

Soil water extraction patterns of lucerne grown on stony soils

Richard E. Sim · Hamish E. Brown · Edmar I. Teixeira · Derrick J. Moot

Received: 22 July 2016 / Accepted: 15 November 2016 / Published online: 24 November 2016
© Springer International Publishing Switzerland 2016

Abstract

Background and aims Lucerne (*Medicago sativa* L.) is often grown under water-limited production conditions due to its capacity to extract water from deep soil layers through an extensive taproot system. These soils often contain stones which cause the roots to become unevenly distributed due to displacement by rock fragments. To improve the estimation of water use by lucerne grown in stony soils, we investigated the temporal pattern of water supply and demand, and how this influences crop growth.

Methods Naturally occurring stones in the silt loam soil profile were used to reduce the plant available water capacity for three lucerne crops. The Monteith model was fitted against observed soil water to obtain estimates of the extraction rate constant (kl , day^{-1}) and extraction front velocity (EFV, mm day^{-1}) of lucerne roots. Crop water demand was represented by transpiration losses driven by intercepted solar radiation based on the “canopy conductance” approach.

Results The Monteith model described the pattern of water extraction for lucerne grown on stony soils. However, a single, constant kl and EFV were

inappropriate for characterising water extraction. The main physiological responses to water stress were (i) a reduction in canopy conductance, (ii) a reduction in canopy expansion and (iii) the rearrangement of leaves into a more vertical position.

Conclusion This study validated frameworks to quantify lucerne water extraction and transpiration demand which can be used to improve the estimation of water use by lucerne crops.

Keywords Alfalfa · Canopy conductance · Evaporation · Rainfed · Stones

Introduction

Lucerne (*Medicago sativa* L.) is a high yielding perennial forage crop used worldwide across a wide latitudinal range (Michaud et al. 1988). The crop is often grown under water-limited production conditions due to its capacity to extract water from deep soil layers through an extensive taproot system (Brown et al. 2005; Sheaffer et al. 1988). The ability to estimate lucerne yield and water use under these conditions is important to further support current efforts to enhance methods for assessing regional and global agricultural productivity and environmental impacts (Rosenzweig et al. 2013; Rötter et al. 2011; Verburg et al. 2007). In particular, the accurate estimation of time and intensity of drought stress is an important determinant of lucerne yield under rainfed environments (Robertson et al. 2002; Sheaffer et al. 1988). These depend on the dynamics of water supply

Responsible Editor: Rafael S. Oliveira.

R. E. Sim (✉) · D. J. Moot
Faculty of Agriculture and Life Science, Lincoln University,
PO Box 7647, Canterbury, New Zealand
e-mail: richard.sim@lincolnuni.ac.nz

H. E. Brown · E. I. Teixeira
The New Zealand Institute for Plant & Food Research Limited,
Private Bag, Christchurch 4704, New Zealand

from the soil (Brown et al. 2009) and demand (Brown et al. 2012) during the period of crop growth.

Monteith (1986) developed an approach to quantify crop water supply as an exponential function of plant available water in different soil layers (Passioura 1983). The Monteith model has been used widely to describe water extraction of annual crops grown on deep silt loam soils that have high plant available water capacity (PAWC) (Dardanelli et al. 1997; Meinke et al. 1993; Robertson et al. 1993a; Singh et al. 1998). Also, for conditions of deep soils, with high PAWC, Monteith's model has been used to estimate water supply for lucerne crops (Brown 2004; Dardanelli et al. 1997). However, often lucerne is grown on shallow, stony soils with low PAWC (Moot et al. 2008; Sim et al. 2015). This is the case for the Canterbury plains of New Zealand, in which lucerne is grown in soils with thin topsoil layers (usually less than 0.3 m of silt loam) on top of gravel layers with more than 50% of the soil volume occupied by rock fragments larger than 2 mm (Di and Cameron 2002). These limiting physical characteristics of stony soils contrast with the uniform distribution of roots assumed in the Monteith's model of water supply (Passioura 1983). In stony soils, primary roots show a preferred downward growth pattern amongst stones, while secondary root proliferation is physically inhibited (Clark et al. 2003; Passioura 1988). This causes roots to become densely 'clumped' in macropores and the rate of soil water extraction declines in response to non-uniform root distribution (Dardanelli et al. 2004). It is unclear if lucerne crops show a similar adaptive response when grown in shallow stony soils and how this influences patterns of water uptake and crop growth.

Crop water demand is the water extracted for transpiration when supply is non-limiting. Potential transpiration demand is commonly calculated using the Penman-Monteith equation from weather variables (Monteith 1965) and adjusted to account for the effect of the crop canopy (French and Legg 1979). The canopy intercepts incoming solar radiation which supplies the radiative energy to drive evaporation, which is also controlled by the vapour pressure deficit (VPD) between the evaporating surface and atmosphere (Penman 1948). For lucerne, a strong positive linear relationship between transpiration and intercepted radiation and VPD indicated that the rate of transpiration per unit of intercepted radiation, or canopy conductance ($\text{mm MJ}^{-1} \text{m}^{-2}$) was conservative for well watered

lucerne crops (Brown et al. 2012). As a consequence, transpiration demand of lucerne grown in a temperate climate was accurately predicted. To further develop this approach to estimate transpiration demand the effect of soil water supply of these stony soils on canopy conductance needs to be determined.

The aim of this study was to determine the temporal pattern of water supply and demand for lucerne crops grown on stony soils, with low PAWC. For that, we first calculated the water supply of both seedling and established (regrowth) lucerne stands from measured soil water using a soil water balance. Then, for these different stages of crop development, the Monteith model was fitted against observed soil water to obtain estimates of the extraction rate constant (kl , day^{-1}) and extraction front velocity (EFV, mm day^{-1}) of lucerne roots (Monteith 1986; Passioura 1983). Then, for regrowth lucerne, crop water demand was represented by transpiration losses driven by intercepted solar radiation based on the "canopy conductance" approach (Brown et al. 2012). Physiological processes influencing solar radiation interception by the canopy, such as leaf area index expansion (Teixeira et al. 2007c) and leaf orientation (Pearce et al. 1967), were quantified to explain changes in plant transpiration and soil evaporation in response to drought stress. Results of this study are expected to support the definition of best agronomic management practices and the improvement of water extraction models for lucerne crops grown under low PAWC conditions.

Materials and methods

Experimental sites and design

Three experiments were conducted using rainfed lucerne (cultivar; Stamina 5, fall dormancy 5), at Lincoln University, Canterbury, New Zealand ($43^{\circ}38'S$, $172^{\circ}28'E$). Measurements were taken from July 2011 to June 2012 on two seedling and three established regrowth crops which were grown under consistent environmental conditions, but on soils which differed in naturally occurring stone content. The three soils are referred to as; (i) stone free, (ii) stony and (iii) very stony and are characterised by their plant available water capacity (PAWC) which is directly influenced by stone content of the soil profile.

The first experimental site was at the Lincoln University main campus, located in paddock 12 of Iversen Fields. The soil is classified as a Wakanui silt loam (*Udic Ustochrept*, USDA Soil Taxonomy) (Cox 1978) which has 1.8–3.5 m of fine textured silt loam overlying gravels (Webb 2003). As a consequence, these soils have 360 mm of plant extractable water to a depth of 2.3 m (Brown et al. 2005; Sim et al. 2015) and are referred to as “stone free”. The second and third experiments were conducted at Ashley Dene Research Farm in paddocks H7 and M2. The soil is classified as a Lismore stony silt loam (*Udic Haplustept* loamy skeletal, USDA Soil Taxonomy) (Cox 1978). These soils have a shallow topsoil containing ~10% stones, by volume, overlaying horizons of sandy loams with a stone content up to 45% (Di and Cameron 2002). The two soils differed in the depth of topsoil and B horizon which lays between the topsoil and alluvial gravels. The B horizon has a lower stone content (20–30%) and higher silt and clay content compared to the deeper gravel layers which can contain up to 30% sand. At the H7 site the topsoil was ~0.35 m and the sandy gravel horizons occurred at ~1 m. As a consequence, the H7 soils have 240 mm of PAWC to a depth of 2.3 m and are referred to as “stony”. In contrast, the M2 site had a shallower topsoil (<0.2 m) and depth to gravels of ~0.5 m (McLenaghan and Webb 2012; Webb 2003). As a consequence, the M2 soils have 130 mm of plant extractable water to 2.3 m (Moot et al. 2008; Sim et al. 2015) and are referred to as “very stony”.

At the stone free and very stony sites lucerne was established as a split-plot within a randomised complete block design, replicated four times as described by Sim et al. (2015). Data from two sub plots (4.2 × 7 m) from each experiment are presented in the current study which consisted of seed sown on two dates (i) 4 October 2010 and (ii) 10 October 2011. This allowed the comparison of established and seedling crops within the same year.

At the stony site in November 2008 lucerne was established in a rotational grazing system, based on six 0.46 ha (48 × 89 m) paddocks as described by Moot et al. (2016). The grazing treatments were first implemented in year two, from 2 October 2010. This involved stock grazing each paddock for ~7 days, creating a 35 to 42 day rotation before the regrowth in the same paddock was regrazed. The current research occurred in the crops third year, and included only data from sub plots (6.3 × 24.5 m) sown to ‘Stamina 5’ in paddock 1, to allow direct comparison with the other experiments. Sub

plots were sown in a randomised complete block design, which was replicated four times.

Prior to sowing, all experimental areas were conventionally cultivated (plough, maxi-til, harrow and roll) and lime coated lucerne seed was sown at 10.5 kg/ha (bare seed equivalent) using an Øyjord cone seeder. This coated seed contains rhizobia (*Sinorhizobium meliloti*) and fungicide, which protects against *Pythium* spp. with additional molybdenum and lime. Seedling crops established 212 ± 32 plants m^{-2} within one month after sowing and populations of regrowth crops at the start of the measurement period (June 2011) were 198 ± 63 , 160 ± 16 and 262 ± 93 plants m^{-2} at the stone free, stony and very stone site, respectively (Sim 2014). Plant density would not have been expected to impact on productivity among crops, which were above the critical threshold of ~50 plants m^{-2} where yield and water extraction are negatively affected (Dolling et al. 2011; Teixeira et al. 2007a).

