Temperature and water availability effects on radiation and water use efficiencies in alfalfa (*Medicago sativa* L.)

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Abstract. Alfalfa, the most important forage crop in Argentina, shows considerable variability in forage production caused by variations in inter-annual rainfall and intra-annual radiation and temperature regimes. Such variation may affect radiation use efficiency and water use efficiency. This paper seeks to study the effects of temperature and water availability on radiation use efficiency and water use efficiency. We conducted the experiment in Córdoba, Argentina, under irrigated and droughted conditions. Drought was imposed by mobile rainout shelters during 3 consecutive periods. We measured forage, intercepted photosynthetically active radiation and water use to calculate radiation use efficiency and water use efficiency between cuttings. Under irrigation, radiation use efficiency and water use efficiency normalised by daytime vapour pressure deficit, were not limited by mean temperature above 21.3 and 21.9°C, respectively. Below those critical values, both variables decreased consistently with temperature decrements. Under drought, radiation use efficiency tended to decrease and water use efficiency tended to increase. In addition, the relationship between relative dry matter and relative water use was not linear, as reported in previous studies for annual crops.

Additional keywords: efficiency, drought, air temperature.

Introduction

Alfalfa (*Medicago sativa* L.) is the most important perennial forage crop in Argentina. There are about 5 million hectares (INDEC 2005) including pure stands and stands mixed with other forage species, growing mostly in the Argentinean Pampa region, between the parallels 30–40°S and the meridians 58–65°W. Due to its adaptability to different environments, excellent nutritional quality, and high forage yields, alfalfa is the basis of milk and beef production.

Average seasonal dry matter (DM) yields under rain-fed conditions across the Pampas are between 10 and 18 t/ha.year (Rossanigo 1996), although a minimum of 5 t/ha.year (Rossanigo *et al*. 1995) and a maximum value of 29 t/ha.year (Rossanigo 1996), have been reported. This high seasonal variability in forage production could be attributed mainly to variability in water supply, caused by variations in rainfall regimes among locations, or considerable variability in inter-annual rainfall patterns within locations (Hall *et al*. 1992), and by fluctuations in watertable depth (Dardanelli and Collino 2002). Both water supply sources (rainfall and watertable), cause periods of alternating adequate or insufficient water balance. Mean annual rainfall values across the Pampas vary between 600 and 1000 mm/year.

Under non-limiting water conditions, radiation and temperature variability constitute the main sources of DM variations. Mean annual incident solar radiation and mean temperature (T_{mean}) values in the Pampas, vary from 15–17 MJ/m^2.day and 14–18°C, respectively (Racca *et al*. 2001). The inter-annual variation in radiation and temperature is less than the variation within the growing season (intra-annual). The ranges of monthly mean maximum and minimum values of solar radiation and temperature across this region are 22–24 to 7–11 MJ/m^2.day, and 20–25 to 7–12°C, respectively. Within these wide air temperature ranges, radiation use efficiency (RUE) might be limited by suboptimal temperatures outside the 25–30°C generic optimal range reported by Doorenbos and Kassam (1979). Temperatures limiting RUE might reduce also water use efficiency (WUE) because environmental limitations to DM production limit also the ratio between DM and transpired water. On the other hand, daytime vapour pressure deficit (VPD) affects WUE (Tanner and Sinclair 1983). Monthly daytime VPD across the region and throughout the seasons varies between 0.5 and 2 kPa. Normalisation of WUE by VPD seems to be a necessary step before defining temperature limitations to WUE.

Under limiting water conditions, drought constitutes another source of RUE and WUE variability. Several reports for annual crops in the Pampas demonstrated that, under drought, RUE decreased for soybean (Andriani *et al*. 1991)

and peanut (Collino *et al.* 2001), and that WUE increased for wheat (Abbate *et al.* 2004) and peanut (Ferreyra *et al.* 2003). However, for a perennial crop such as alfalfa, the RUE and WUE responses to environmental variations like temperature, solar radiation and drought, are more complex than for annual crops because each growth period between cuttings is exposed to different combinations of solar radiation, temperature and water regimes.

The objective of this paper was to study the effects of temperature throughout the growing season on alfalfa RUE and WUE, for both non-limiting and limiting water availability conditions.

