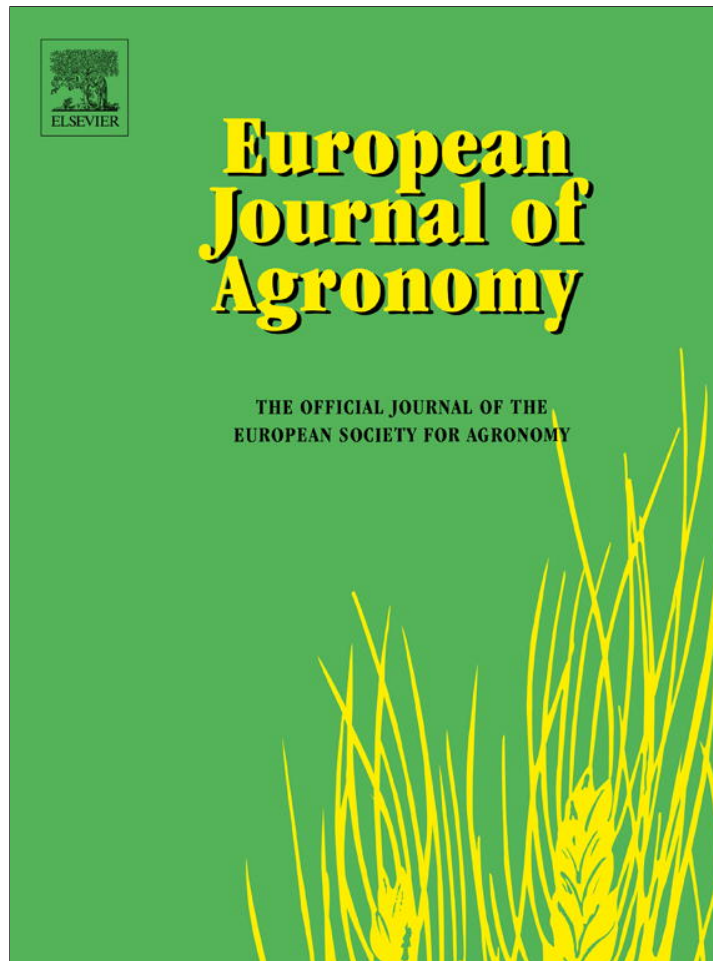


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Yield components, light interception and radiation use efficiency of lucerne (*Medicago sativa* L.) in response to row spacing

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ABSTRACT

Lucerne sowing is characterized by a rectangular spatial arrangement, *i.e.* greater distance between sowing rows than between plants in the row. Therefore, the reduction of row spacing generates more square spatial arrangements that can influence intraspecific competition and resource utilization, especially radiation, and thus biomass. The experiment included different row spacings (10–15–17.5–20 and 30 cm) at the same plant density in a pure lucerne crop during the first production year. Total aerial dry matter (ADM) was increased by narrow spacing (more square arrangements) up to an optimal distance (around 13 cm) ($R^2 = 0.60$). ADM ranged from 2292 to 1670 g DM m⁻² for 15 and 30 cm row spacing, respectively. Plant density was the forage yield component most affected by row spacing and it increased with narrow spacing ($0.15 \geq R^2 \leq 0.5$). ADM responses to reduced row spacing were positive as revealed by both a linear increase in radiation interception (PAR_{ia}) ($R^2 = 0.76$) and an optimal pattern in radiation use efficiency (RUE) ($R^2 = 0.45$). PAR_{ia} in the first year showed an increase of 8 MJ cm⁻¹ of spacing reduction. RUE values ranged from 2.0 to 1.6 g DM MJ⁻¹ for 15 and 30 cm row spacing, respectively. The leaf area index (LAI) was also affected by row spacing. Additionally, seasonal variation was found for the main variables but did not interact with row spacing. In conclusion, reducing row spacing to an optimal distance is a practice that allows for more favourable spatial arrangements of a lucerne crop and has a positive impact on forage production.

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1. Introduction

Row spacing is an agronomical practice that determines the spatial distribution of the plants, which affects canopy structure, light interception and radiation use efficiency and consequently, biomass production in forage cropping systems. Lucerne pastures have very limited capacity for reseeding, which means that the spatial distribution of the plants remains uniform for many years and thus determines the timing of canopy closure after every defoliation. Lucerne sowing is characterized by greater distance between rows than between plants in the row, thereby showing a markedly rectangular arrangement. It is worth noting that if the row spacing decreases at the same density, the distance between plants in the

row increases, thus generating a more square spatial arrangement. This could lead to improved canopy closure and biomass accumulation at each regrowth. The effects on biomass production can be analysed through changes in forage yield components such as the number of plants per area, the number of shoots per plant and the mass per shoot (Volenc et al., 1987). Complementary, biomass production can be studied by analyzing the radiation model components: the photosynthetically active radiation (PAR) intercepted and accumulated during the crop cycle (PAR_{ia}) and the radiation use efficiency (RUE) or PAR conversion into biomass (Monteith, 1977). For this study, we performed both analyses to generate knowledge about the mechanisms involved in the biomass response to row spacing in pure lucerne crops.

Different spatial arrangements produced by changes in row spacing can affect resource competition relationships at both the intraspecific and the interspecific levels (*e.g.* affecting recruitment of weed species). Intraspecific competition has three effects: (i) density-dependent mortality, (ii) trade-offs between size and density, and (iii) population size structure alteration (Park et al., 2003). The first two effects can be inferred by changes in average forage yield components, while the distribution of plant sizes in the crop provides information about the population structure. The

Abbreviations: ADM, aerial dry matter; LAI, leaf area index; PAR, photosynthetically active radiation; PAR_{ia} , amount of photosynthetically active radiation intercepted and accumulated during crop cycle; $fPAR_i$, fraction of photosynthetically active radiation intercepted by the canopy; $fPAR_e$, fraction of photosynthetically active radiation transmitted through the canopy; RUE, radiation use efficiency.

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combination of two agronomic practices, plant density and row spacing, defines the spatial arrangement of plants. Density effects were clarified in a two-year experiment performed by Volenec et al. (1987), with a uniform distance between plants (square arrangement) for all density treatments. These authors determined that increased plant density had a positive effect on lucerne biomass production due to a higher shoot number per unit area, though the average plant size was reduced. Conversely, the focus of our work was to analyse how row spacing affected forage yield components, light interception, radiation use efficiency and biomass production at the same plant density in lucerne's first production year, where greater effects were previously found (Mattera et al., 2009).