Meteorological conditions

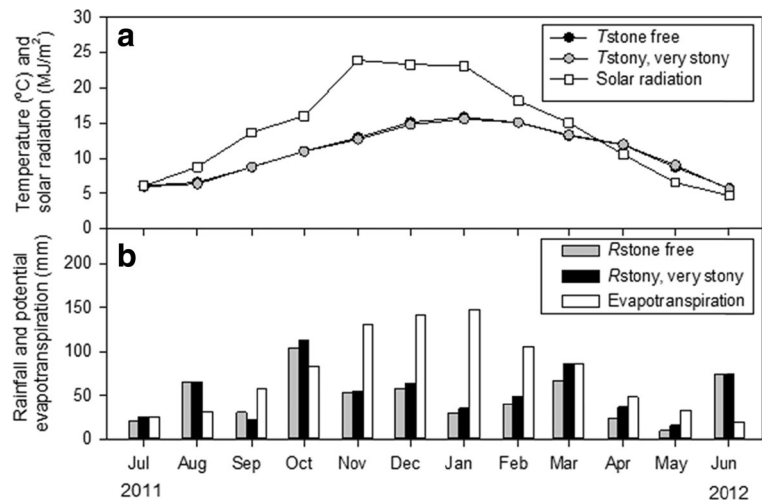
Meteorological data (solar radiation, Penman potential evapotranspiration and vapour pressure deficit) were measured at Broadfields Meteorological Station (NIWA, National Institute of Water and Atmosphere Research, New Zealand) which is located 2 km north of the Lincoln University main campus. Rainfall and air temperature were also recorded at the individual experimental sites. Mean monthly temperature was consistent between locations and ranged from 6°C in July to 17°C in January (Fig. 1a). Mean monthly total solar radiation ranged from 4 to 22 MJ $m^{-2} day^{-1}$ over the same period. Total rainfall (1 July 2011 to 30 June 2012) experienced by the lucerne crops was 580 mm at the stone free site and 645 mm at both stony sites which was accumulated in 52 rain days (>1 mm). Total Penman potential evaporation (P_{ET}) (French and Legg 1979) was 910 mm, and exceeded rainfall from about September to May. Long term mean annual rainfall for Lincoln is 630 mm and annual mean P_{ET} is 1095 mm.

Agronomic management

Crop management

Chemical analysis of the topsoil (0–150 mm) prior to the start of the measurement period showed that pH was adequate (5.8 to 6.5) and available P and K where

Fig. 1 Mean monthly (a) air temperature (T) and daily solar radiation and total monthly (b) rainfall (R) and Penman potential evapotranspiration experienced by rainfed lucerne crops grown in Iversen Fields paddock 12 (stone free) and Ashley Dene paddock H7 (stony) and M2 (very stony) at Lincoln University, Canterbury, New Zealand



moderately high (Olsen P 16 to 19 mg/kg; available K 160 to 190 mg/kg). However, to ensure soil fertility did not limit growth, the stone free and very stony sites received 300 kg/ha potassic super sulphur (8% P; 5% K; 10% S) and the stony site received 2.8 t/ha lime and 500 kg/ha sulphur super (8% P; 15% S) in September 2011. Plots were kept weed free as required by chemical control and hand weeding.

Defoliation

Seedling lucerne crops, defined as the growth phase from sowing to first defoliation, were cut when 50% of 10 marked stems per plot had an open flower. Subsequent regrowth phases were defoliated when 50% of marked stems had a visible flower bud. The exceptions were the first spring defoliation which occurred when crop height reached 0.35 to 0.40 m to prevent lodging and one regrowth cycle during late summer, when defoliation was delayed to allow 50% of marked stems to have an open flower. A final defoliation occurred once growth stopped in May/June. This management resulted in crops in the first year being defoliated 3 to 4 times and 5 to 7 times in the second year at the stone free and very stony sites. Defoliations were undertaken mechanically using a lawn mower to a height of ~50 mm. The exception was for the established crop at the very stony site, which was grazed with approximately 100 ± 20 ewes for a duration of 4 to 8 days.

The grazing system was first imposed at the stony site on 27 September 2011. Ewes with twin lambs were

rotated around paddocks 1 to 6 twice, and then a further four times with weaned lambs. Stocking rate was 12 ewes/ha (over all six paddocks) and grazing duration was 5 to 7 days per paddock. Plots were destocked from 7 February to 29 March 2012 to allow seven weeks of regrowth to recharge perennial reserves as recommended for commercial farm practice (Moot et al. 2003).

Measurements

Shoot biomass

Shoot biomass was measured at 7 to 14 day intervals using a single 0.2 m quadrat, cut just above crown height (~50 mm) using hand shears. Measurements were taken systematically each season to avoid re-cutting previously sampled areas. Areas within 1 m of the neutron probe access tubes were also avoided. All samples were dried in a forced air oven (60°C) to a constant weight.

Leaf area index

Leaf area index (LAI; m² leaf m⁻² soil) was calculated from destructive green area index (GAI) measurements from a sub-sample of 20 shoots taken from the quadrat used to measure shoot biomass. To measure GAI, shoots were laid flat with leaves spread apart and passed through a belt area meter (LICOR 3100, Licor Inc. Lincoln, USA). Shoot samples were dried in a forced air oven (60°C) to a constant weight and GAI was calculated using specific leaf weight (SLW; g DM m²

GAI). GAI was converted to LAI by a calibration process where samples of 20 shoots were passed through the leaf meter, then the leaves were removed from each stem and both were separately passed back through the area meter. This showed GAI systemically underestimated LAI, mainly due to leaves overlapping around the apex of the shoot and GAI values were multiplied by a factor of 1.30 to convert to LAI. The calibration process was repeated on five occasions throughout the season which showed the correction factor was consistent for lucerne crops and across the experimental sites ($n = 91$, $a = 0$, $b = 1.30$, $R^2 = 0.99$).

Soil water content

Volumetric soil water content was measured in 22 layers of the soil profile to a depth of 2.3 m at 10 to 14 d intervals. The top layer (0–0.2 m) was measured with a time domain reflectometer (TDR; Trace system, Soil Moisture Equipment, Santa Barbara, California, USA) with 0.2 m long stainless steel rods. The remaining 21 layers were measured at their mid-point using a neutron probe (Troxler Electronic Industries Inc., Research Triangle Park, North Carolina, USA). Neutron probe access tubes were installed to a depth of 2.3 m in the centre of each plot. Conventional auger installation was not possible at Ashley Dene due to the stony soil profiles. Thus, access holes were created by driving a 50 mm steel spike into the soil with a vibrating plate attachment on a 20 t excavator. Aluminium tubes were then installed. To maintain consistency this method was used at all experimental sites. Previous experience in a similar soil type using this installation method showed no effect on actual soil moisture (Mills 2007) most likely because the highly compacted gravel layers meant minimal displacement of silt and sand particles away from the access tubes. Access tubes were installed ~5 days following sowing, to allow mechanical sowing of the entire plot, but prevent damage to seedling lucerne.

Calculations

Soil water balance calculations

Total evapotranspiration (ET) between each measurement period was calculated from the soil water balance (Eq. 1) which accounted for rainfall (R), the change in measured soil water content to 2.3 m depth (ΔSWC) and

drainage (D). The soils in the present study are free draining (Webb 2003) and Eq. 1 assumes no water runoff which is consistent with field observations. ET was extrapolated to daily values (ET_d), in relation to Penman evaporation transpiration (P_{ET}) for the same period, and daily P_{ET} ($\text{P}_{\text{ET}d}$) (Eq. 2). ET_d was close to zero when an extended dry period followed canopy defoliation. This limited water loss to both transpiration and soil evaporation. ET_d reached a maximum of 8.2 mm day^{-1} for the crop grown on the stone free soil in mid summer.

$$\text{ET} = \text{R} - \Delta\text{SWC} - \text{D} \quad (1)$$

$$\text{ET}_d = (\text{ET}/\text{P}_{\text{ET}}) * \text{P}_{\text{ET}d} \quad (2)$$

Drainage was calculated as daily rainfall in excess of the drained upper limit (DUL) to 2.3 m depth from the calculated daily soil water content. DUL was defined as the maximum stable soil water content which was measured during winter when plant growth was negligible. SWC measurements were taken about five days after complete soil recharge, to allow for drainage. Complete recharge occurred in all soils when rainfall exceeded ET and was also recorded for bare soil at the stone free and very stony sites which were chemically fallowed for the first season, and received ~600 mm of rainfall with no plant water extraction.

Evapotranspiration was partitioned into soil evaporation (E_s) and transpiration (T) using the two phase approach (Ritchie 1972) described by Jamieson et al. (1995) for a *Udic Ustochrept* soil in the same environment. Briefly, E_s is assumed to be energy limited during the first phase and 9 mm was evaporated. From then, the soil surface is sufficiently dry to restrict water loss and E_s is diffusion limited. The soil diffusion constant was $4.4 \text{ mm day}^{-1/2}$. Potential E_s is set by P_{ET} , and reduced proportional to ground cover (French and Legg 1979) which was calculated daily from interpolated LAI measurements. It was assumed E_s only occurred in the top 0.2 m of soil, and to avoid overestimation, the Ritchie calculation was modified to account for additional soil drying by crop roots (Brown et al. 2004). To do this, a water balance for the 0.2 m soil layer was run parallel to the E_s calculation, which assumes water was preferentially extracted from the uppermost layer first (Brown et al. 2009; Sheaffer et al. 1988). E_s occurred when the SWC content of the top layer was greater than the lower

limit for evaporation. The lower limit for evaporation was the minimum volumetric soil water content measured in the top layer of bare soil plots adjacent to the experiments and was 15 and 25% for the stone free and very stony soil types, respectively (Sim 2014). To partition ET calculated during grazing, it was assumed LAI decreased exponentially to zero halfway through the grazing period based on observations of preferential grazing of leaf material by stock. ET calculated during grazing was included in the subsequent regrowth phase.

