Influence of contrasting availabilities of water and nutrients on the radiation use efficiency in C_3 and C_4 grasses

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Abstract   The radiation use efficiency (RUE) model is one of the most used tools to generate large spatial and temporal scale net primary productivity (NPP) estimations by remote sensing. It involves two key issues to make accurate estimations of NPP: the estimation of the fraction of photosynthetically active radiation (PAR) intercepted by vegetation (fPAR) and the estimation of the plant RUE. The objectives of this work were to quantify the above-ground RUE under optimal water and nutrient conditions in two C_3 and one C_4 grass species and to analyse the effect of restrictions in these factors upon RUE by comparing both metabolic pathways. Grasses were cultivated from seeds and four treatments combining contrasting availabilities of water and nutrients were applied. RUE values were calculated from measurements of the incoming PAR, fPAR and productivity. In each of the species, plants with sufficient water and nutrients showed the highest RUE ($2.61–3.52$ g MJ^{-1}), whereas those with deficiencies in both resources presented the lowest RUE ($1.15–2.39$ g MJ^{-1}). *Cynodon dactylon* (C_4) was the species with higher value of RUE and no significant differences were detected between treatments. However, no significant differences were detected between *C. dactylon* and *D. glomerata* under no stress treatment (N1W1) and between *C. dactylon* and *L. perenne* under water stress treatment (N1W0). RUE values of *Dactylis glomerata* (C_3) diminished if only one of the two stress factors was presented, while *Lolium perenne* (C_3) only when both stress factors were present. The decreases under stress treatments were between 35% and 60% compared with the no stress treatment. When regional NPP is estimated it is therefore important to take into account the decrease in the RUE, especially in areas under severe stress.

Key words: grassland, light-use efficiency, primary productivity, remote sensing, stress.

INTRODUCTION

Nowadays there is an increasing interest in describing and understanding the dynamics of carbon fluxes and the variables that exert a control over them. The objectives behind this interest vary from the quantification of the amount of energy available in the food web (McNaughton *et al*. 1989, 1991) to the construction of complex models that simulate and compare the functional aspects of different ecosystems (Cramer *et al*. 1999; Ostle *et al*. 1999). The primary productivity (PP) of ecosystems is the key variable that defines the input of carbon into any ecosystem. Its quantification and the study of its dynamics are the first steps in any analysis at the ecosystem level. Particularly in areas with an extensive livestock production, where pastures and grasslands are the main forage resources that sustain cattle production, accurate estimations of the above-ground net primary productivity (ANPP) are considered as a primordial necessity to adjust the grazing pressure and

to improve the sustainable management. Because of the interaction of numerous factors, the ANPP is highly variable both spatially and temporally. Because of the spatial explicitly of remote sensing data and their high temporal repeatability, some models that deal with the estimation of ANPP have incorporated the use of remote sensing data (Nagendra 2001; Kerr & Ostrovsky 2003; Di Bella *et al*. 2008). However, the transformation of satellite information into reliable ANPP estimations remains a major challenge. The radiation use efficiency (RUE) model (Kumar & Monteith 1982) is a simple model frequently used to estimate this variable. It relates ANPP with the photosynthetically active radiation absorbed by vegetation (APAR) as well as with the RUE of vegetation. RUE is defined as the energy conversion coefficient of absorbed radiation into above-ground biomass (Field *et al*. 1995). APAR can be calculated by multiplying the fraction of radiation intercepted by vegetation (fPAR) by the incoming photosynthetically active radiation (PAR). Therefore, this model can be written as follows:

$$ANPP \equiv RUE * \sum APAR \equiv RUE * \left(fPAR * \sum PAR \right)$$

(1)

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The simplicity of this model adds a further advantage as it incorporates the possibility of using spectral information provided by remote sensing to estimate fPAR. In consequence, it can generate large spatial and time scale ANPP estimations. To estimate fPAR, the Normalized Difference Vegetation Index (NDVI) is the most used spectral index (Dye & Goward 1993; Sellers *et al.* 1994; Turner *et al.* 2002; Di Bella *et al.* 2004). This index integrates information from the differential reflectance values on the red and infrared bands of the electromagnetic spectrum.

