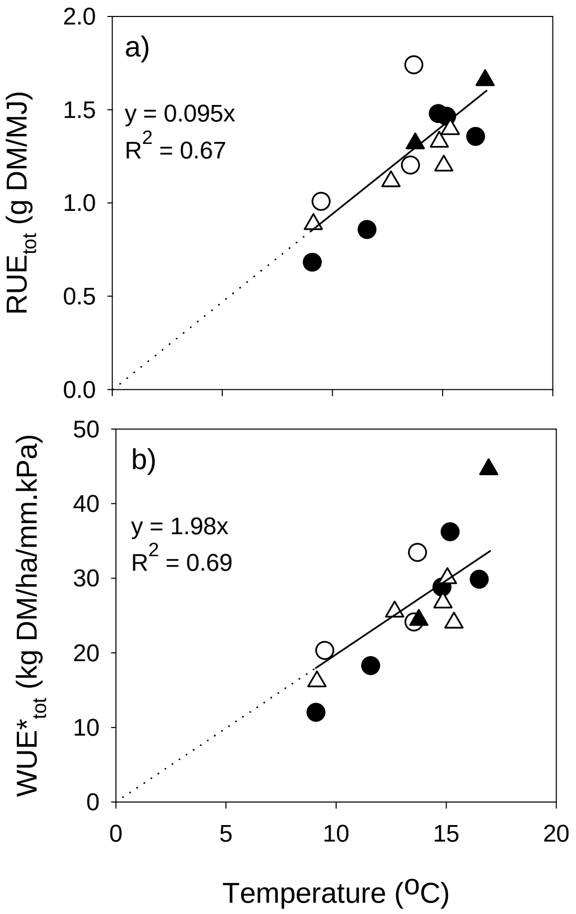

Figure 3. a) Estimated total radiation use efficiency (RUE) and b) Estimated total water use efficiency (WUE) of fully irrigated lucerne in relation to mean daily temperature. Data from different field season combinations (I8$_{00/01}$ ●, I8$_{01/02}$ ○, I9$_{00/01}$ △, I9$_{01/02}$ ▲)

Discussion

This research has shown that the concepts of RUE and WUE can also be applied to lucerne with strong linear relationships for DM accumulation with intercepted radiation and transpiration respectively (Figure 1). However, the assumption that RUE and WUE* are constant did not hold and the effects of DM partitioning and temperature needed to be accounted for.

Dry matter partitioning

Figure 2 showed a distinct seasonal pattern of DM partitioning between shoots and perennial organs. This pattern was consistent with Khaiti and Lemaire (1992) who reported DM partitioned to shoots was 80% in summer and dropped abruptly to 45% in autumn. The highest partitioning of DM to shoots in the spring is not well documented but is implied by many studies that show lucerne yields that are greatest in spring and decrease in summer and autumn regrowth periods (Frame *et al.*, 1998). The seasonal pattern of P_{shoot} was then used to calculate RUE_{tot} and $WUE*_{tot}$ which explicitly account for any seasonal effects of changes in partitioning on RUE and WUE*.

Temperature responses of RUE_{tot} and WUE^*_{tot}

Both RUE_{tot} and WUE^*_{tot} showed a similar linear increase with increased temperature (Figure 3). These data were collected over two years, from two separate fields within each year which suggests this is a crop response to the environment. Sadras *et al.* (1991) and Singh and Sri Rama (1989) also demonstrated the link between RUE and WUE*, but this relationship is not widely recognised. A few authors have reported temperature responses in RUE (van Keulen and Seligman, 1987; Wilson *et al.*, 1995), but such responses are also not widely recognised for RUE or WUE*. In a detailed review of the subject (Sinclair and Muchow, 1999) made no mention of the effects of temperature on RUE. However, variation in RUE and WUE* are important for simulation models that use these parameters. The link between them implies that any change invoked for RUE should also be invoked for WUE*.

Theoretical justification of temperature responses

In spite of the limited recognition of temperature responses of RUE and WUE*, analysis of the underlying theory explains why the two parameters are linked and why they respond to temperature. A crops RUE, is proportional to its photosynthetic assimilation rate (A) per unit of radiation intercepted (I) (Monteith, 1977) and can be represented as:

Equation 1

$$RUE = \frac{A}{I} = \frac{\left(\dfrac{C_a - C_i}{R_g + R_m}\right)}{I}$$

Where C_a and C_i are CO_2 concentrations in the atmosphere and inside the leaf, respectively. R_g is gas phase resistance (stomatal and boundary layer) and R_m is mesophyl resistance which is proportional to the crops photosynthetic capacity (Evans and von Caemmerer, 1996). Respiration is assumed to increase as a constant proportion of A under the environmental conditions experienced in this research (Dewar *et al.*, 1999) so is not included in this discussion. Solar radiation is the primary factor controlling A with an increase in I giving a proportional decrease in R_g (stomatal opening) and R_m (increased photon supply to photosystems) so RUE remains constant.

A crops water use efficiency can be represented in a similar way:

Equation 2

$$WUE = \frac{A}{T} = \frac{\left(\dfrac{C_a - C_i}{R_g + R_m}\right)}{\left(\dfrac{V_i - V_a}{R_g}\right)}$$

Where T is transpiration, V_a and V_i are water vapour pressures in the atmosphere and inside the leaf respectively. V_i - V_a is represented by VPD and is accounted for in the normalisation of WUE (WUE*). Solar radiation is also the primary factor driving T through decreased R_g so an increase in I will increase A and T in proportion and WUE* will remain constant. However, other environmental factors, such as temperature, can influence A without influencing I or T and any such change in A will influence both RUE (Equation 1) and WUE* (Equation 2) in the same manner (i.e. $RUE \propto WUE^*$).

To understand how temperature influences RUE and WUE* it is necessary to consider the individual components of A (Equation 1). Firstly, we can assume that C_a is constant. Solar radiation is the primary driver of A and T through changes in R_g and R_m. At a given level of I (or T) we can assume R_g and R_m are constant and A will be proportional to C_i. Thus, any temperature effects on C_i will also influence RUE and WUE*. The C_i of a crop can be written as (Jarvis and Morison, 1981):

Equation 3

$$C_i = C_a \frac{g_g}{(g_g + g_m)}$$

Where g_g and g_m are gas phase and mesophyll conductance, given by the reciprocal of R_g and R_m, respectively. Changes in solar radiation will change g_g and g_m in the same proportion so C_i (and RUE and WUE*) will remain constant (Jarvis and Morison, 1981). However, lower temperatures can reduce the photosynthetic capacity of a crop through limiting biochemical reaction rates (von Caemmerer, 2000). Thus, at lower temperatures it is reasonable that g_m will decrease relative to g_g, increasing C_i, reducing A and explaining the reduction in RUE and WUE*. The influence of C_i upon WUE* is well recognised (Farquhar *et al.*, 1989) and carbon isotope discrimination is widely used as a surrogate measure of C_i in crop breeding programmes that aim to increase WUE* (Richards *et al.*, 2002). However, the influence of temperature on C_i and subsequent WUE* and RUE is not widely recognized. These temperature responses will need to be incorporated into simulation models which use RUE or WUE* within their mechanisms if they are to accurately predict DM production and water extraction in temperate climates.

Conclusions

1. The proportion of total DM lucerne partitioned to shoots decreased from 0.9 in September to ~0.65 from November – January then decreased abruptly to 0.4 in March.
2. Lucerne RUE_{tot} and WUE^*_{tot} showed liner increases from 0 at 0 °C to a maximum at 17 °C.

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