The established lucerne crops most likely extracted water below the depth of maximum SWC measurement because the extraction front arrived at the 2.3 m soil layer before the maximum soil water deficit was attained. The additional water extracted by the crops was estimated by assuming the relationship between transpiration and radiation interception (T/R_i) was constant within individual regrowth cycles. This was consistent with cycles when the extraction front was <2.3 m, and has also been demonstrated for other lucerne crops (Brown et al. 2012). Thus, for regrowth phases where the extraction front was ≥ 2.3 , water was added to actual SWC measurements until T/R_i displayed a linear relationship. This resulted in 63 ± 21 mm extra water in regrowth cycles 5 and 6 at the stone free site and 21 ± 8 mm at the stony site in cycles 4 and 5 and in cycle 3 at the very stony site.

The model for water extraction

The Monteith model (Monteith 1986) was used to describe the measured soil water and indicated the pattern of crop water extraction. In a certain layer, soil water content (θ) is constant (Eq. 3), until the arrival of the extraction front which is identified by an exponential decrease in θ (Passioura 1983) (Eq. 4).

$$\theta = \theta_u \quad t \leq t_c \quad (3)$$

$$\theta = \theta_1 + ((\theta_u - \theta_1) * \exp(-kl*(t - t_c))) \quad t > t_c \quad (4)$$

where θ ($\text{mm}^3 \text{mm}^{-3}$) equals the initial soil water content (θ_u) until θ decreases exponentially at t_c . θ_1 is the lower limit of extractable water, $\theta_u - \theta_1$ is the extractable water content and $t - t_c$ is the duration (days) of the exponential decay. kl is the extraction rate constant, which aggregates root length density (l ; cm root cm^{-3} soil) and the diffusion coefficient (k ; $\text{cm}^2 \text{day}^{-1}$)

(Passioura 1983), neither of which were measured in the current study.

For seedling crops, the function was fitted from sowing (10 October 2011) to maximum SWD which occurred on 28 May 2012. For established crops, water extraction was observed to start in early September 2011, however a 60 mm rainfall event returned θ to DUL on 21 October 2011. Therefore, measurements prior to this were excluded, and θ was analysed from this point to maximum SWD which occurred on 14 February, 22 February and 28 May 2012 at the very stony, stony and stone free sites, respectively. The function was not fitted to the 0–0.2 m layer because of water loss due to soil evaporation. The extraction front velocity (EFV; mm day^{-1}) was determined by the slope of the linear regression of t_c as a function of depth. The lag phase for the descent of the drying front, i.e. x -intercept, was not observed in established crops because the initial period of water extraction in early spring was excluded due to the October 2011 rainfall event.

Quantifying water stress

Water stress (T/T_D) was quantified as the ratio between water supply and demand (Jones et al. 2003; Robertson et al. 2002). Water supply was crop transpiration (T), calculated from the soil water balance. Crop transpiration demand (T_D) was the amount of water required to maintain transpiration rates of a fully irrigated crop in the same environment. On a daily time step, T_D was calculated using the canopy conductance approach (Brown et al. 2012), which predicts transpiration from the product of daytime averaged vapour pressure deficit (VPD, kPa), intercepted radiation (R_i ; MJ m^{-2}) and a canopy conductance coefficient (Θ_T) (Eq. 5).

$$T_D = \text{VPD} * R_i * \Theta_T$$

where daytime averaged vapour pressure was calculated from hourly wet and dry bulb temperatures using the methodology presented by Wang et al. (2004) and hours of daylight were calculated by time of year and latitude (Goodspeed 1975). Daily VPD ranged from 0.09 to 1.18 kPa. A Θ_T of $0.45 \text{ mm MJ}^{-1} \text{ kPa}^{-1}$ was shown by Brown et al. (2012) to accurately predict transpiration ($\pm 0.05 \text{ mm day}^{-1}$) for lucerne crops grown in Canterbury, New Zealand and was therefore used in this current study. Mean T/T_D was calculated for each

regrowth phase and then compared in relation to the rate of canopy expansion to determine the effect of water stress on intercepted radiation.

Thermal time

Thermal time (T_t , °Cd) was calculated following the method of Jones and Kiniry (1986) from daily mean air temperature using a broken-stick threshold model, where T_t is assumed zero below the base temperature (T_b) of 1.0°C. T_t is accumulated linearly at a rate of 0.7 °Cd °C⁻¹ up to 15°C and then at a rate of 1.0 until 30°C (Moot et al. 2001; Teixeira et al. 2011). This method calculates T_t at three hourly intervals which are integrated over a day.

Extinction coefficient and light interception

The extinction coefficient (k) was used to represent the canopy architecture and determine the fraction of radiation intercepted by each unit of LAI among the crops. The value of k was determined from the negative slope of the regression between the natural log of fractional radiation interception and LAI (Monsi and Saeki 2005), measured independently. Fractional radiation interception by the canopy was measured directly, on 40 occasions using a Sunscan plant canopy analyser system (Delta-T Devices Ltd., Burwell, Cambridge, England). For this, incident and transmitted radiation measurements were made during stable light conditions. Eight below and above canopy readings were taken per plot, perpendicular to drill rows. Measurements were regressed against destructive LAI measurements taken at the same time.

The fractional solar radiation intercepted by the canopy (R/R_o) was calculated as a function of LAI and canopy architecture (k) using the Beer-Lambert law (Eq. 6) which describes the exponential reduction of light through the canopy (Sinclair 2006).

$$R/R_o = 1 - \exp(-k \cdot \text{LAI}) \quad (6)$$

Daily intercepted radiation (MJ m⁻²) was calculated from interpolated LAI from fitted logistic curves that described ($R^2 > 0.70$) the sigmoidal shape of leaf area expansion over time for each growth cycle.

Leaf area expansion rate

The mean leaf area expansion rate (LAER; m² leaf m⁻² soil °Cd⁻¹) was calculated for individual growth cycles as the linear slope between LAI and thermal time accumulation. To ensure the linear phase of leaf area expansion was analysed, data points between 5% and 95% of maximum LAI were used (Teixeira et al. 2011).

Analysis of results

The model of water extraction was accepted as having accurately predicted θ when $R^2 > 0.75$. When models failed, often due to lack of data points during extraction on the stony soil, but a systematic change in θ was observed, consistent with the descent of the drying front, both the θ_u and θ_l were fixed and θ reanalysed. kl differences were compared over depth with a split-split plot ANOVA. Because there was no apparent pattern in kl over depth, kl was averaged to the depth of maximum extraction and compared using a split-plot analysis of variance (ANOVA). To summarise results, mean kl was presented for seven 0.3 m soil layers. ANOVA was performed using general linear models, when differences occurred, indicated with a P -value ≤ 0.05 , means were separated by Fishers least significant difference (lsd) at the 5% level. The extraction model, linear regressions and ANOVA were calculated using GENSTAT (version 14.1) (Lawes Agricultural Trust, IACR, Rothamsted, U.K.).

Results

Shoot yield

Total annual shoot yield for the seedling crop, sown on 10 October 2011 on the stone free soil was 12.1 ± 1.2 t DM ha⁻¹, compared with ($P < 0.001$) 3.1 ± 0.2 t DM ha⁻¹ on the very stony soil (Fig. 2). The yield from established lucerne was up to 21.5 ± 1.5 t DM ha⁻¹ in the same year, when grown on the stone free soil, compared with ($P < 0.001$) 12.3 ± 0.2 t DM ha⁻¹ for the crop at the stony site and 6.7 ± 0.7 t DM ha⁻¹ at the very stony site. Shoot yield at the end of growth cycles ranged from 0.3 to 4.5 t DM ha⁻¹ throughout the season. For established lucerne, the contribution of spring regrowth cycles, (July to December) to total shoot yield was 40% at the stone free site and 60% at the very stony site.

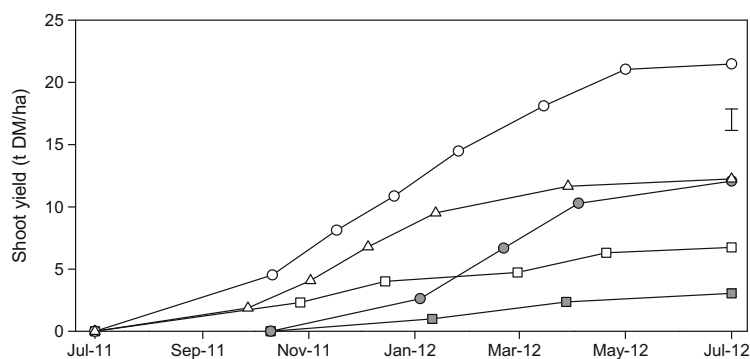


Fig. 2 Accumulated shoot yield (t DM/ha) from 1 July 2011 to 30 June 2012 for seedling, sown 10 October 2011 (closed symbols) and established (open symbols) crops of ‘Stamina 5’ rainfed

lucerne grown on three sites; stone free (○) stony (△) and very stony (□) at Lincoln University, Canterbury, New Zealand. Note: error bar represent standard error of the mean at final harvest

Soil water extraction and use

Soil water deficit

The initial soil water deficit (SWD) was <15 mm at sowing, and did not exceed 50 mm until ~50 days after sowing (Fig. 3a). As a consequence of 180 mm of rainfall during this period, 66 mm of drainage below 2.3 m depth was estimated from the soil water balance at both sites (Table 1). Soil water extraction exceeded rainfall until the maximum SWD was reached on 28 May 2012 for both first year crops. This showed the maximum extractable water for first year lucerne was 232 ± 11.4 mm for the crop on the stone free soil, which was greater ($P < 0.001$) than the crop on the very stony soil which extracted 99 ± 5.0 mm.