Materials and methods

Crop management and experimental design

The study was conducted at the Institute of Phytopathology and Plant Physiology (IFFIVE)-INTA in Córdoba, Argentina (31°24′S, 61°11′W). The soil is a silty loam Enthic Haplustoll (USDA Soil Taxonomy) with the horizons A, AC, and C, 0–23, 23–54, and >54 cm, respectively, with a silt content ranging from 67 to 69%, and with pH 7.1–7.7. The soil profile does not present any physical constraints to root development.

Alfalfa var. Victoria SP INTA (moderately dormant), was seeded on 15 March 2000, with a 300 seed/m^2 density and 0.2 m row spacing. The experiment was performed under 3 mobile rainout shelters (each 5 by 21 m). Under each shelter, 2 treatments were used: irrigated, IRR, and water-stressed, WS, arranged in a completely randomised design with 3 replicates. Plot size was 5 by 3 m. In all plots, rainfall was withheld during the imposed drought period by covering plots only during rainfall events, but IRR plots were watered to maintain an available water content level greater than 60% within 0–250 cm soil profile. Irrigation was applied using a drip system. The WS plots, each one under a different shelter, received no irrigation during 3 consecutive drought periods. The start date, end date, and duration of each drought period were: shelter 1 — 5 October 2000 to 16 January 2001 (104 days); shelter 2 — 17 January 2001 to 8 August 2001 (204 days); and shelter 3 — 9 August 2001 to 8 March 2002 (212 days). At the beginning of the 1st drought period, the available water content within the 0–585 cm soil profile was 90% of the potential extractable soil water, defined as the available water between the drained upper limit and the lower limit. At the beginning of the 2nd and 3rd drought periods, soil profile was 75% of the potential extractable soil water. During the 3 imposed drought periods, WS plots received no water until measured crop water use practically ceased and plants showed severe stress symptoms. Weeds were eliminated by combining clethodim (Select, Bayer Argentina SA) applications with hand weeding. Aphids were controlled using pirimicarb (Aficida, Zeneca SAIC).

Sampling and experimental analysis

The forage DM (g/m^2) of each cutting was obtained from each replicate by harvesting 11 m^2 samples when the first flowers appeared (10% flowering) or when new crown shoots reached 5 cm in height. Plant material was oven-dried at 100°C until constant weight.

Daily values of maximum and minimum temperature, relative humidity, incident solar radiation, and rainfall were recorded from a weather station located close to the trial.

The daily incoming photosynthetically active radiation (PAR) (MJ/m^2.day), was estimated by multiplying the incident solar radiation by 0.5, as suggested by Monteith (1972). The fraction of PAR intercepted by the crop (*f*), was calculated for the IRR and WS treatments as follows:

$$f = 1 - \frac{I}{I_0} \tag{1}$$

where *I* is the PAR (μmol/m^2.s) measured at ground level and I_0 is the incoming PAR (μmol/m^2.s) at the top of the canopy. Both *I* and I_0 were measured at 1200 hours, 5–6 times at regular intervals across each growth period, with a LI-1000 data-logger connected to a LI-191SA line quantum sensor (Li-Cor, Inc., USA). Daily *f* was estimated by linear interpolation between successive *f* measurements.

The cumulative intercepted PAR (PAR$_i$) (MJ/m^2), for each growth period between cuttings was calculated as:

$$PAR_i = \sum_{N=1}^{N} f \times PAR \tag{2}$$

where *N* is the number of days for any single growth period. The radiation use efficiency (RUE, g/MJ) for each cutting was calculated as the ratio between DM and PAR$_i$.

Soil moisture was measured every 6–9 days on each experimental plot at intervals of 15–40 cm down to 585 cm using a Troxler 4301 neutron probe (Troxler Electronic Laboratories Inc., USA). The volumetric water content of each layer was accumulated across depths to calculate the water stored within the soil profile. The water use (WU) (mm) for each growth period between cuttings was determined by accumulating the water use between successive soil moisture measurements using the following equation:

$$WU = \sum_{N=1}^{N} \Delta S + 1 \tag{3}$$

where *N* is the number of soil moisture measurements taken during the growth period, ΔS is the change (mm) in stored water within the soil profile, and *I* is the irrigation (mm). In WS plots, *I* was equal to zero during the 3 growth imposed periods. Water losses by drainage below the measured zone were disregarded.