Row spacing was studied in numerous experiments in grain and industrial crops following the radiation model. As a result, in several crops narrow spacing increased the proportion of the radiation intercepted by the canopy ($fPAR_i$), resulting in higher PAR_{ia} . This response was observed in grain crops such as corn (*Zea mays* L.) (Barbieri et al., 2000; Andrade et al., 2002; Sharratt and McWilliams, 2005), sorghum [*Sorghum bicolor* (L.) Moench] (Steiner, 1986), soybean [*Glycine max* (L.) Merr.] (Board et al., 1992; Andrade et al., 2002) and sunflower (*Helianthus annuus* L.) (Zaffaroni and Schneider, 1989). The $fPAR_i$ increase was also reported for industrial crops as sugarcane (*Saccharum* spp.) (Singels and Smit, 2009) and fiber hemp (*Cannabis sativa* L.) (van der Werf et al., 1995). The higher $fPAR_i$ was mainly explained by changes in leaves disposition; in other words, a more equidistant arrangement of the plants ensured a more uniform distribution of leaves in the canopy (Zaffaroni and Schneider, 1989; van der Werf et al., 1995; Flenet et al., 1996; Barbieri et al., 2000; Sharratt and McWilliams, 2005). Other authors have reported that more square arrangements increased the leaf area index (LAI) (Steiner, 1986; Board and Harville, 1992; Singels and Smit, 2009) also enhancing $fPAR_i$. The effects of row spacing on biomass production are also determined by what occurs in the second component of the radiation model, the RUE. For corn, soybean, and sunflower, the positive grain yield responses were associated with increments in PAR_{ia} (Andrade et al., 2002). However, yield increases were not as proportional as the increase in PAR_{ia} suggesting a lower RUE or harvest index in narrow spacings. For corn, RUE also dropped at post-flowering, counteracting the positive effects of higher PAR_{ia} in narrow rows during the same period (Maddonni et al., 2006). The mechanisms that explain RUE reduction in narrow spacing are still under study. Maddonni et al. (2006) suggested that both light attenuation within the canopy and red/far red ratio at lower leaf stratum could have depressed photosynthesis and consequently RUE. In forage crops, the existing information reported biomass increments by row spacing reduction (for pure lucerne: Roufai, 1975; Lutz and Morley, 1982; Mattera et al., 2009; and associated with grasses: Jefferson and Kielly, 1998), but the studies were not completely detailed in terms of both forage yield and radiation model components. In crowded populations, the asymmetric competition due to light determines the death of smaller plants (Weiner et al., 1990). Self-thinning processes are common in lucerne crops (Rowe, 1988; Teixeira et al., 2007a), and unlike annual crops, changes in yield components through the years can determine size density compensation. However, in a preliminary work for a period of three years, we have found that the row spacing affected both plant size and density through the initial period (Mattera et al., 2009). We proposed the current experiment to investigate forage yield components with exhaustive detail to scrutinize these processes during the first year.

Lucerne is one of the most important forage crops due to its elevated production of high quality forage. The objectives of this work were: (i) to study the impact of row spacing on intraspecific competition by analyzing forage yield components (plant density, shoots $plant^{-1}$ and weight shoot $^{-1}$) and (ii) to analyse the effects of row spacing on light interception and radiation use efficiency and

its relation to aerial biomass production. The experiment included measurements at five different row spacings (10–15–17.5–20 and 30 cm) at the same plant density established by thinning, in a pure lucerne crop (cv. Monarca) during five subsequent regrowths in the first production year. To the best of our knowledge, this is the first quantitative study to deal with the yield components, light interception and radiation use efficiency of forage crops in response to row spacing. We hypothesized that the decrease of row spacing generates more square spatial arrangements which increase biomass production in lucerne crops. Specifically, we predicted that narrow spacings would increase forage yield components due to lower intraspecific competition. Although there exists a trade-off between intra-row and inter-row distances, in the case of lucerne crops, where plants are much closer in the row than between rows, the intra-row distance would limit growth first. Therefore, narrow spacing (greater intra-row distance) would delay the onset of competition. Second, narrow spacings would reach the critical LAI faster due to a plant arrangement closer to a square, increasing the time of the regrowth with optimal interception. Third, we also predicted that the spacing would not affect RUE in the range of biomass commonly explored by lucerne crops for forage production, though this could occur if a closer distribution of the plants changes light penetration through the canopy.

2. Materials and methods

2.1. Study site

The experiment was carried out from March 2009 to January 2010 on an area of flat land at the Rafaela INTA Experimental Station, Santa Fe, Argentina (31°12'S and 61°30'W). The climate of the region is subhumid humid and mesothermal, and Rafaela is characterized by annual rainfall of 957 mm with little precipitation in winter. The annual mean temperature is 19°C, with the mean monthly lowest temperature in July (12°C) and the maximum in January (26°C). The soil is a "Rafaela" silt loam (USDA Soil Taxonomy: Typic Argiudoll, fine, mixed, thermic) (Mosconi et al., 1981), being the top horizon (first 20 cm) characterized by 3.4% of organic matter, 0.2% of total nitrogen, 37 mg kg $^{-1}$ of nitrates-N, 67 mg kg $^{-1}$ of extractable P, 9 mg kg $^{-1}$ of sulfates-S and a pH of 6.3.

2.2. Crop establishment, experimental design and treatments

The lucerne cultivar used was Monarca SP INTA (Produce S.A., Pergamino, Argentina) (without winter dormancy), with a thousand seed weight of 2.3 ± 0.1 g and germination power of $93 \pm 1\%$, seeds were uncoated without treatment and inoculation. Before sowing, the seedbed was prepared by a disc harrow and a tine harrow. The experiment was hand-seeded, put in rows at a sowing depth of around 1 cm, in early autumn of 2009. Precipitation during the time of sowing was sufficient to assure a good establishment of the crop (358 mm from February to April). During the rest of the experimental period, precipitation was abundant (770 mm), exceeding lucerne evapotranspiration in every regrowth, except in October, where irrigation ($\cong 15$ mm) was done to avoid severe water stress. Weeds were hand controlled. Pesticides were applied to control insects and diseases when necessary. Degree day accumulation during each regrowth was calculated as the sum of averages of daily absolute lowest and highest temperatures, considering a base temperature of 5°C (Fick et al., 1988).

Rhizobia infection was expected given the previous history with lucerne in the paddock. The experimental design was a randomized complete block with five replicates. Each experimental unit consisted in a plot of 1 m \times 1.5 m. Treatments were established at sowing as five row spacings: 10–15–17.5–20 and 30 cm

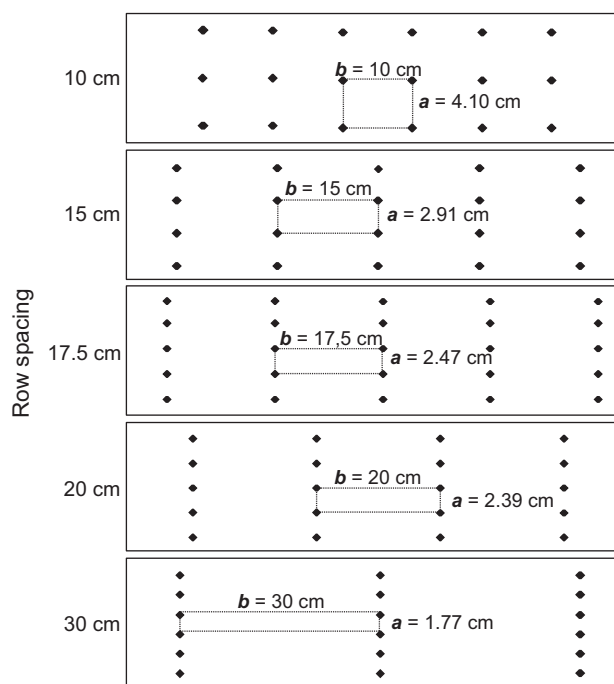


Fig. 1. Scheme of the spatial arrangement of lucerne cultivated at five row spacings (10–15–17.5–20 and 30 cm) at Rafaela, Santa Fe, Argentina. This scheme was developed from the average distance between plants in the row at the beginning of the experimental period (September). Note that distance between plants in the row is represented by letter *a*, while letter *b* identifies row spacing.