For established crops, the initial SWD on 1 July 2011 at both stony sites was <10 mm and the SWD did not exceed 65 mm until late October (Figure 3 b). As a consequence of 150 mm of rainfall during this period, these crops experienced 31 mm of drainage (Table 1). In contrast, the initial SWD was 180 mm at the stone free site, (Fig. 3b), and no drainage was estimated. For established crops, SWD steadily declined from late October until the maximum deficit was reached first at the very stony site on 14 February, then 22 February for the stony site and 28 May 2012 at the stone free site. This showed the maximum extractable water was ($P < 0.05$) 130 ± 13.4 mm, 237 ± 37.9 mm and 355 ± 38.6 mm for crops grown on the very stony, stony and stone free soil, respectively. Therefore, the difference in soil stoniness created a three-fold range in the soil water available for extraction by these rainfed lucerne crops grown in the same climate.

Transpiration, soil evaporation and drainage

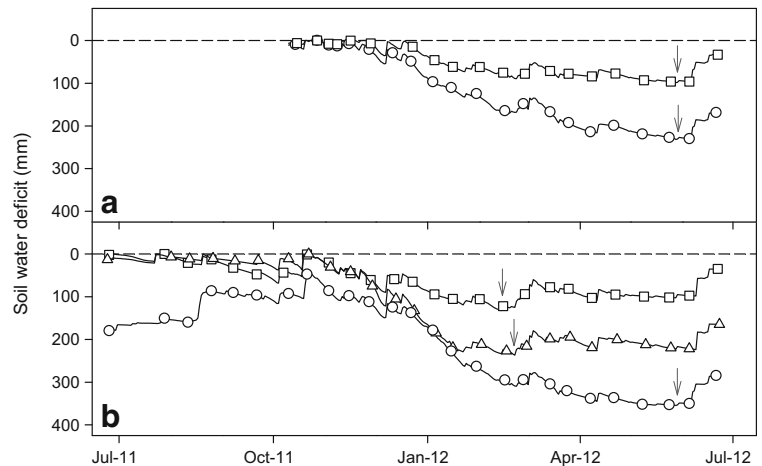
Transpiration (T) was highest ($P < 0.001$) for the established crop grown on the stone free soil at 621 mm (Table 1). This, accounted for 81% of the total water balance for that soil. In contrast, the crop grown on the very stony soil transpired 50% less, or 316 mm, which represented 53% of total water for that soil. Soil evaporation (E_s) was highest ($P < 0.05$) for both stony soils with a mean of 251 mm. However, because the crop on the stony soil transpired an extra 130 mm, E_s represented 34% of the total water balance, compared with 42% for the crop on the very stony soil.

Transpiration for seedling crops, was highest ($P < 0.05$) for the crop grown on the stone free soil at 415 mm, compared with the crop on the very stony soil at 150 mm. As a consequence of the water balance starting at sowing for first year crops, mean E_s was 140 mm compared with 200 mm for the established crops because the period from July–September was excluded. This was when bare ground was exposed for the longest duration in established crops. However, E_s represented a larger percentage of the total water balance for seedling crops, with up to 46% of water partitioned to E_s in the very stony soil.

Water extraction rate (kl)

The temporal pattern of SWC in individual layers agreed with the Monteith model which gave an accurate description (R^2 of 0.65 to 0.99) of the exponential decline in SWC when the extraction front arrived at an individual layer (Sim 2014).

Fig. 3 Soil water deficit to 2.3 m from 1 July 2011 to 30 June 2012 for (a) seedling (b) and established ‘Stamina 5’ rainfed lucerne grown on three sites; stone free (○), stony (△) and very stony (□) at Lincoln University, Canterbury, New Zealand. Note dashed line is the drained upper limit. Arrows mark time of maximum soil water deficit



There was no systematic pattern in kl over depth, so it was averaged over the depth of extraction for each crop (Table 2). There was an interaction between site and growth stage ($P < 0.01$) for kl . For established lucerne, kl was highest for the crop grown on the very stony soil with a mean of 0.049 day^{-1} , twice that of the crop on the stone free soil with a value of 0.025 day^{-1} . However, site did not affect the kl for seedling crops, which was conservative at 0.036 day^{-1} .

Table 1 Transpiration (T ; mm), soil evaporation (E_s ; mm) and drainage (mm) calculated from the soil water balance for seedling (10 October 2011 to 30 June 2012) and established (1 July 2011 to 30 June 2012) ‘Stamina 5’ rainfed lucerne crops grown on three sites at Lincoln University, Canterbury, New Zealand

Site and growth stage	T	E_s	Drainage
Seedling			
Stone free	415 _a	96 _b	62 _a
Very stony	150 _b	185 _a	69 _a
SEM	9.7	27.3	8.4
Probability	$P < 0.05$	$P < 0.05$	<i>ns</i>
Established			
Stone free	621 _a	148 _b	0 _b
Stony	446 _b	249 _a	29 _a
Very stony	316 _c	252 _a	32 _a
SEM	21.0	20.5	4.4
Probability	$P < 0.001$	$P < 0.05$	$P < 0.001$

SEM is the standard error of the mean, *ns* = not significant. Means within a column with different letters are significantly different ($\alpha = 0.05$) according to Fishers lsd test

Extraction front velocity (EFV)

For seedling crops, the soil drying cycle started 30 days after sowing. The extraction front descended the soil profile linearly at $\sim 14 \text{ mm day}^{-1}$ to the maximum depth of extraction of 1.5 m in late February, 145 days after sowing. The relationship was strongest for the crop grown on the stone free soil (Fig. 4a) compared with the seedling crop on the very stony soil ($R^2 = 0.68$). The EFV was 0.5 mm day^{-1} from sowing to early December (Fig. 4c). This was followed by a rapid descent of the extraction front at $\sim 40 \text{ mm day}^{-1}$ from 0.5 to 1.0 m of depth.

For established crops, the drying cycle began on 24 October 2011 following rain events which returned the soil profile to DUL at both stony sites and a minimum deficit of 47 mm at the stone free site. The EFV was $14.2 (\pm 1.06) \text{ mm day}^{-1}$ for the crop grown on the stone free soil (Fig. 4a), or less than half that ($P < 0.001$) of the crops grown on both stony soils where EFV was $33.0 (\pm 1.41) \text{ mm day}^{-1}$ (Fig. 4b, c). As a consequence, water extraction reached the maximum depth of measurement (2.3 m) on 24 December 2011 for both crops grown on the stony soils, 80 days earlier ($P < 0.001$) than the crop on the stone free soil which occurred on 11 March 2012.

Determining the effect of water stress on crop canopy expansion

In an attempt to explain the influence of water supply on plant transpiration and soil evaporation, crop water stress was quantified and related to canopy expansion. To do this, water stress was quantified by the ratio between transpiration calculated from the soil water

Table 2 Values of the extraction rate constant (kl , day^{-1}) of seven soil layers for seedling and established 'Stamina 5' rainfed lucerne crops grown on three sites at Lincoln University, Canterbury, New Zealand

Depth (m)	Seedling		Established		
	Stone free	Very stony	Stone free	Stony	Very stony
0.2–0.5	0.039	0.018	0.019	0.023	0.044
0.5–0.8	0.043	0.041	0.026	0.033	0.051
0.8–1.1	0.040	0.027	0.031	0.040	0.062
1.1–1.4	0.030	0.047	0.025	0.038	0.065
1.4–1.7			0.035	0.034	0.046
1.7–2.0			0.021	0.044	0.054
2.0–2.3			0.019	0.035	0.022
Mean	0.038 _b	0.033 _{bc}	0.025 _c	0.035 _b	0.049 _a
SEM	0.011	0.008	0.006	0.005	0.010
Probability					
Site	<i>ns</i>				
Growth stage	<i>ns</i>				
Interaction	$P < 0.01$				

SEM is the standard error of the mean. Means within a row with different letters are significantly different ($\alpha = 0.05$) according to Fishers lsd test, *ns* = not significant

balance and transpiration demand of a fully watered crop, which was determined from intercepted radiation and daytime averaged VPD using the canopy conductance approach. Only data from the established crops which included all three sites were included in the analyses.

Leaf area index and rate of expansion

Leaf area index (LAI) at the end of regrowth cycles ranged from 0.45 to 5.5 throughout the season (Fig. 5). The maximum leaf area expansion rate (LAER) was $0.018 \pm 0.001 \text{ LAI } ^\circ\text{Cd}^{-1}$ which was attained in the late