The WUE (g/kg) was calculated between cuttings as the quotient of DM and WU. A normalised water use efficiency (WUE$_n$) (g/kg.kPa) was calculated by multiplying WUE by the VPD (kPa), as suggested by Tanner and Sinclair (1983). The VPD values used for WUE$_n$ calculations were estimated daily as the difference between the average daily saturated vapour pressure (e$_a$) and the actual vapour pressure (e$_d$), using daily maximum and minimum temperature (T$_{max}$, T$_{min}$) and daily maximum and minimum relative humidity, following the procedure of Allen *et al.* (1998). Because evapotranspiration occurs during the day, daytime VPD is likely to be a better estimator than daily mean VPD (Howell 1990). Then e$_a$ was estimated using a weighing parameter equal to 0.72, as reported by Abbate *et al.* (2004), for the same location under study. Thus, e$_a$ was calculated as:

$$e_a = e_{aT_{max}}0.72 + e_{aT_{min}}0.28. \tag{4}$$

This procedure gives more weight to T$_{max}$, which corresponds to daytime VPD values.

The relationships between RUE, WUE and WUE$_n$ and mean air temperature for all growth periods between cuttings were set using data from IRR plots. To evaluate if changes in these relationships across temperature between groups of cuttings occurred, different linear regression models were compared. Statistical analysis was carried out using InfoStat (InfoStat 2002).

Results and discussion

The 10-day average values of minimum and maximum temperature, incident solar radiation and daytime vapour pressure deficit throughout the experimental period, ranged from 3.4–22.9°C, 15.3–33.5°C, 6.2–26.0 MJ/m^2.day and 0.49–2.21 kPa, respectively (Fig. 1). Growth periods between cuttings occurred under a wide range of combinations of climatic conditions.

In the IRR treatment, we studied temperature effects on RUE. We first considered a simple linear relation between RUE and T_{mean}, obtaining the following fitted equation:

$$RUE = -0.154 + 0.061T_{mean} \qquad (5)$$

with root mean squared error (RMSE) = 0.154 and $r^2 = 0.684$.

An examination of the residuals suggested that a more complex model should be considered. A quadratic model improves the fit, but the residuals suggested that a fit with 2 separate linear models with one joint point (Hocking 1996) might be more acceptable, with a change in slope at about 20–22°C. We then fitted 2 line segments to describe the relationship using a dummy variable (Drapper and Smith 1998) to split the data in the above-mentioned range of T_{mean}. Statistical differences between group slopes were evaluated at $\alpha = 0.05$. Maximum differences between slopes were used to suggest a joint point of mean air temperature.
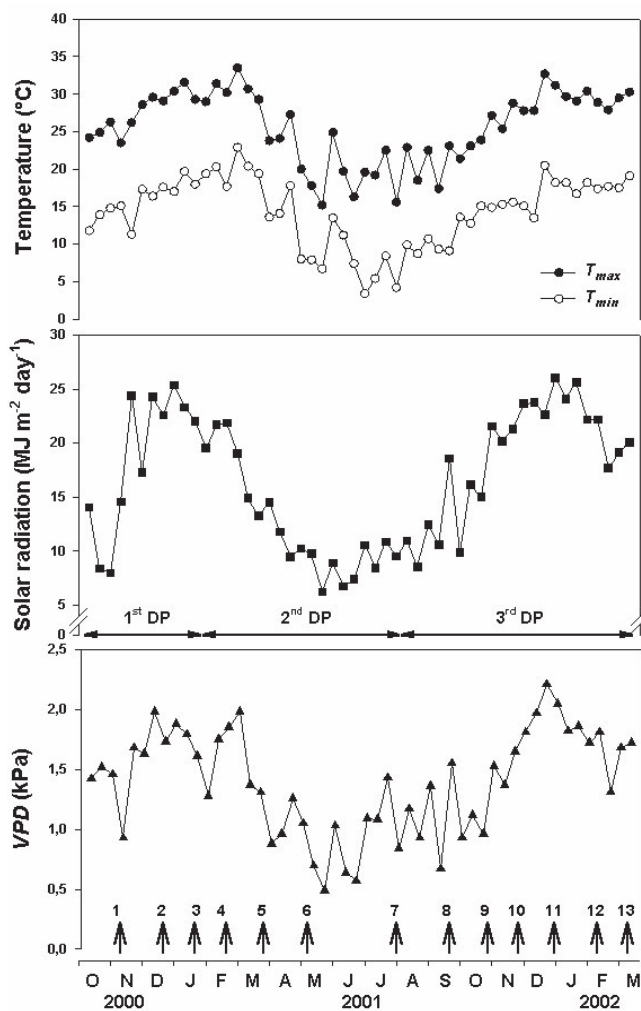
A maximum slope difference between both linear segments was attained at 21.3°C ($P = 0.021$). Finally, we fitted the data to the following model to obtain goodness of fit measures for the joint point model:

$$RUE = -0.408 + 0.0759T_{mean} - 0.0419z(T_{mean} - 21.3) \qquad (6)$$

where z is a dummy variable which assumes a value equal to 1 if T_{mean} is ≥21.3°C, otherwise $z = 0$. The improvement over the simpler linear fit was apparent since RMSE = 0.149 and $r^2 = 0.713$ for this model containing a joint point at 21.3°C. Figure 2 shows the segmented regression fit to RUE and the joint-point temperature value.

The slope of a linear regression from the 2nd segment did not differ from 0 ($P = 0.569$) indicating that within the T_{mean} range values above 21.3°C (21.4–26.0°C) included in this study, air temperature did not limit RUE. Below the critical 21.3°C value, RUE decreased consistently with mean temperature decrements.

Doorenbos and Pruitt (1977) reported a generic 25–30°C optimum range for crop growth. Al-Hamdani and Todd (1990), found no decrease in alfalfa canopy net photosynthesis until 34°C. In our study, maximum temperatures rarely surpassed this value, as deduced from decadic maximum temperature values shown in Figure 1. The critical value obtained in this study and its corresponding mean daily amplitude (12°C) is in agreement with the Patterson (1993) findings. In this study, performed under controlled chambers, maximum dry weight was obtained with a minimum and maximum temperature of 18 and 29°C, respectively (23.5°C mean temperature), and was reduced with a minimum and maximum temperature of 15 and 25°C, respectively (20°C mean temperature). Al-Hamdani and Todd (1990) found a net photosynthesis decrease below 21°C and Doorenbos and Pruitt (1977)

Figure 1. Ten-day average maximum (T_{max}) and minimum (T_{min}) temperature, incident solar radiation and daytime vapour pressure deficit (VPD), during the experimental period. The arrows represent the cuttings, and the horizontal segments represent the 1st, 2nd, and 3rd drought period (DP).
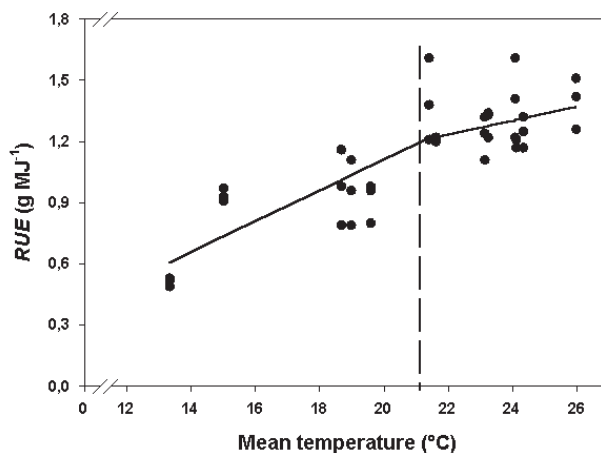

Figure 2. Radiation use efficiency (RUE) as a function of mean temperature. The solid line represents the segmented regression fit to RUE. The dashed line indicates the 21.3°C joint-point mean temperature value.

reported 25°C as a generic critical value below which alfalfa vegetative growth decreases.