(Fig. 1). The purpose was to generate a spatial arrangement gradient where narrow spacings had arrangements closer to a square while wide spacings had markedly rectangular arrangements. Plots were seeded at high densities (20 kg ha^{-1}) and after a month, a seedling thinning was performed (following the spatial arrangement assigned to each plot) to give all plots the same density ($250 \text{ plants m}^{-2}$), assuming that all seedlings had emerged at that moment. Due to the spacing treatments, the number of rows per plot varied, with 12, 9, 8, 7 and 5 rows per plot for spacings of 10–15–17.5–20 and 30 cm, respectively.

2.3. Measurements

2.3.1. Plant density and rectangularity index

Plant density was followed throughout the experiment by counting plants marked with rings in two fixed segments along the rows. During each treatment, the length of the segment was adjusted (66 cm, 44 cm, 38 cm, 33 cm and 22 cm length for spacings of 10–15–17.5–20 and 30 cm, respectively) to create an equal plot surface. Rings were moved to live shoots of the same plant when shoot mortality occasionally occurred on target plants. Countings were done four times during the spring–summer season: in September, October, December and at the end of the experiment (January 2010). On each of the counting dates, the spatial arrangement of the plants was assessed by measuring the distance between plants in the row of the segments used to register plant density. A rectangularity index was then calculated as the ratio between row spacing and the average distance between plants in the row (Willey and Heath, 1969).

2.3.2. Biomass production and forage yield components

Aerial dry matter (ADM) was evaluated in consecutive regrowths, from the first cut of the pasture (date: 31/08) and five subsequent regrowths from the beginning of the spring till the end of the summer. The phenological stage at cutting was between early

and late flowering. Biomass was harvested on an equal surface for all spacings (as was plant density, Section 2.3.1); four segments along the rows were harvested per plot and date. Cuttings were done manually with a scissor 7 cm above ground level avoiding the borders of each plot. The harvested biomass was dried to constant weight in a forced air oven at 60°C . Additionally, in four regrowths, the number of shoots in all the corresponding harvested biomass was counted and dry mass per shoot was calculated as the ratio of ADM to shoot number. Finally, the number of shoots per plant was estimated as the ratio between shoot number and plant density. During the last harvest, plant bases were excavated to characterize crown–tap root weight and dimensions. Individual plants were processed to register the dry weight of the crown, the crown area resulting from the product of the greater diameter and its respective perpendicular diameter, and finally, the upper taproot diameter.

2.3.3. Light interception and radiation use efficiency

Light interception and radiation use efficiency were studied in five consecutive regrowths following the first cutting. During regrowth incident PAR was measured periodically (every 2–7 days) above and below the canopy with a 1 m linear ceptometer (Cavadevices, Buenos Aires, Argentina) to estimate the proportion of the radiation transmitted ($f\text{PAR}_t$) through the canopy in each spacing. Measurements were done at noon on sunny days by positioning the ceptometer at ground level in homogenous sectors of the plots across rows. The $f\text{PAR}_i$ was calculated as $(1 - f\text{PAR}_t)$. The values of $f\text{PAR}_i$ between measurements were obtained by linear interpolation. The incident global radiation was provided by a meteorological station located at INTA-Rafaela and a coefficient of 0.45 was used to obtain incident PAR. The PAR_{i_a} in each regrowth was calculated as the sum of the product of daily incident $\text{PAR} \times f\text{PAR}_i$. Additionally, the PAR_{i_a} of the entire experimental period was estimated for each plot as the sum of partial PAR_{i_a} . The RUE was estimated as the ratio between ADM and PAR_{i_a} for each regrowth and also globally estimated as the ratio of ADM and PAR_{i_a} sums for the entire experimental period. To confirm this estimate, the RUE was also calculated as the slope of the relationship between the accumulation of ADM and PAR_{i_a} throughout the experimental period.

2.3.4. Canopy characteristics: leaf:stem ratio, LAI, *k* and leaf greenness

In four regrowths (September, October, December and January), one of the subsamples of aerial biomass was dissected into leaves and stems to estimate the leaf:stem ratio as an indicator of forage quality. In December and January regrowths, the specific leaf area was obtained by measuring the area of the leaves of fifteen randomly selected shoots (representing more than 500 cm^2) with digital photography and scanning and then weighting its dry weight. These measurements were used to estimate LAI by multiplying the lamina proportion by the specific leaf area and ADM. Additionally, the light extinction coefficient (*k*) was estimated as $k = -\text{LN}(f\text{PAR}_t)/\text{IAF}$ (Fleuret et al., 1996). Differences in light attenuation can drive changes in nitrogen concentration and distribution through the canopy, and consequently altering photosynthesis levels. As a result, leaf greenness was measured in fully expanded leaves of three different layers of the canopy using a portable chlorophyll meter (Model SPAD-502, Minolta, Ramsey, NJ, USA). The SPAD-Minolta gives an estimate of the chlorophyll content of the leaves and was associated in other legumes crops to N concentration [faba bean (*Vicia faba* L.); Abdelhamid et al., 2003] and to photosynthetic rates (soybean; Ma et al., 1995). Each layer was defined as 1/3 of the average canopy height (60 cm and 45 cm for December and January, respectively). Within each layer, fifteen randomly selected leaves were measured to obtain an average SPAD value.

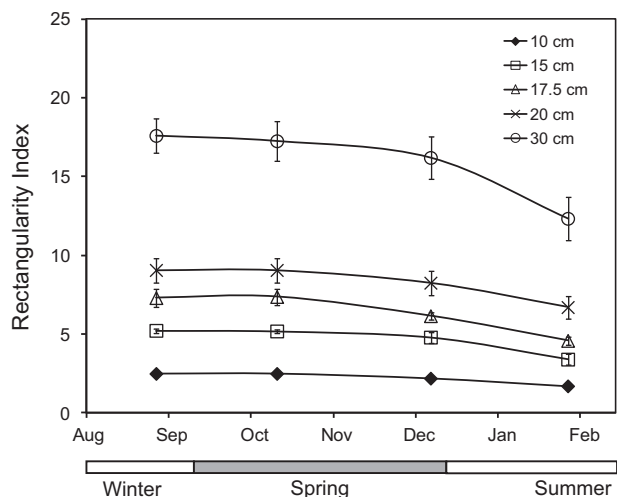


Fig. 2. Evolution of the rectangularity index of lucerne cultivated at five row spacings (10–15–17.5–20 and 30 cm) during the spring–summer of the first production year at Rafaela, Santa Fe, Argentina. Plots were thinned at post-emergence to uniform plant density (250 plants m^{-2}). Rectangularity index was calculated as the ratio of the distance between rows and the distance between plants in the row. Values are means \pm SE of five replicates.