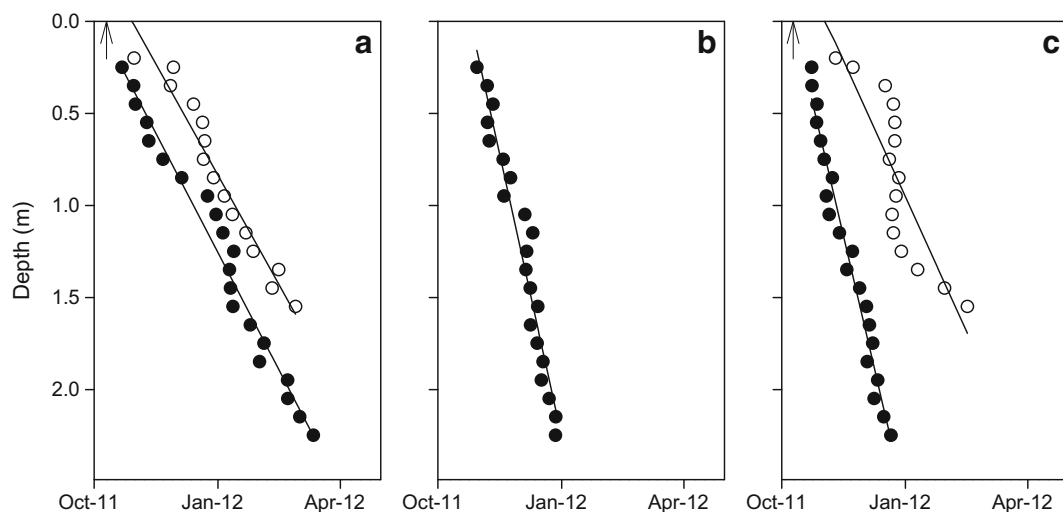
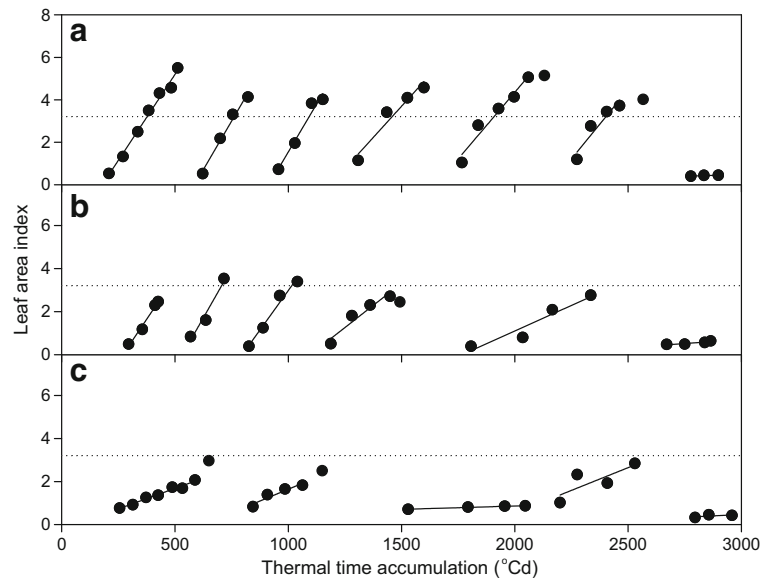


Fig. 4 Time of water extraction for each individual soil layer for seedling (○) and established (●) 'Stamina 5' rainfed lucerne crops grown on three sites; (a) stone free, (b) stony and (c) very stony in 2011/2012 at Lincoln University, Canterbury, New Zealand. Start dates were 10 and 21 October 2011 for first year and established

year crops, respectively. Extraction front velocities (\pm standard errors): a) ○ – 12.9 (± 1.02) mm/d, $R^2 = 0.95$, ● – 14.2 (± 1.06) mm/d, $R^2 = 0.97$. b) ● – 33.3 (± 1.62) mm/d, $R^2 = 0.93$. c) ○ – 15.1 (± 2.45) mm/d, $R^2 = 0.68$, ● – 32.6 (± 1.19) mm/d, $R^2 = 0.96$. Arrows mark the sowing date for first year crops

Fig. 5 Leaf area index against thermal time accumulation from 1 July 2011 to 30 June 2012 for established ‘Stamina 5’ rainfed lucerne crops grown on three sites; (a) stone free, (b) stony and (c) very stony at Lincoln University, Canterbury, New Zealand. Note: dotted line represents calculated critical leaf area index from Fig. 6



spring regrowth cycles (500–1000 °Cd) of the crops grown on the stone free and stony soils (Fig. 5a, b). In contrast, the early season LAER of the crop grown on the very stony soil was 0.005 LAI °Cd⁻¹ ($P < 0.001$), or 70% less (Fig. 5c). Generally, the LAER declined as the season progressed, with the exception of the crop on the very stony soil which had a LAER of 0.006 LAI °Cd⁻¹ in the fourth regrowth cycle, or a five-fold increase ($P < 0.001$) compared with the previous cycle. LAER was minimal (<0.001 LAI °Cd⁻¹) beyond ~2500 °Cd with the onset of frosts when minimum air temperature < 0°C.

Extinction coefficient

The pattern of increasing fractional light interception with LAI differed ($P < 0.001$) seasonally among crops (Fig. 6). The data could be separated into two groups which indicated the lucerne grown on the stone free soil and the spring (Sep–Nov) and autumn (Feb–Apr) regrowth cycles for crops on both stony soils achieved 95% light interception, or the critical leaf area index (LAI_{crit}), at an LAI of 3.2. As a result, the extinction coefficient (k) for these crops was 0.94 ± 0.014 . In contrast, the summer regrowth cycles for crops on both stony soils intercepted 88% of incoming radiation at an LAI of 3.2, and as a consequence k was 0.66 ± 0.013 . Therefore, a single k value was unsuitable to determine the fractional light interception from LAI data (Eq. 6),

which needed to be adjusted seasonally for crops grown at both stony sites.

Transpiration in relation to radiation interception

Total intercepted radiation (R_i) of 3160 MJ m⁻² for the crop grown on the stone free soil was 27% more ($P < 0.05$) than the crops grown on both stony soils at 2315 MJ m⁻². The relationship between accumulated T

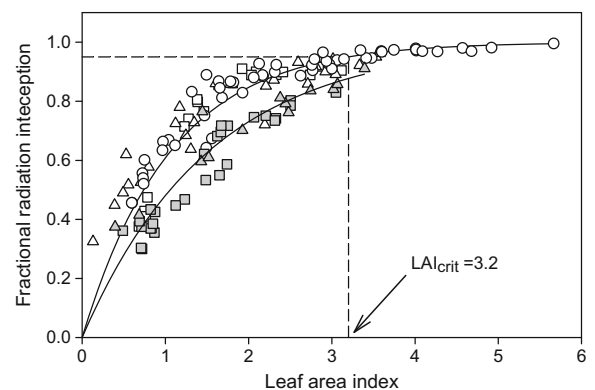


Fig. 6 The relationship between leaf area index and the fractional radiation interception of established ‘Stamina 5’ rainfed lucerne crops grown on three sites; stone free (○) stony (△) and very stony (□) in 2011/2012 at Lincoln University, Canterbury, New Zealand. Data were grouped and two regressions fitted ($P < 0.001$) to; (i) all data points from the crop grown on the stone free soil and spring (Sep–Nov) and autumn (Mar–May) regrowth cycle data points for crops on both stony soils (open symbols) and (ii) summer data points for crops grown on both stony soils (closed symbols)

and R_i was constant for all regrowth periods ($R^2 > 0.97$), with the exception of the final cycle when canopy expansion was affected by frost (Fig. 7). However, the slope of the regression (T/R_i) differed ($P < 0.001$) among regrowth cycles and ranged from 0.09 to 0.22 $\text{mm MJ}^{-1} \text{m}^{-2}$ (Fig. 8). For irrigated lucerne this variation may be closely related to daytime averaged VPD (Brown et al. 2012), which agrees with the T/R_i of non-water stressed growth cycles for the crops grown on the stone free and stony soil (Fig. 8). These crops also displayed close to maximum LAER (Fig. 5a, b), when SWD was less than 35% of the maximum in spring (Fig. 3b). The consistency shown among unstressed crops, albeit over a narrow VPD range (0.34 to 0.49 kPa) gave confidence in the determination of transpiration demand of the crops using the canopy conductance approach (Brown et al. 2012).

Quantifying water stress

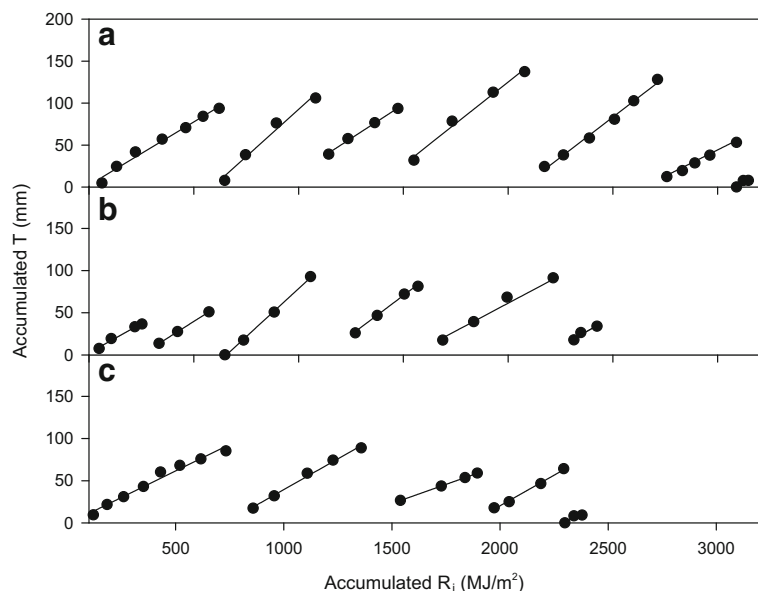
Total transpiration demand (T_D) was 690 mm for the crop grown on the stone free soil, compared with 560 mm for both crops on soils with stones. T_D was greater than T (Table 1) for all crops, which indicates T was limited by water supply and all crops experienced water stress. Water stress was quantified by the ratio between T and T_D (T/T_D) for individual growth cycles (Fig. 9). The T/T_D was 0.98 ± 0.10 for the unstressed growth cycles in spring for the crops grown on the stone

free and stony soils (Fig. 9a, b). For these crops, water stress increased with subsequent growth cycles and T/T_D decreased to ~ 0.65 for the autumn (April) regrowth cycle. In contrast, T/T_D was 0.70 for the first spring growth cycle for the crop on the very stony soil and decreased to 0.33 in the third regrowth cycle (Fig. 9c). T/T_D increased back to 0.63 for the autumn regrowth cycle, which was consistent with the other crops at the same time.

Water stress and LAER

Figure 10 shows the relationship between the rate of canopy expansion and water stress, which was derived from LAER (Fig. 5) and T/T_D (Fig. 9) for individual regrowth phases. The data can be analysed by regression which showed LAER declined with water stress, but the spread of data ($R^2 = 0.22$) suggests canopy expansion response had more than one cause. For example, when T/T_D was ~ 0.80 , LAER ranged from close to zero to 0.015 $\text{LAI } ^\circ\text{Cd}^{-1}$. Therefore, the asymptotic line drawn through the highest LAER at different levels of water stress is used to indicate maximum potential LAER. This showed potential LAER declined linearly from a maximum of 0.018 $\text{LAI } ^\circ\text{Cd}^{-1}$ when $T/T_D \geq 0.90$ to a LAER of zero when $T/T_D = 0.30$.