To our knowledge, no previous critical temperature values for RUE have been determined for alfalfa. However, Duru and Langlet (1989) in experiments carried out in Toulouse, France, found significant RUE reductions under non-limiting water and nitrogen supplies in fall cuttings as compared with late spring-summer cuttings. In this environment, fall cuttings grow under cooler temperatures. Our 1.30 ± 0.14 g/MJ mean average RUE, corresponding to groups of cuttings growing under a non-limiting range of temperatures, was lower than the 1.71 ± 0.12 g/MJ value reported by Duru and Langlet (1989) and the 1.76 RUE value reported by Gosse *et al.* (1986), if considered late spring and summer cuttings. The lower value found in our study might be attributed to several factors such as differences in total radiation and the proportion of diffuse radiation, different temperature regimes, DM partitioning between shoots plus leaves and crown plus roots, among other possible causes. Further research is necessary to elucidate such differences.

In the IRR treatment, WUE for individual cuttings ranged from 0.90 to 2.39 g/kg. For the same location and variety, López *et al.* (1997) reported 1.34–2.54 g/kg. Bolger and Matches (1990) in Texas (USA) reported that in individual cuttings WUE varied from 1.19 to 2.91 g/kg. Guitjens (1990) reviewed the results of several experiments and reported a wide variation among individual cuttings from 0.6 to 3.0 g/kg including both rain-fed and irrigated experiments. This wide variation among cuttings throughout the growing season might be attributed to different radiation, temperatures, VPD combinations, and dormancy response. In our study, no effect of T_{mean} on WUE was observed (Fig. 3*a*). However, when WUE was normalised by daytime VPD, temperature effects on WUE_n followed a similar pattern to that observed for RUE. A comparison between 2 linear models (with and without joint point), as described for T_{mean} and RUE relationship, was then performed. The fitted equation using the simple linear model was:

$$WUE_n = -0.366 + 0.134 T_{mean} \qquad (7)$$

with RMSE = 0.554 and $r^2 = 0.446$. An improved goodness of fit was obtained with 2 separate linear models with one joint point:

$$WUE_n = -1.286 + 0.1868 T_{mean} - 0.1934z(T_{mean} - 21.9) \quad (8)$$

with RMSE = 0.537 and $r^2 = 0.493$.

The 21.9°C joint point was previously obtained by calculating the maximum differences between slopes of groups of cuttings under T_{mean} lower and higher than the joint point temperature ($P = 0.027$). This joint point value (Fig. 3*b*) was close to the 21.3°C obtained for RUE. The slope of a linear regression from the 2nd segment did not differ from 0 ($P = 0.673$) indicating that within the T_{mean} range values above 21.9–26.0°C (range observed in this

study) air temperature did not limited WUE_n. Below the critical 21.9°C value, WUE_n decreased consistently with mean temperature decrements.

We may assume that temperature affected WUE_n in the same way as was observed for RUE, limiting DM production, because DM is the common numerator of both RUE and WUE_n equations. WUE normalisation allowed us to separate the effect of VPD on WUE from the effect of other environmental variables such as mean temperature. Asseng and Hsiao (2000) demonstrated that, on a seasonal basis, alfalfa WUE normalised by pan evaporation was similar among different environments. To our knowledge, no previous studies normalising alfalfa WUE by VPD have been reported. Abbate *et al.* (2004) demonstrated that VPD was the best meteorological index to normalise contrasting wheat WUE values across the Argentine Pampa region. In our study, normalisation above the critical temperature allowed us to reduce the variation coefficient from 21 (WUE) to 17% (WUE_n). For this group of cuttings, mean WUE and WUE_n values were 1.69 g/kg and 2.86 g/kg.kPa, respectively.