2.4. Statistical analysis

All the statistical analyses were performed using SAS v9.1.3 statistical software (SAS Institute, Cary, NC, 2004). The dynamics of biomass production, yield components, PAR_{ia} and RUE were analysed by rmANOVA with a randomised complete block design and repeated measures. Polynomial contrasts were performed to evaluate the existence of linear and/or quadratic relations of each variable as a function of row spacing. Coefficients used for the calculations of the contrasts were obtained with the macro ORPOLY for unequal spacing. For the variables analysed only in summer regrowths (LAI and SPAD), ANOVAs were done separately for each regrowth. Fisher's least significant difference (LSD) was used to detect differences between treatments ($p < 0.05$) or trends ($0.05 < p < 0.10$). Crown and taproots traits were analysed by ANOVAs with randomised complete block design and subsampling (each plant) with four replicates. Rectangularity index, leaf:stem ratio, crown weight and crown area were natural log transformed to accomplish analysis assumptions. Regression and correlation analysis were used to analyse relationships between variables, and F tests for differences between slopes. Additionally, it was estimated the joint point and the respective slopes of the bi-linear regression (Draper and Smith, 1998) adjusted for ADM response to spacing. The degrees of freedom for the error term were 21 (all the replicates were used to adjust the model).

3. Results

3.1. Spatial arrangement

The differences in the spatial arrangement of lucerne plants caused by row spacing were reflected in the rectangularity index (rmANOVA; $p < 0.0001$) (Fig. 2). The index approached unity as row spacing was reduced, implying a more equidistant arrangement between plants. The spatial arrangement of the widest row spacing (30 cm) was (rectangularity index = 15.1) on average seven times more rectangular than it was for the narrowest spacing (10 cm; rectangularity index = 2.1). Linear regressions for each counting date between row spacing and the rectangularity index resulted in high determination coefficients (0.89–0.93), showing a close relationship of both variables during the experiment. Due to plant

mortality, there was a slight decrease ($p < 0.0001$) of the rectangularity index during the experiment. The interaction between row spacing and time was not significant (rmANOVA; $p = 0.86$), although the reduction seems to be more pronounced in 30 cm spacing. However, great differences among all row spacing treatments were evident throughout the experiment (Fig. 2), confirming that the gradient of spatial arrangement required to test the hypotheses was kept during all the experimental period.

3.2. Aerial biomass and forage yield components

As expected, ADM was affected by row spacing (rmANOVA; $p = 0.0003$) (Fig. 3a). When the six different harvests were analysed, the results showed a significant linear increase (polynomial contrasts; $p < 0.0001$) of biomass production as spacing was reduced. On average, the highest yielding distance (15 cm) accumulates 40% more biomass than the less productive distance (30 cm). ADM was also influenced by time ($p < 0.0001$) but did not interact with row spacing ($p = 0.37$). September and November regrowths were the most productive (386 and 438 $g DM m^{-2}$, respectively), while during the initial growth, October and December the ADM was intermediate (331, 310 and 319 $g DM m^{-2}$, respectively), and the lowest ADM occurred in January (236 $g DM m^{-2}$). After the analysis by regrowth, a bi-linear regression was adjusted between total ADM and row spacing in order to reflect the occurrence of an optimal spacing, which was determined to be 13 cm between rows (Fig. 3b). The function explained 60% of the variation ($p < 0.0001$) (Fig. 3b) with an initial positive slope (50 $g DM cm^{-1}$) up to 13 cm after which the slope was negative ($-38 g DM cm^{-1}$).

Plant density dynamics was affected by row spacing (rmANOVA; $p = 0.0097$). A significant linear increase (polynomial contrasts; $p = 0.0008$) was detected, denoting a higher plant density as spacing was reduced (Fig. 4a). This response occurred despite the fact that all spacing treatments started with a similar number of plants (due to thinning). Time also affected plant density ($p < 0.0001$), with increasing mortality leading to a plant density reduction of 10% by December and other 26% by January. The other two yield components, the number of shoots per plant (Fig. 4b) and dry mass per shoot (Fig. 4c), were not affected by row spacing, although a trend was detected for the latter (rmANOVA; $p = 0.76$ and $p = 0.09$, respectively). The interaction between row spacing and time was not significant ($p > 0.1$) for any of the yield components. The structural traits of the crown and taproots of the plants may provide information on plant vigour. But we were unable to confirm that row spacing had any significant effects on lucerne crowns and taproots (ANOVA; $p > 0.05$; data not shown), with mean values of 0.54 g, 1.6 cm^2 and 0.32 cm, for crown weight, crown area and taproot diameter, respectively. However, in 15 and 17.5 cm spacings, the distribution of sizes in the population did present changes, with a higher value of the upper quartile for crown traits: the upper quartile was 54% greater for crown weight and 24% for crown area, which implies that individual plants with bigger crowns were present in those row spacings, suggesting a different plant hierarchy.

3.3. Light interception and radiation use efficiency

Canopy interception was influenced by row spacing throughout the experimental period (Fig. 5). Narrow spacings (10 cm and 15 cm) intercepted higher $fPAR_i$ during the entire regrowth period. In September, all distances reached an interception of 0.95, but the critical value was achieved faster as row spacing was reduced. In November and December, 10 and 15 cm spacings were the only treatments that exceeded 0.95 $fPAR_i$ by the end of the regrowth period. While in October and January, the critical value was not reached in any spacing but the maximum values (around 0.9)