Fig. 7 Accumulated transpiration (T) in relation to accumulated intercepted radiation (R_i) for individual regrowth periods of established ‘Stamina 5’ rainfed lucerne crops grown on three sites; (a) stone free, (b) stony and (c) very stony from 1 July 2011 to 30 June 2012 at Lincoln University, Canterbury, New Zealand



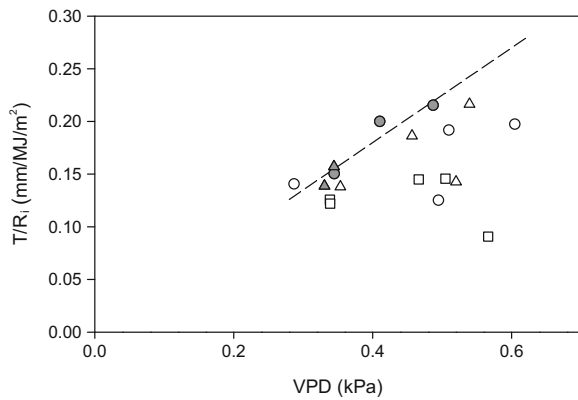


Fig. 8 Transpiration per unit of interception radiation (T/R_i) in relation to mean daytime vapour pressure deficit (VPD) for individual regrowth periods of established ‘Stamina 5’ rainfed lucerne crops grown on three sites; stone free (○) stony (△) and very stony (□) from 1 July 2011 to 30 June 2012 at Lincoln University, Canterbury, New Zealand. The closed symbols represent regrowth periods where leaf area expansion rate > 90% maximum. The dashed line is from Brown et al. (2012) ($T/R_i = 0.45 * VPD$) and represents the T/R_i for fully watered ‘Kaituna’ lucerne grown in the same location and with similar management as the crop grown on the stone free soil

Discussion

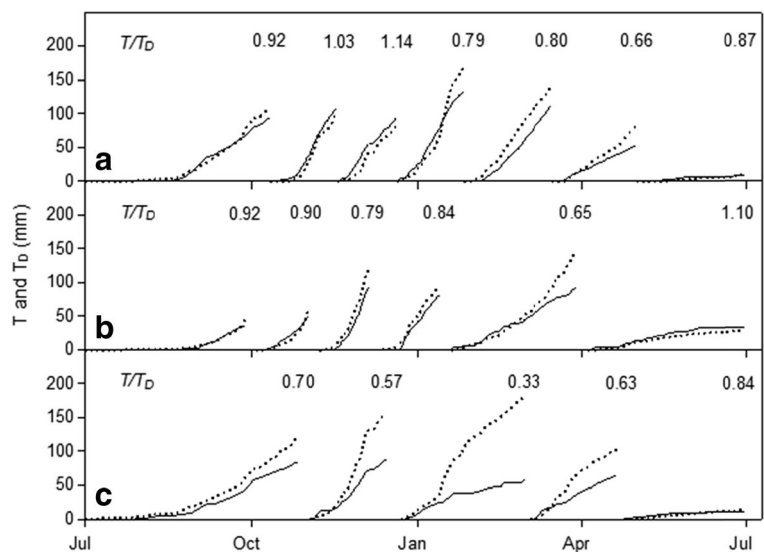
The temporal pattern of lucerne water extraction can be determined by the minimum of transpiration demand and water supply from the soil. Transpiration demand was calculated from the product of intercepted radiation, constant canopy conductance and daytime average VPD. To create supply limited crops, the volume of soil available to be exploited by the root system was

changed through the naturally occurring stone content in the soil profile. The main physiological responses of lucerne to water stress observed in this study were (i) a reduction in canopy conductance, (ii) a reduction in canopy expansion and (iii) the rearrangement of leaves into a more vertical position as demonstrated by a decline in the canopy extinction coefficient. These adaptive changes explained the reduced transpiration and radiation interception observed in water stressed lucerne crops.

Lucerne transpiration demand

The canopy conductance approach proposed by Brown et al. (2012) was appropriate for determining transpiration demand of lucerne crops grown on a range of soils. This was because transpiration was linearly related to intercepted radiation for all crops (Fig. 7) and the canopy conductance coefficient (Θ_T) of $0.45 \text{ mm MJ}^{-1} \text{ kPa}^{-1}$ presented by Brown et al. (2012) appeared to be stable and constant for lucerne grown in Canterbury, New Zealand. This was demonstrated by the agreement between the Θ_T of fully watered lucerne and spring regrowth phases (Fig. 8), which were considered to have adequate water supply due to canopy expansion rates consistent with fully watered lucerne in the same environment (Teixeira et al. 2011). The prediction of T_D meant, in the absence of a fully watered reference crop, the degree of water stress could be quantified as actual transpiration relative to transpiration demand (Fig. 9).

Fig. 9 Transpiration (T ; —) compared with transpiration demand (T_D ; ····) for individual regrowth periods of established ‘Stamina 5’ rainfed lucerne crops grown on three sites; (a) stone free, (b) stony and (c) very stony from 1 July 2011 to 30 June 2012 at Lincoln University, Canterbury, New Zealand. Values above each growth cycle represent transpiration relative to transpiration demand (T/T_D)



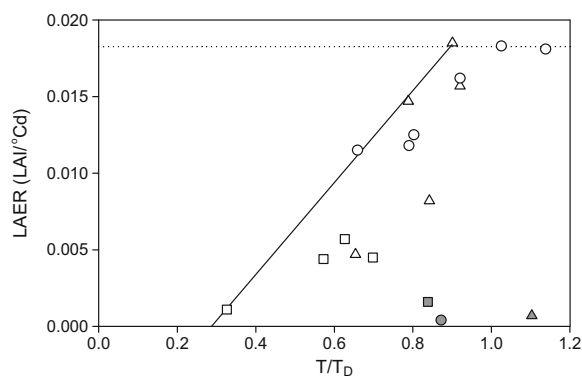


Fig. 10 Leaf area expansion rate (LAER) in relation to crop water stress (T/T_D) for individual regrowth periods of established ‘Stamina 5’ rainfed lucerne crops grown on three sites; stone free (\circ) stony (Δ) and very stony (\square) from 1 July 2011 to 30 June 2012 at Lincoln University, Canterbury, New Zealand. The regression (—; $y = 0.03x - 0.009$) estimates the potential LAER in relation to water stress. Note: the closed symbols are the final regrowth period where crops experienced minimum air temperature $< 0^\circ\text{C}$

Soil water supply

Predicted transpiration demand (Fig. 9), exceeded actual transpiration calculated from the soil water balance for all crops (Table 1). Therefore, the rate of extraction needs to be quantified to determine the temporal supply of water, which bounds transpiration in water limited environments.

The Monteith model (Monteith 1986) described the pattern of water extraction for lucerne grown on stony soils. This extends the applicability of the water extraction framework to a wider range of soil types. However, a single, constant kl and EFV were inappropriate to characterise water extraction for all of these lucerne crops. The EFV for seedling lucerne was $\sim 14 \text{ mm day}^{-1}$ (Fig. 4a, c), which may be set by the primary root extension velocity, as for annual crops (Bland and Dugas 1989; Robertson et al. 1993b). This result was consistent with other studies (Brown 2004; Dardanelli et al. 1997; Meyers et al. 1996) when seedling lucerne root growth is not inhibited by hostile soil conditions, such as acidic or sodic sub soils or compacted layers (Dolling et al. 2005). In contrast, the EFV of the established lucerne root systems increased two-fold to 33 mm day^{-1} (Fig. 4), when grown on a stony silt loam. This rapid descent of the extraction front has not been reported previously for lucerne and is comparable to that of annual crops, where EFV ranges from 23 to 49 mm day^{-1} (Dardanelli et al. 1997; Meinke et al. 1993; Robertson et al. 1993a; Singh et al. 1998).

The EFV of established lucerne is not directly comparable to that of lucerne during the seedling phase. The initial descent of the drying front was independent of the primary root, which was already at least 1.5 m, determined from the depth of soil water extraction in the seedling phase (Fig. 4a, c). The EFV may be the result of the production of fine roots on the existing taproot (Luo et al. 1995; Pietola and Smucker 1995). However, these roots do not appear to renew at a constant rate and therefore are not a strong indicator of the EFV, which varies depending on crop transpiration demand and precipitation (Brown 2004; Singh et al. 1998). This is because lucerne extracts water via the shortest path (Brown et al. 2009; Sheaffer et al. 1988). Extraction begins in a certain layer when the transpiration demand of the shoots exceeds the supply of the overlaying layers. However, the upper limit of the extraction front appeared to be 33 mm day^{-1} for these lucerne crops grown on stony soils of low PAWC at Lincoln, New Zealand.

When grown on stony soil lucerne increased the rate of water extraction. This was shown by a two-fold increase in the extraction rate constant (kl) which aggregates root length density (l) and soil water diffusion properties (k) (Passioura 1983). Differences in k among soil types are likely due to soil texture. The coarse sandy loams of the Lismore soils (stony and very stony sites) generally have greater hydraulic conductivity, compared to the predominately silt textured loams of the Wakanui soil (stone free site) (Di and Kemp 1989; Webb 2003). This may allow greater root exploration due to increased porosity (Jones 1983; Saxton et al. 1983) which would support greater water extraction. Also, if lucerne increased root length density in response to decreasing PAWC this would increase kl . However, there was a relatively consistent EFV and kl values for established crops over the full soil profiles to the point of severe water stress. This suggests lucerne did not alter root morphology to increase the rate of water extraction in response to low PAW. Rather, when supply limited, often the rate of water extraction declines (Asseng et al. 1998) due to a decrease in total root length density (l) (Clark et al. 2003). A proposed explanatory hypothesis is l was intrinsically higher because the roots occupied about half the volume of soil due to the stones, which may have supported the two-fold increase in kl .