Seasonal WUE was 1.61 g/kg. Alfalfa WUE reported in the literature varies widely ranging from 0.85 (Saeed and El-Nadi 1997) to 2.31 g/kg (Grimes *et al.* 1992). The WUE
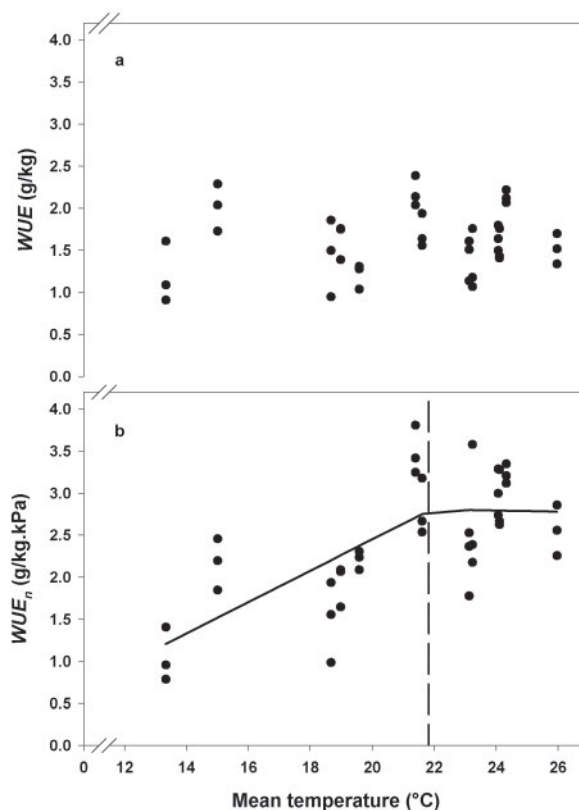
Figure 3. (*a*) Water use efficiency (WUE) and (*b*) water use efficiency normalised by daytime vapour pressure deficit (WUE_n), as a function of mean temperature. The solid line represents the segmented regression fit to WUE_n. The dashed line represents the 21.9°C joint-point mean temperature value.

value found in our study is similar to values reported by Bauder *et al*. (1978), Wright (1988), Bolger and Matches (1990), and Guitjens (1990) with 1.59, 1.72, 1.74 and 1.52 g/kg, respectively. López *et al*. (1997) reported seasonal WUE for the same location and variety of 1.86 g/kg, higher than the value found in our study. This difference is caused by alfalfa WUE variation between years in relation to environmental variation, in agreement with conclusions of Smeal *et al*. (1992).

In WS treatments, at the end of the 3 consecutive imposed drought periods, available water was depleted to 250 cm (Fig. 4). Below 250 cm, total water extraction was similar by the end of the 2nd and 3rd drought periods and greater than that observed at the end of the 1st period. These results indicate that during the 1st drought period, the root system was not completely developed. This is consistent with results of Borg and Grimes (1986), who reported that the alfalfa root system completes its development during the 2nd harvesting season. In our study, the 2nd harvesting season started close to the beginning of the 2nd drought period. As consequence of drought, DM, PAR$_i$ and WU, were rapidly reduced before the onset of the 3 drought periods (Fig. 5*a–c*) because the alfalfa variety used in this study demonstrated the lowest potential soil water extraction rate among several crops (Dardanelli *et al*. 1997). On the other hand, this low rate of water uptake allowed the crop to tolerate long drought periods (e.g. 212 days for the 3rd drought period), before plants showed severe stress symptoms.

Average PAR$_i$ reductions observed in WS plots for the 1st, 2nd and 3rd drought periods were 14, 23 and 40%, respectively, compared to IRR treatment, indicating that the 3rd drought period was the most severely stressed. Although the soil water content at the end of the 2nd and 3rd drought periods was similar (Fig. 4), the atmospheric demand was

greater along the 3rd period and so the supply:demand was lower, as shown in Figure 1. One possible explanation for the reductions in PAR$_i$, observed for each drought period in the WS treatments after the 2nd cutting, might be that the leaf expansion was decreased. A significant RUE reduction (expressed by linear regression slope differences between IRR and WS treatments), was observed only for the 3rd period (Table 1), when the drought intensity was the highest. In summary, we can suppose that PAR$_i$ reductions (caused mainly by leaf expansion reductions) might be more relevant than RUE reductions (caused by stomata closure) on DM reductions observed under drought (Fig. 5*a*).