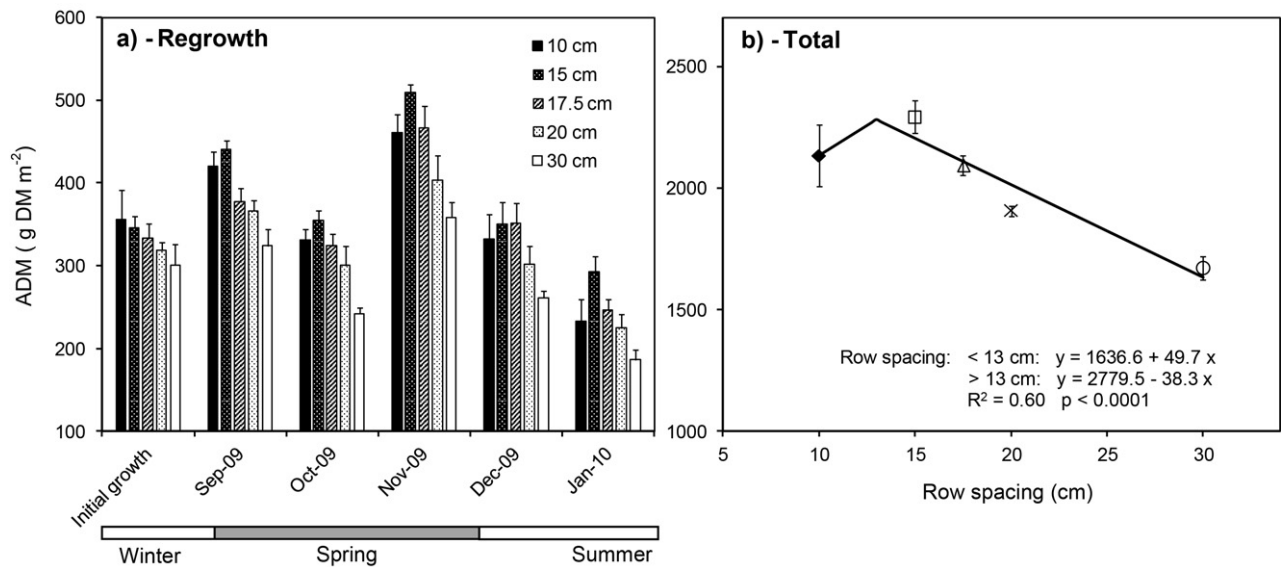


Fig. 3. (a) Evolution of aerial dry matter (ADM) per regrowth of five row spacings (10–15–17.5–20 and 30 cm) and (b) total ADM of lucerne as a function of row spacing during the spring–summer of the first production year at Rafaela, Santa Fe, Argentina. Plots were thinned at post-emergency to uniform plant density (250 plants m⁻²). Values are means ± SE of five replicates.

were registered again in 10 and 15 cm spacings. Consequently, the higher $fPAR_i$ in narrow spacings resulted in a significant increase in the PAR_{ia} by the crop during regrowths (rmANOVA; $p < 0.0001$; Appendix A). As row spacing was reduced PAR_{ia} increased linearly (polynomial contrasts; $p < 0.0001$). No interaction with time was detected so we performed a linear regression including the sum of radiation intercepted during five regrowths as a function of row spacing (Fig. 6a). Remarkably, we found a significant function ($p < 0.0001$) that explains 76% of PAR_{ia} variation, with an increase of 8 MJ cm⁻¹ of spacing reduction (Fig. 6a).

Radiation use efficiency was also affected by row spacing (rmANOVA; $p = 0.0013$), and no interaction with time was detected (Appendix A). This variable presented an optimal pattern, with the highest RUE values at 15 and 17.5 cm and decreases for narrower and wider spacings. A significant linear relation (polynomial contrasts; $p = 0.0019$) associated with linear reductions was observed when moving away from optimal spacings, and a quadratic relation (polynomial contrasts; $p = 0.0084$) was also detected in relation to the existence of the optimal range previously mentioned. The optimal pattern of RUE in each regrowth was clearly confirmed when the RUE of the entire period was estimated as the ratio of ADM and PAR_{ia} sums (Fig. 6b). In this case, a quadratic polynomial function ($p = 0.0036$) explained 45% of RUE variation. The optimum global RUE was observed for 15 cm spacing (1.98 g DM MJ⁻¹), where RUE was 25% higher than the widest spacing (30 cm) and 13% higher than the narrowest spacing (10 cm). Coincidentally, the RUE estimated as the slope of the relationship between the accumulation of ADM and PAR_{ia} of the overall period (Appendix B) was higher at 15 cm spacing (2.17 g DM MJ⁻¹) ($p < 0.05$) than at 30 cm and 10 cm (1.73 and 1.93 g DM MJ⁻¹, respectively).

Although no interaction was detected between time and row spacing, time had a significant effect on both variables (rmANOVAs; $p < 0.0001$; Appendix A). In September PAR_{ia} was the highest (273 MJ m⁻²) followed by November (194 MJ m⁻²); was intermediate in October and December (164 and 162 MJ m⁻²) and lowest in January (149 MJ m⁻²). The highest RUE values were registered during the middle of the spring and beginning of the summer (October 1.89 g DM MJ⁻¹, November 2.24 g DM MJ⁻¹ and December 1.97 g DM MJ⁻¹), with the lowest values at the beginning and the end of the experimental period (September 1.40 g DM MJ⁻¹

and January 1.57 g DM MJ⁻¹). A significant linear relationship was detected between temperature and RUE ($p = 0.0127$) that explained 25% of the variation. The function was substantially improved when January regrowth was excluded from the analysis (64% of the variation explained, $p < 0.0001$) with a RUE increase of 0.06 g DM MJ⁻¹ per degree increase.

3.4. Canopy characteristics

The leaf:stem ratio did not change with row spacing (rmANOVA; $p = 0.26$) and though it was affected by time ($p < 0.0001$), it did not interact with spacing ($p = 0.56$). During spring regrowths, the canopy was leafy, with the highest leaf:stem ratio in October (1.60), followed by September (1.48). In summer regrowths, stems represented a greater proportion of biomass, with a consequently lower leaf:stem ratio (0.74).

Row spacing influenced the LAI of the lucerne crop in both regrowths studied (December and January) (Table 1), and this was related with the $fPAR_i$ as LAI directly affects light capture. First, in December the widest spacing (30 cm) had lower LAI than other spacings, with an average reduction of 25%. In January, 30–20 and 10 cm spacings had lower LAI than the 15 cm spacings. The LAI of those row spacings was 32% lower on average. According to these results, it can be concluded that significant differences in LAI between spacings occurred in those with more contrasting ADM (Fig. 3a). No significant differences were found for the extinction coefficient k (data not shown), with a value of 0.72 in December

Table 1

Leaf area index (LAI) average values of lucerne canopy cultivated at five row spacings (10–15–17.5–20 and 30 cm) of two regrowths (December and January) of the first production year at Rafaela, Santa Fe, Argentina.

	LAI (December)	LAI (January)
Row spacing (cm)		
10	4.10 ^{a*}	2.25 ^b
15	3.64 ^a	3.03 ^a
17.5	3.87 ^a	2.31 ^{ab}
20	3.69 ^a	2.09 ^b
30	2.87 ^b	1.86 ^b

* Different letters in the column show significant differences at 5% level (LSD).