The stony Lismore soils have an increasingly high stone content by volume of up to 45% below 0.5 m (Di

and Cameron 2002). This explains why these soils had only half the extractable water compared with the deep silt loam soil (Fig. 3b), and as a consequence of water stress produced up to 70% less shoot biomass (Fig. 2). The response of lucerne root morphology in these stony soils has not been reported in the literature, most likely because it is impractical to sample these layers (Webb 2000). The effect of stones may be similar to root ‘clumping’ in macropores due to soil compaction (Dardanelli et al. 2004; Passioura 1988), which increases apparent l for the volume of soil exploited by the roots. This leads to higher rates of water extraction from the soil within the confined root mass. However total extracted water declines, because the greater rate of extraction does not compensate for the decrease in soil volume. This was clearly demonstrated in the first spring regrowth cycle where, although the kl increased two-fold for the crop grown on the very stony soil, actual water extracted only met 70% of demand (Fig. 9c) and the crop experienced water stress.

In addition to the ‘clumping effect’, the high stone content meant the EFV probably did not represent primary root growth of seedling lucerne (Fig. 4c). Roots which are deflected by physical barriers become unevenly distributed, which means a preferred root pathway occurs in seedlings, until extensive lateral roots are developed (Clark et al. 2003). This would decrease the initial volume of soil available for extraction and is associated with the low EFV after sowing for the crop grown on the very stony soil (Fig. 4c).

A similar effect has been reported when seeds are direct-drilled into wet soil and the drill slot is smeared (Passioura 2002). Initial growth is often slow until roots develop the turgor pressure to penetrate the smeared slot created by the drill. Once lateral roots are developed, l rapidly expands and water extraction increases proportionally (Passioura 1983). This was demonstrated in the present study after a 60 mm rainfall event which resulted in an observed almost vertical descent of the extraction front of ~ 40 mm day⁻¹ from soil layers at 0.5 to 1.0 m (Fig. 4c). Asseng et al. (1998) found a similar result when droughted wheat was rewatered, water extraction increased to twice that of a fully watered control due to the rapid renewal of nodal roots. Thus, the linear model of the drying front is a poor indicator of water supply under these circumstances. Rather, water extraction is the minimum of crop demand and supply from the soil and EFV appears to have an upper threshold dependant on soil type.

Transpiration and radiation interception in response to water supply

Water stress reduced radiation interception and transpiration by up to 27% (Fig. 5) and 50% (Table 1), respectively. To do this, lucerne simultaneously reduced Θ_T and the rate of leaf area expansion, which agrees with previous reports for lucerne under water stress (Brown et al. 2012; Brown et al. 2009). A reduction in Θ_T to a minimum rate of 0.09 mm MJ⁻¹ m⁻² (Fig. 8) means less water is transpired per unit of intercepted radiation, probably due to partial stomatal closure to regulate loss of water vapour (Carter and Sheaffer 1983). Maximum potential LAER rate declined linearly from 0.018 LAI °Cd⁻¹, when $T/T_D \geq 0.90$ to zero when T/T_D was 0.30 (Fig. 10). This result corresponds with the same response shown by Brown et al. (2009) and indicates the minimum water requirement of lucerne to sustain leaf area expansion and growth. Canopy expansion rates below the potential were most likely limited by other factors, such as frost damage which increases the rate of leaf senescence (Barlow et al. 2015) which was observed in the autumn regrowth cycles and preferential partitioning of assimilate to perennial organs in response to drought (Sim et al. 2015).

When water stress was sustained over a longer period of time for crops grown on the stony soils, a secondary mechanism to reduce radiation loading was a decline in the extinction coefficient from 0.94 to 0.66 (Fig. 6). Changes in leaf morphology induced by water stress were observed by Moran et al. (1989) who showed lucerne distributed leaves more vertically due to a 25% decrease in leaf angle, which increased the light penetration through the canopy (Pearce et al. 1967). As a consequence, transpiration demand declined because the proportion of radiation intercepted per unit of LAI was reduced. This means changes in extinction coefficient need to be accounted for when determining T_D , which has a larger effect on the amount of intercepted radiation in water stressed, open canopies.

Agronomic implications

Seedling lucerne could be strategically used within a farm system to provide forage when established lucerne has exhausted soil water and growth has ceased. This is because when lucerne is sown the extraction of water is limited by the descent of the drying front which appears to have been constrained by the rate of primary root

extension. This means the time of sowing of new lucerne crops could be manipulated so first defoliation coincides with the approach of maximum SWD in established crops. To maximise the available water supply for seedling crops the soil profile should be fallowed to obtain the drained upper limit to the expected maximum rooting depth prior to sowing. This was ~1.5 m for lucerne in the first season on soil types used in this study. Incomplete soil water recharge below the rooting depth of seedling lucerne will reduce drainage from rainfall events during establishment, which can be extracted the following year when the taproot extends below 2.3 m. Also, these results suggest seedling lucerne would respond to irrigation when grown on stony soils, due to inadequate soil water extraction. However, this may require greater weed control because frequent wetting of the soil surface and an incomplete canopy promotes weed germination in open canopies (Palmer 1982).

To maximise water use efficiency, radiation capture should be maximised in spring when the VPD is lowest. This is because lucerne transpires less water per unit of intercepted radiation (Fig. 8), and when scaled up to the crop level, water use efficiency is greatest (Brown et al. 2005). Agronomic management which reduces the optimum canopy expansion rate such as water stress (Fig. 10), inadequate nitrogen supply (Avice et al. 2003; Teixeira et al. 2008), or short defoliation intervals (Teixeira et al. 2007b), will reduce radiation interception, and therefore shoot yield. Furthermore, by maintaining the crop canopy by delaying spring defoliation, a lower proportion of water may be lost via soil evaporation, which was recently shown in wheat by Harrison et al. (2011). This is because the relatively even distribution of annual rainfall in this environment (Fig. 1b) maintains the water content of the upper layer above the lower threshold for soil evaporation for a large portion of the year. However, an increase in crop yield in response to delayed spring defoliation may be offset by a decrease in forage quality as the unpalatable fraction increases with shoot biomass (Brown and Moot 2004).

Conclusions

This study has highlighted that the rate of lucerne water extraction differed with soil type and crop transpiration demand. Water supply from lucerne roots grown on stony soils was described by the Monteith model, although roots were unevenly distributed due to

displacement by rock fragments. This extends the applicability of the framework to a wider range of soil types. However, a single, constant kl and EFV were inappropriate for characterising water extraction on these soils. The canopy conductance approach was suitable to determine transpiration demand of lucerne. This was because transpiration was linearly related to radiation interception and the canopy conductance coefficient of $0.45 \text{ mm MJ}^{-1} \text{ kPa}^{-1}$ was stable for lucerne grown at Lincoln, New Zealand. Water limitation reduced lucerne yield through a reduction in radiation interception due to a linear decrease in leaf area expansion rate in response to water stress and also a decline in the canopy extinction coefficient from 0.94 to 0.66. These results further the understanding of the temporal pattern of lucerne water use which improves the ability to estimate lucerne yield and productivity when grown on a range of soil types. The strong relationship between leaf area index and transpiration demand offers insight into the potential of canopy management to manipulate water use to support greater productivity in water scarce environments.

Acknowledgements The William Machin Trust funded Richard Sim's Ph.D. research, and Lincoln University and Beef + Lamb NZ assisted financially through the Pastoral 21 programme to allow preparation of this manuscript.

References

- Asseng S, Ritchie JT, Smucker AJM, Roberston MJ (1998) Root growth and water uptake during water deficit and recovering in wheat. *Plant Soil* 201:265–273
- Avice JC et al (2003) Vegetative storage proteins in overwintering storage organs of forage legumes: roles and regulation. *Can J Bot* 81:1198–1212
- Barlow KM, Christy BP, O'Leary GJ, Riffkin PA, Nuttall JG (2015) Simulating the impact of extreme heat and frost events on wheat crop production: a review. *Field Crop Res* 171:109–119
- Bland WL, Dugas WA (1989) Cotton root growth and soil water extraction. *Soil Sci Soc Am J* 53:1850–1855
- Brown H.E., 2004. Understanding yield and water use of dryland forage crops in New Zealand. Ph.D. Thesis, Lincoln University, Lincoln, New Zealand, 288 pp.
- Brown HE, Moot DJ (2004) Quality and quantity of chicory, lucerne and red clover production under irrigation. *Proceedings of the New Zealand Grassland Association* 66: 257–264
- Brown HE, Moot DJ, McKenzie BA (2004) Field validation of empirical functions used to predict crop water use, proceedings of the 4th international crop science congress. Australian Agronomy Society, Brisbane, Australia