Our interpretation is supported by the general concept developed by Hsiao and Acevedo (1974), who concluded that leaf expansion is more sensitive to drought than to stomata control. Reports for annual crops in the Pampas,
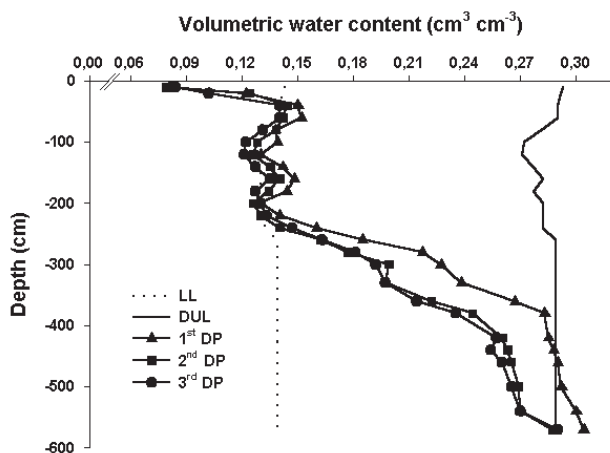
Figure 4. Volumetric water content over soil depth at the end of the 1st, 2nd and 3rd drought period (DP). The solid line indicates the drained upper limit (DUL) and the dashed line indicates the lower limit (LL).
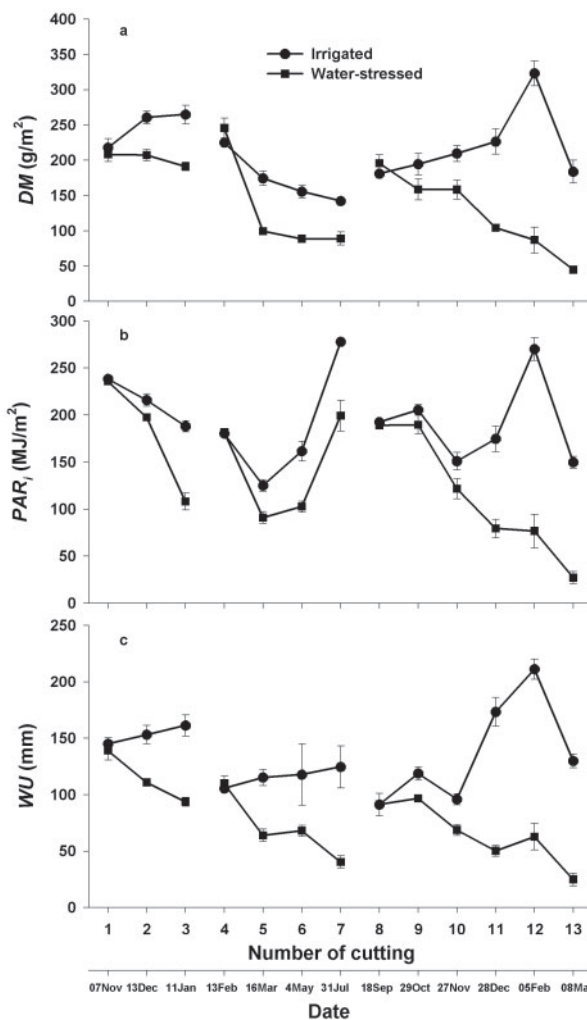
Figure 5. (*a*) Forage dry matter (DM), (*b*) accumulated intercepted photosynthetically active radiation (PAR$_i$) and (*c*) accumulated water use (WU) obtained for each growth period between cuttings, under irrigated and water-stressed conditions. The vertical segments represent the mean standard errors.

such as soybean (Andriani *et al*. 1991) and peanut (Collino *et al*. 2001), showed that, under imposed drought, DM was reduced as a result of either PAR$_i$ and RUE decreases. As neither LAI nor stomatal resistance were measured in this experiment however, our supposition requires more research to be confirmed. Successive forage harvests throughout the alfalfa growth season also make this crop only partially comparable to annual crops.

WUE was not modified by drought during the 1st and 2nd drought period (as observed for RUE) but was significantly increased during the 3rd drought period (Table 1). Collino *et al*. (1997), for the same location and variety under study, did not find differences in WUE between irrigated and drought treatments, under drought intensity similar to our 1st and 2nd drought periods. Guitjens (1984) showed a non-significant linear trend between declining annual WUE and increasing annual water consumption. These reported results agree with our findings for the 1st and 2nd drought period but not with those corresponding to the 3rd period, in which a significant WUE increase (expressed by statistical differences in the linear regression slopes between IRR and WS treatments), was observed. These results suggest that during the 3rd drought period (more severely water stressed) stomata control might become more manifest, resulting in a reduction of water losses (expressed by WU), rather than photosynthesis reductions (expressed by DM). Following Sinclair *et al*. (1984), we may suppose that DM in low to high water-availability environments did not relate linearly with relative WU during all the imposed drought periods, although this behaviour was clearly expressed only under severe drought.