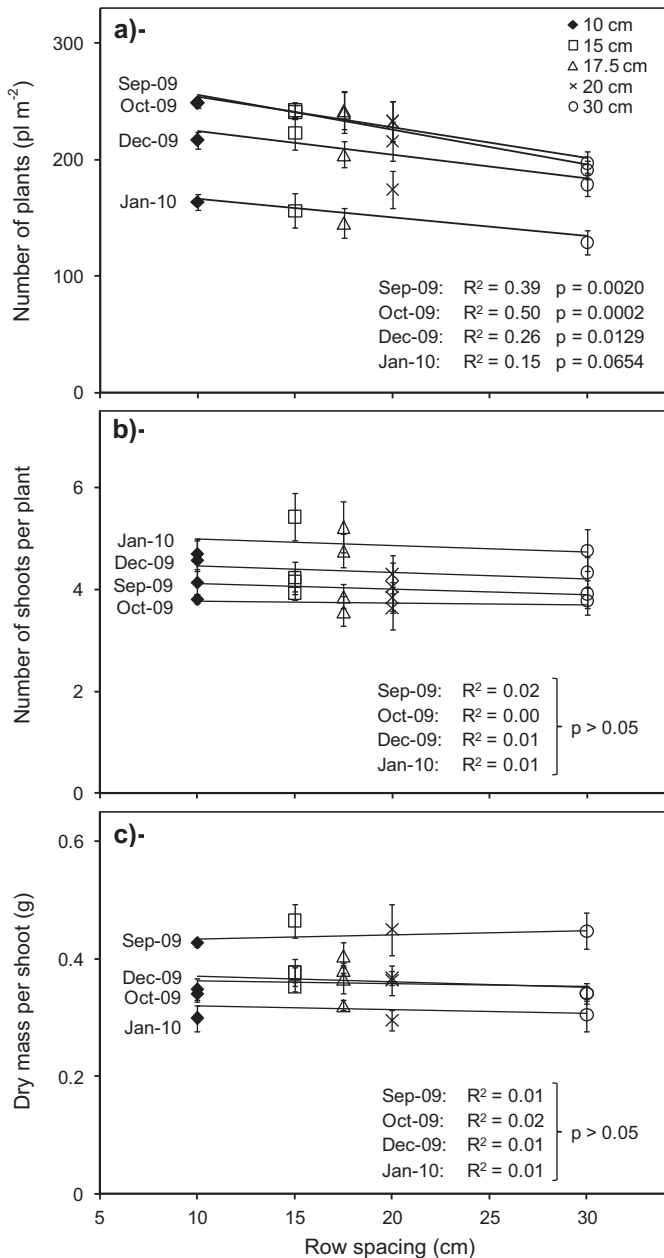


Fig. 4. Forage yield components: (a) plant density, (b) number of shoots per plant, and (c) dry mass per shoot of lucerne as a function of row spacing (10–15–17.5–20 and 30 cm) of four regrowths in the spring–summer of the first production year at Rafaela, Santa Fe, Argentina. Plots were thinned at post-emergence to uniform plant density ($250 \text{ plants m}^{-2}$). Values are means \pm SE of five replicates.

and 0.95 in January and high variability in both ($CV = 15$ and 23% , respectively).

Row spacing significantly influenced SPAD along the canopy structure. The SPAD values were similar for all treatments when comparing the high and middle layers of the canopy; however, reductions due to narrow row spacing were registered in the lower stratum of the canopy (Table 2). A trend was identified in December (ANOVA; $p = 0.08$), with lower values in 10 cm than 20 and 30 cm spacings. This was later confirmed in January (ANOVA; $p < 0.05$) with lower SPAD values in 10 and 15 cm than in 30 cm spacings. The reduction of the SPAD values was 12% on average.

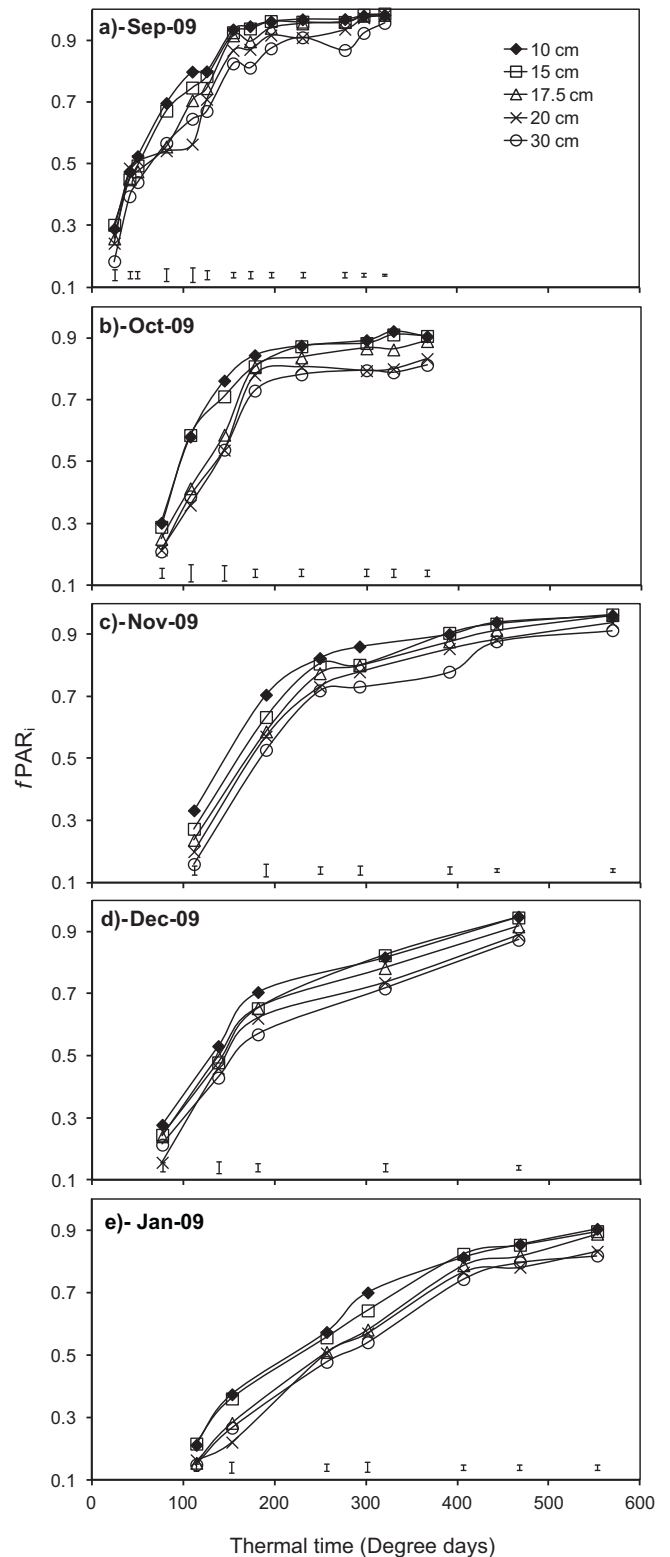


Fig. 5. Fraction of photosynthetically active radiation intercepted ($fPAR_i$) by lucerne canopy as a function of thermal time cultivated at five row spacings (10–15–17.5–20 and 30 cm) of five regrowths in the spring–summer of the first production year at Rafaela, Santa Fe, Argentina. Values are means of five replicates. Vertical bars denote SE per sampling date.

Table 2

Leaf greenness (SPAD units) average values of three layers (low, middle and high) of lucerne canopy cultivated at five row spacings (10–15–17.5–20 and 30 cm) of two regrowths (December and January) of the first production year at Rafaela, Santa Fe, Argentina.