- Brown HE, Moot DJ, Pollock KM (2005) Herbage production, persistence, nutritive characteristics and water use of perennial forages over 6 years on a Wakanui sil loam. *N Z J Agric Res* 48:423–439
- Brown HE, Moot DJ, Fletcher AL, Jamieson PD (2009) A framework for quantifying water extraction and water stress responses of perennial lucerne. *Crop and Pasture Science* 60(8): 785–794
- Brown HE, Jamieson PD, Moot DJ (2012) Predicting the transpiration of lucerne. *Eur J Agron* 43:9–17
- Carter P, Sheaffer C (1983) Alfalfa response to soil water deficits. II. Plant water potential, leaf conductance, and canopy temperature relationships. *Crop-Science* 23(4):679–680
- Clark LJ, Whalley WR, Barraclough PB (2003) How do roots penetrate strong soil? *Plant Soil* 93:93–104
- Cox, J.E., 1978. Soils and agriculture of Paparua County, Canterbury, New Zealand, 34. New Zealand Soil Bureau Bulletin.
- Dardanelli JL, Bachmeier OA, Sereno R, Gil R (1997) Rooting depth and soil water extraction patterns of different crops in a silty loam haplustoll. *Field Crop Res* 54:29–38
- Dardanelli JL, Ritchie JT, Calmon M, Andriani JM, Collino DJ (2004) An empirical model for root water uptake. *Field Crop Res* 87:59–71
- Di HJ, Cameron KC (2002) Nitrate leaching and pasture production from different nitrogen sources on a shallow stoney soil under flood-irrigation dairy pasture. *Aust J Agric Res* 40: 317–334
- Di HJ, Kemp RA (1989) Variation in soil physical properties between and within morphologically defined series taxonomic units. *Aust J Agric Res* 27:259–273
- Dolling PJ, Latta RA, Ward PR, Roberson MJ, Asseng S (2005) Soil water extraction and biomass production by lucerne in the south of Western Australia. *Aust J Agric Res* 56:389–404
- Dolling PJ, Lyons AM, Latta RA (2011) Optimal plant densities of lucerne (*Medicago sativa*) for pasture production and soil water extraction in mixed pastures in South-Western Australia. *Plant Soil* 348:315–327
- French BK, Legg BJ (1979) Rothamsted irrigation 1964–76. *Journal of Agricultural Science, U.K.* 92(1):15–37
- Goodspeed, M.J., 1975. Computer routines for solar position, daylength and related quantities. CSIRO Australia Division of Land Use Research Technical Memorandum 75/11.
- Harrison MT, Evans JR, Dove H, Moore AD (2011) Recovery dynamics of rainfed winter wheat after livestock grazing I. Growth rates, grain yields, soil water use and water-use efficiency. *Crop and Pasture Science* 62:947–959
- Jamieson P, Francis G, Wilson D, Martin R (1995) Effects of water deficits evapotranspiration from barley. *Agric For Meteorol* 76(1):35–44
- Jones CA (1983) Effect of soil texture on critical bulk densities for root growth. *Soil Sci Soc Am J* 47:1208–1211
- Jones CA, Kiniry JR (1986) CERES-maize: a simulation model of maize growth and development. Texas A&M University Press, College Station, 194 pp
- Jones JW et al (2003) The DSSAT cropping system model. *Eur J Agron* 18:235–265
- Luo Y, Meyerhoff PA, Loomis RS (1995) Seasonal patterns and vertical distributions of fine roots of alfalfa (*Medicago sativa* L.). *Field Crop Res* 40(2):119–127
- McLenaghan R. and Webb T., 2012. Soil properties and fertility of Ashley Dene: the challenge., Lucas, D., Gow, N. and Nicol, A. (Eds). Ashley Dene Lincoln University farm - the first 100 years: Lincoln University, 17–22.
- Meinke H, Hammer GL, Want PJ (1993) Potential soil water extraction by sunflower on a range of soils. *Field Crop Res* 32:59–81
- Meyers LL, Russelle MP, Lamb JFS (1996) Fluridone reveals root elongation differences among alfalfa germplasms. *Agron J* 88:67–72
- Michaud R, Lehman WF, Rumbaugh MD (1988) World distribution and historical development. Alfalfa and Alfalfa Improvement, American Society of Agronomy, Madison, U.S.A.
- Mills A (2007) Understanding constraints to cocksfoot (*Dactylis glomerata* L.) based pasture production. Ph.D. Thesis, Lincoln University, Lincoln, New Zealand
- Monsi M, Saeki T (2005) On the factor light in plant communities and its importance for matter production. *Ann Bot* 95(1): 549–567
- Monteith JL (1965) Evaporation and environment. In: Fogg GE (ed) The state and movement of water in living organisms. Academic press, New York, pp. 205–234
- Monteith J.L., 1986. How do crops manipulate water supply and demand? Philosophical transactions of the Royal Society of London, A(316): 245–258.
- Moot DJ, Robertson MJ, Pollock KM (2001) Validation of the APSIM-Lucerne model for phenological development in a cool-temperate climate. Hobart, pp:1–5
- Moot DJ, Brown HE, Teixeira EI, Pollock KM (2003) Crop growth and development affect seasonal priorities for lucerne management. In: Moot DJ (ed) Legumes for Dryland Pastures. New Zealand Grassland Association: Christchurch, Lincoln University, New Zealand, pp. 201–208
- Moot DJ, Brown HE, Pollock K, Mills A (2008) Yield and water use of temperate pastures in summer dry environments. *Proceedings of the New Zealand Grassland Association* 70: 51–57
- Moot DJ, Bennett SM, Mills AM, Smith MC (2016) Optimal grazing management to achieve high yields and utilisation of dryland lucerne. *J New Zealand Grasslands Assoc* 78:27–34
- Moran SM, Pinter PJ, Clothier BE, Allen SG (1989) Effect of water stress on the canopy architecture and spectral indices of irrigated alfalfa. *Remote Sens Environ* 29:251–261
- Palmer TP (1982) Weeds in lucerne, why are they there, what harm do they do. In: Wynn-Williams RB (ed) Lucerne for the 80's. Agronomy Society of New Zealand, Palmerston North, pp. 33–35
- Passioura JB (1983) Roots and drought resistance. *Agric Water Manag* 7(1–3):265–280
- Passioura JB (1988) Water transport in and to roots. *Annu Rev Plant Physiol Plant Mol Biol* 39:245–265
- Passioura JB (2002) Soil conditions and plant growth. *Plant Cell Environ* 25:311–318
- Pearce RB, Brown RH, Blaser RE (1967) Photosynthesis in plant communities as influenced by leaf angle. *Crop Sci* 7:321–324
- Penman H.L., 1948. Natural evaporation from open water, bare soil and grass. *Proceedings of the Royal Society of London, A*, 194: 120–145.

- Pietola LM, Smucker AJM (1995) Fine root dynamics of alfalfa after multiple cuttings and during a late invasion by weeds. *Agron J* 87:1161–1169
- Ritchie JT (1972) Model for predicting evaporation from a row crop with incomplete cover. *Water Resour Res* 8(5):1204–1213
- Robertson MJ, Fukai S, Ludlow MM, Hammer GL (1993a) Water extraction by grain sorghum in a sub-humid environment. I Analysis of the water extraction pattern. *Field Crops Research* 33(1–2):99–112
- Robertson MJ, Fukai S, Ludlow MM, Hammer GL (1993b) Water extraction by grain sorghum in a sub-humid environment. II. Extraction in relation to root growth. *Field Crop Res* 33:99–112
- Robertson MJ et al (2002) Simulation of growth and development of diverse legumes species in APSIM. *Aust J Agric Res* 53(4):429–446
- Rosenzweig C et al (2013) The agricultural model Intercomparison and improvement project (AgMIP): protocols and pilot studies. *Agric For Meteorol* 170:166–182
- Rötter RP, Carter TR, Olesen JE, Porter JR (2011) Crop-climate models need an overhaul. *Nat Clim Chang* 1:175–177
- Saxton KE, Rawls WJ, Romberger JS, Papendick RI (1983) Estimating generalized soil-water characteristics from texture. *Soil Sci Soc Am J* 50:1031–1036
- Sheaffer CC, Tanner CB, Kirkham MB (1988) In: Hanson AA, Barnes DK, Hill RRJ (eds) *Alfalfa water relations and irrigation. Alfalfa and alfalfa improvement*. American Society of Agronomy, Madison, pp. 373–409
- Sim R.E., 2014. Water extraction and use of seedling and established dryland lucerne crops. PhD Thesis. Ph.D. Thesis, Lincoln University, Canterbury, New Zealand.
- Sim RE, Moot DJ, Brown HE, Teixeira EI (2015) Sowing date affected shoot and root biomass accumulation of lucerne during establishment and subsequent regrowth season. *Eur J Agron* 68:69–77
- Sinclair TR (2006) A reminder of the limitations in using Beer's law to estimate daily radiation interception of vegetation. *Crop Sci* 46:2343–2347
- Singh P, Monteith JL, Lee KK, Rego TJ, Wani SP (1998) Response to fertiliser nitrogen and water of post-rainy season sorghum on a Vertisol. 2. Biomass and water extraction. *J Agric Sci, UK* 131:429–438
- Teixeira EI, Moot DJ, Brown HE, Fletcher AL (2007a) The dynamics of lucerne (*Medicago sativa* L.) yield components in response to defoliation frequency. *Eur J Agron* 26(4):394–400
- Teixeira EI, Moot DJ, Mickelbart MV (2007b) Seasonal patterns of root C and N reserves of lucerne crops (*Medicago sativa* L.) grown in a temperate climate were affected by defoliation regime. *Eur J Agron* 26(1):10–20
- Teixeira EI, Moot DJ, Pollock KJ, Brown HE (2007c) How does defoliation management affect yield, canopy forming processes and light interception in lucerne (*Medicago sativa* L.) crops? *Eur J Agron* 27(1):154–164
- Teixeira EI, Moot DJ, Brown HE (2008) Defoliation frequency and season affected radiation use efficiency and dry matter partitioning to roots of lucerne (*Medicago sativa* L.) crops. *Eur J Agron* 28(2):103–111
- Teixeira EI, Brown HE, Moot DJ, Meenken ED (2011) Growth and phenological development patterns differ between seedling and regrowth lucerne crops (*Medicago sativa* L.). *Eur J Agron* 35:103–111
- Verburg K, Bond WJ, Hirth JR, Ridley AM (2007) Lucerne in crop rotations on the Riverine Plains. 3*. Model evaluation and simulation of analyses. *Aust J Agric Res* 58:1129–1141
- Wang E, Smith CJ, Bond WJ, Verburg K (2004) Estimations of vapour pressure deficit and crop water demand in APSIM and their implications for prediction of crop yield, water use and deep drainage. *Aust J Agric Res* 55:1227–1240
- Webb TH (2000) Quantifying variability of soil physical properties within soil series to address modern land-use issues on the Canterbury Plains, New Zealand. *Aust J Soil Res* 38:1115–1129
- Webb TH (2003) Identification of functional horizons to predict physical properties for soils from alluvium in Canterbury, New Zealand. *Aust J Soil Res* 41:1005–1019