However, we could suppose that the relationship between relative DM and relative WU (both with respect to the corresponding IRR treatment) might be non-linear, as demonstrated by Abbate *et al*. (2004) on wheat across several environments (including our experiment site).
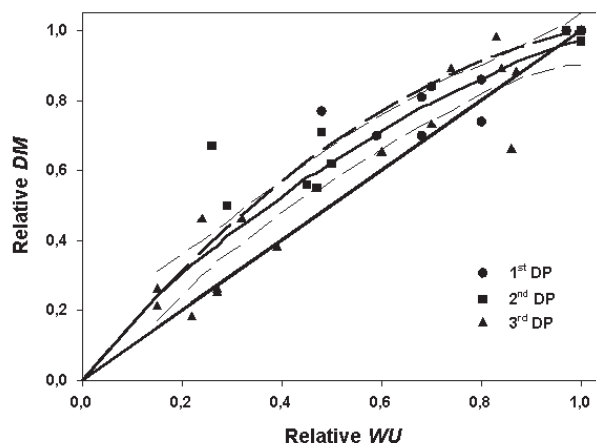
A curvilinear model, without intercept:

$$y = 1.543x - 0.575x^2 \qquad (9)$$

for the relationship between relative DM (*y*) and relative WU (*x*) resulted in a better fit than a linear model without intercept, with RMSE = 0.317 and r^2 = 0.853. The data arrangement (Fig. 6) suggests that the crop behaviour was similar under the 3 drought imposed periods.

Thus, the form of the relationship does not agree with the linear theoretical model proposed by Hanks (1974), which assumes that relative DM is equal to relative WU at every drought level. This linear model is widely known and it was adopted in several models (Howell 1990). Moreover, the 95% confidence limits for the fitted curvilinear model (Fig. 6), clearly shows that, except for extreme values of *x*, the mean trend is not one of a model like that of Hanks (1974), with unitary slope.

Our model fitting line is close to the model obtained by Abbate *et al*. (2004), showing the similarities between both models. These quadratic models show that WUE increased under conditions of water stress. This pattern is in agreement with the results of Ferreyra *et al*. (2003), who demonstrated non-linear effects of water stress on peanut growth.

The Abbate *et al*. (2004) finding arose from experiments conducted in the Pampas and at multiple sites around the world, under very varied environmental conditions. In our

Table 1. Regression coefficients for cumulative dry matter *v*. cumulative intercepted photosynthetically active radiation (RUE) and *v*. cumulative water use (WUE) for the three drought periods

General equations are RUE = *a* + *b*DM and WUE = *a* + *b*DM
P<0.05 indicate significant differences between the linear regression slopes obtained for irrigated and water-stressed treatments

Drought period	Treatment	Regression coefficients		r^2	*P*-value
		a	*b*		
		RUE			
1st	IRR	−94.38	1.291	0.985	0.527
1st	WS	−90.78	1.229	0.976	
2nd	IRR	129.82	0.799	0.926	0.070
2nd	WS	152.05	0.668	0.881	
3rd	IRR	−80.41	1.222	0.996	0.017
3rd	WS	−30.37	1.107	0.973	
		WUE			
1st	IRR	−69.52	1.634	0.970	0.088
1st	WS	−58.95	1.921	0.989	
2nd	IRR	103.31	1.298	0.982	0.485
2nd	WS	110.50	1.366	0.785	
3rd	IRR	65.57	1.545	0.976	0.038
3rd	WS	36.42	1.812	0.979	

Figure 6. Relationship between relative forage dry matter (DM) and relative water use (WU), when observations under water-stressed plots are expressed relative to irrigated plots, using pooled data from the 3 drought periods (DP). The solid straight line represents the Hanks (1974) relationship; the solid curvilinear line is our quadratic regression (with thin dashed lines representing 95% confidence intervals). Thick dashed line shows the quadratic regression obtained for wheat by Abbate *et al*. (2004)

study, different combinations of environmental variables throughout the year allowed us to obtain contrasting environmental conditions for different cuttings. The above-mentioned non-linear relationships agree with Sinclair *et al*. (1984), who reported that stomata control acting to prevent high transpiration rates could significantly improve WUE. In particular, they postulated that stomata closure during midday periods of high evaporative demand would be a very useful strategy for increasing WUE.

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