Layer (cm)	SPAD (December)			SPAD (January)		
	Low (0–20)	Middle (20–40)	High (40–60)	Low (0–15)	Middle (15–30)	High (30–45)
Row spacing (cm)						
10	29.6	37.7	44.9	34.9 ^{b*}	42.2	51.0
15	32.6	38.9	45.3	35.5 ^b	43.4	51.0
17.5	33.0	39.0	45.1	36.6 ^{ab}	44.1	51.2
20	33.2	37.7	43.3	37.7 ^{ab}	43.9	49.4
30	34.0	38.6	44.0	40.0 ^a	45.2	50.1

* Different letters in the column show significant differences at 5% level (LSD).

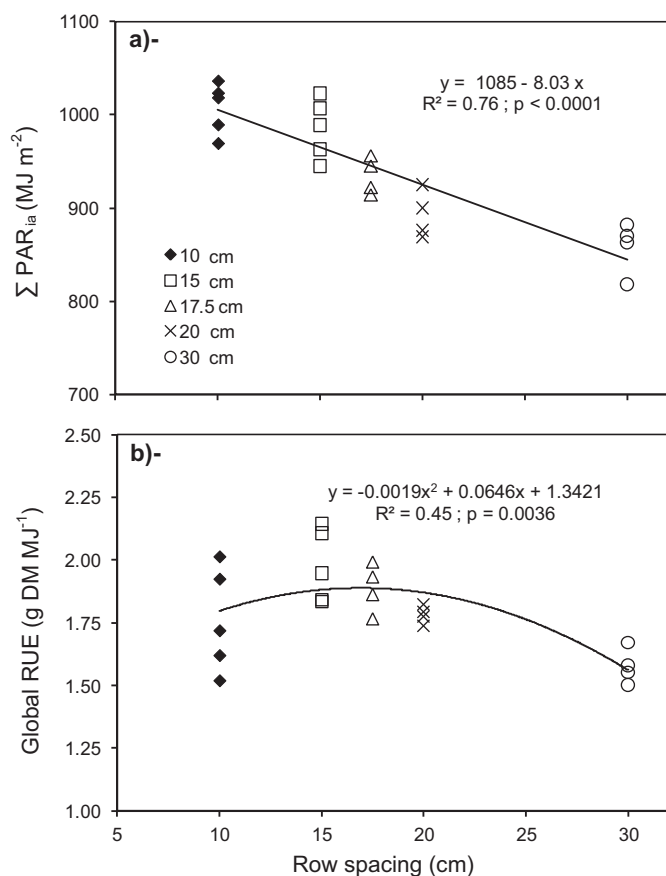


Fig. 6. (a) Intercepted and accumulated PAR ($\sum PAR_{ia}$) of five regrowths and (b) global radiation use efficiency (RUE) of lucerne as a function of row spacing (10–15–17.5–20 and 30 cm) in the spring–summer of the first production year at Rafaela, Santa Fe, Argentina. Global RUE was calculated as the ratio between total aerial dry matter (ADM) and $\sum PAR_{ia}$ of five regrowths (September–January). There are presented values of five replicates.

4. Discussion

4.1. Effects of row spacing on biomass production and plant density

By using the gradient generated in plant spatial arrangement due to row spacing treatments and maintained during the experimental period (Figs. 1 and 2), we were able to test the hypothesis of this work. The results demonstrate that there was a significant linear relationship of ADM increase as row spacing was reduced until an optimal distance (around 13 cm), below which biomass accumulation tended to decrease. A bi-linear regression was adjusted to represent that pattern, explaining 60% of the variability (Fig. 3b). An increased ADM in more square spatial arrangements coincides with the proposed hypothesis and also with previous experiences

in Australia (Roufai, 1975) and Argentina (Mattera et al., 2009), where ADM increases (around 5–20%) were found in long-term trials of row spacing reduction. In the present experiment, the higher relative increase (between 16 and 42%) was probably the result of assessing spring and early summer regrowths, when row spacing effects are concentrated (Mattera et al., 2009) and partition to crown and roots of the lucerne plants is still relatively lower (Khaiti and Lemaire, 1992; Brown et al., 2006), enhancing the effects on aerial growth. Otherwise, as expected biomass was affected by regrowth. It is remarkable the biomass reduction during summer, being consistent with reports of lower yields under well-watered conditions (Evans and Peaden, 1984) that were associated with warmer temperatures that reduced growth period duration. As lucerne is a long-day plant (Major et al., 1991) similar effect could also be produced by longer photoperiods.

The forage yield component that changed among spacings was plant density, which increased with spacing reduction (Fig. 4). Although plant density was initially established by thinning, it was an important determinant of crop production. In many species, plant mortality rates are related to the distance of the nearest neighbour (Skinner, 2005), which coincides with our results as narrow spacing increased intra-row distance between plants (Fig. 1). As spacing was reduced, plant mortality decreased, sign of less intense intraspecific competition within the crop canopy. The differences in size hierarchy, with plants with bigger crowns in narrow spacing (15 and 17.5 cm), could also be an indicator of more favourable growing conditions (Park et al., 2003). Moreover, could be that compensatory growth was operating at those spacings, in coincidence with both higher RUE and dry mass per shoot (trend). Instead, for wide spacings by the end of the first year there was no evidence of compensation. We speculate that biomass in the following year would have continued being higher in narrow spacings, especially in 15 and 17.5 cm spacings. The registered changes in radiation interception and canopy characteristics produced by row spacing suggest that plant density dynamic was mainly influenced by the light environment, although competition for belowground resources cannot be fully discarded. As lucerne is usually sown at high densities to assure uniform crop canopy cover, plant mortality is expected to follow self-thinning law (Matthew et al., 1995) caused by competition for light (Sackville Hamilton et al., 1995). Our data suggest different trajectories between row spacings as higher plant density with the same plant size were found in narrow spacings that may be due to reduced competition for light, and requires to be studied in a long-term experiment. For narrow spacings, it may be more feasible to find a higher plant density that increase biomass production (Volencic et al., 1987). However, one could assume that if the response of plant density is not accompanied by an improvement in the plant spatial arrangement, there would not be a biomass increase, as was observed for 15 cm spacing in a previous experiment at Rafaela-Argentina (Mattera et al., 2009). Additionally, neither dry mass per shoot nor shoots per plant were affected by row spacing, a finding that contrast with previous research on lucerne that have found an important role of the dry

mass per shoot in biomass responses to fertilization (Berg et al., 2005) and defoliation frequency (Teixeira et al., 2007a). Our results reveal the significant improvement of plant density with lower intraspecific competition under narrow spacings, though this did not happen for the other forage yield components.

4.2. Row spacing effects on light interception and radiation use efficiency

Radiation interception increased as row spacing was reduced (Fig. 6a). This response was observed for many grain and industrial crops, though this is the first report for a pasture canopy. The effects on interception were explained by the improved canopy closure, *i.e.* greater interception during regrowth and faster reach of the critical LAI in narrow spacings (Fig. 5). In a lucerne crop, then, the generation of more square arrangements by reducing row spacing improved radiation interception, increasing biomass production. Similarly, we found a significant increase of LAI at the time of cutting (Table 1), but the differences were only confirmed for the most contrasting spacings in yield terms (Fig. 3). In other crops, narrow spacings were reported to improve radiation interception by changes in canopy architecture, *i.e.* greater light extinction coefficient (k) (corn: Flenet et al., 1996 and Barbieri et al., 2000; soybean: Flenet et al., 1996; sunflower: Zaffaroni and Schneider, 1989 and Flenet et al., 1996). In our experiment, the extinction coefficient k showed no differences among spacings. However, it should be noted that the coefficient was estimated with data obtained just before cutting, so the way k evolved during the course of the regrowth is not known. In lucerne, the nitrogen distribution profile is associated with light distribution profile (Lemaire et al., 1991) and the lower SPAD values found in a low canopy stratum in narrow spacings suggest greater light attenuation that could be associated with higher k during regrowth. On the other hand, k in lucerne has shown stability (Varella, 2002; Teixeira et al., 2007b, 2011), probably associated with an efficient canopy given by the expression of various leaf angles between layers and the ability of the leaflets to move following the sun (Travis and Reed, 1983; Heichel et al., 1988). The clarification of this aspect requires further experimental investigation.

The relative change in biomass accumulation (up to 40%) among spacings was greater than the interception change (up to 16%) and was related to the response observed in the RUE. Unexpectedly, we found that RUE was optimal around the 15 cm spacing (Fig. 6b). We propose two complementary explanations for this. First, RUE diminished in 10 cm spacing, which had the lowest SPAD values of the lower canopy stratum (Table 2). This would be associated with the early canopy closure, and the strong relationship between the light that reaches the leaves and its nitrogen content (Lemaire et al., 1991). In this case, the lower SPAD values would be an indicator of reduced photosynthesis in this stratum, and also greater leaf senescence, both of which negatively affect the RUE. Similarly, other authors also found RUE reductions in response to narrow spacing (Board et al., 1994; Maddonni et al., 2006). Second, lower RUE was correlated with a lower LAI at the time of cutting (Fig. 7). This fact could explain the lower RUE values above the optimal spacings, especially in 30 cm spacing, which possessed the lowest LAI value, probably associated with an enhanced self-thinning process. A relation between RUE and LAI was previously reported for other crops (Sinclair and Horie, 1989; Ruíz and Bertero, 2008). The effect of LAI on RUE was mostly observed at low LAI values (Sinclair and Horie, 1989), where a greater proportion of the leaves were light saturated thus lowering the crop's quantum efficiency. This would be the case in our experiment because lucerne grew for short periods, and the majority of the regrowths passed with low LAIs. In conclusion, row spacing would have changed leaf irradiance within the canopy, as spacing was reduced leaves would have been exposed

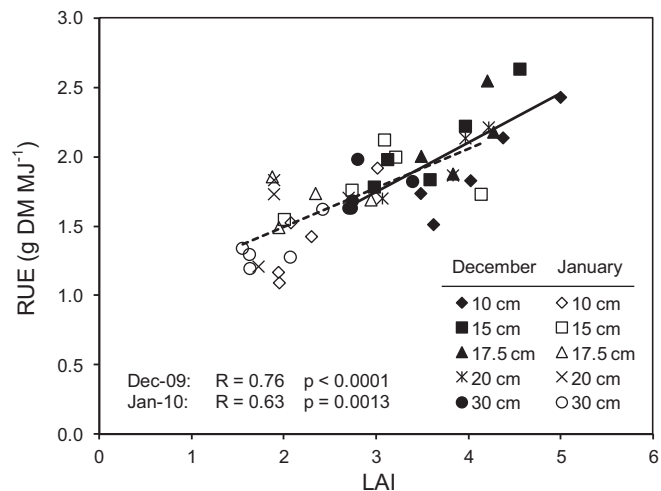


Fig. 7. Relationship between leaf area index (LAI) and radiation use efficiency (RUE) for lucerne cultivated at five row spacings (10–15–17.5–20 and 30 cm) of two regrowths in the spring–summer of the first production year at Rafaela, Santa Fe, Argentina.

to lower irradiance due to higher LAIs, thus increasing RUE. However, it should exist a minimum leaf irradiance, reached near 15 cm spacing, below which some leaves senesce, reducing RUE, as was observed in 10 cm spacing. Other hypothesis interrelated is about partition between shoots/roots, relevant in lucerne crops (Khaiti and Lemaire, 1992; Teixeira et al., 2008); at low irradiance plants allocate more assimilates to shoot preferentially to roots (Poorter and Nagel, 2000; Poorter et al., 2012), that would have increased RUE based on aerial biomass in narrow spacings. Further research is necessary to study these hypotheses.

The RUE was also affected by regrowth (*i.e.* seasonality) which is consistent with previous reports that showed the correlation between RUE and air temperature, with linear increases of RUE as temperature rises (Collino et al., 2005; Brown et al., 2006). However, our results indicated a weak relationship between RUE and air temperature, coinciding with Brown et al. (2006) when RUE was estimated with aerial biomass, as temperature effects can be confounded with changes in partition between shoots/roots. In the case of the last harvest (January, when temperatures exceeded 25 °C) RUE decreased, probably associated with the beginning of a higher partition process to belowground structures. This seasonal trend also coincides with the pattern registered by Thiébeau et al. (2011) in lucerne regrowth crops, where partition to belowground organs raised with thermal time accumulation and reached higher values at the summer season. Thus, the relationship between RUE and temperature was more evident when this last harvest was excluded, being then comparable to the temperature framework developed by Collino et al. (2005) in a similar environment.

5. Conclusions and implications

A more square spatial arrangement in narrow spacings promoted a lower intraspecific competition that allowed for greater plant survival without reductions in plant size, which resulted in the increase of biomass production. As it has been observed for other agronomic practices such as defoliation frequency (Teixeira et al., 2007b, 2008), both radiation model components (*i.e.* PAR_{ia} and RUE) were affected by row spacing: the response was linear for the PAR_{ia} and optimum for the RUE. The bi-linear response of ADM to row spacing was determined by the optimal pattern of RUE. Lucerne has been characterized as an efficient species for radiation capture (Heichel et al., 1988; Travis and Reed, 1983); however, the results presented here evidence the limits of plasticity to compensate for changes in plant spatial arrangement. In the future,

the study of row spacing effects on light extinction coefficient and LAI at different moments during the course of the regrowth could provide greater understanding of the mechanisms involved. In addition, the nutritive value of the forage was not affected by row spacing for the trait evaluated here, *i.e.*, the leaf:stem ratio. Thus, narrow spacing is a practice which could contribute to land intensification use in husbandry systems by helping to achieve forage yield potential. The current machinery design seems to go against such agronomical management, because in Argentina, sowing equipment tends to greater separation between rows. Additionally, other aspects should be considered when determining the optimum spacing for the lucerne crop such as type of cultivars (*i.e.* dormancy and foliation), the cost of equipment, the prevalence of disease and the competitiveness of weeds.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.eja.2012.10.008>.

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