The Kumar and Monteith model (1982), with incorporation of satellite data, included two key issues to make accurate estimations of ANPP: the type of relationship between fPAR and NDVI and the RUE value. Although the relationship between fPAR and NDVI is usually taken as linear, many authors have demonstrated that the relationship may have other forms (Ruimy *et al.* 1994; Turner *et al.* 2002; Cristiano *et al.* 2010). On the other hand, less attention has been paid to variations in the RUE values, and this variability has probably more impact on ANPP estimations from remote sensing data (Piñeiro *et al.* 2006). Moreover, as major efforts have been made on cultivated species, there is a lack of RUE data on grasslands. Monteith (1972, 1977) observed that the relationship between APAR and ANPP in many crop species was linear and thus postulated that RUE was a constant parameter. However, in recent years, the RUE values estimated for different species and conditions have shown a great variability between species with different metabolic pathways (C_3 and C_4 plants), phenological states and environmental restrictions (such as water and nitrogen availability) (Ruimy *et al.* 1994; Turner *et al.* 2002, 2003). Environment characteristics, such as historical and current mean annual precipitation, minimum and mean temperature and vapour pressure deficit, also influence the RUE values (Piñeiro *et al.* 2006; Garbulsky *et al.* 2010). As the main factor which controls plant growth is water availability (Lauenroth 1979; Sala & Paruelo 1997; Garbulsky *et al.* 2010), water stress can reduce RUE by preventing the use of photosynthetic compounds for growth (Collino *et al.* 2001), and its influence may be different between the two metabolic pathways (C_3 and C_4 plants). As C_4 species show greater water use efficiency (Bahrani *et al.* 2010), lesser impact is expected on C_4 than on C_3 RUE values under water restriction conditions. Without water restrictions, nitrogen (N) availability is the main factor controlling the rate of biomass accumulation (Serrano *et al.* 2000). Under nitrogen limitation, specific symptoms of deficiency are developed and plant growth decreases. A general feature is the change of allocation pattern between above- and below-ground biomass (Evans & Edwards 2001). The final RUE value depends on plant response to the interaction of all stress factors. Therefore, it becomes crucial to address the above-mentioned

issues by incorporating the RUE variations into the global models of NPP and carbon cycling. For this reason, the aims of this work were: (i) to quantify the above-ground RUE without limitations in water or nutrient availability in two C_3 and one C_4 characteristic species of the Pampa grasslands in Argentina; (ii) to analyse the effects of water and nutrient restrictions on their RUE; and (iii) to compare these effects between species with different photosynthetic pathways. Our hypothesis was that the restriction of water and/or nutrient resources as well as the metabolic pathway might differentially affect the RUE of grass plants. The predictions were that water restriction has a greater impact on RUE values than nitrogen restriction and that C_4 species present greater RUE values than C_3 plants regardless of the water and nitrogen conditions.

MATERIALS AND METHODS

Two C_3 and one C_4 grass species were used to carry out two experiments at the field of INTA Castelar, Buenos Aires, Argentina (31°36′S; 58°40′W). The C_3 species were *Lolium perenne* L. (perennial ryegrass) and *Dactylis glomerata* (orchard grass), with different canopy architecture. These species were selected for being very common forage plants used in the Pampa grasslands of Argentina. The C_4 species was *Cynodon dactylon* (Bermuda grass), a non-cultivated and invasive species but very common in the field. Two experiments were carried out, because of the different growth cycles of the species: one with both C_3 species (between 22 May and 7 November 2006) and one with the C_4 species (between 18 January and 29 June 2007). Seeds were sown in small plastic pots with sand and, approximately 10 days after germination transplanted to 5-l pots filled with a soil-sand mixture (2:1 v/v) with 0.1–0.15% N. When the plants were established, only two plants were left in each pot to ensure initial low fraction of intercepted photosynthetically active radiation (fPAR) values but a high cover percentage at the end of the experiment. All the pots were placed below an open permanent shelter of transparent polycarbonate to avoid natural rainfall on plants. At the beginning of the experiment, all pots were uniformly irrigated to ensure the successful establishment of plants and, after this, the treatments were applied. All the pots were rotated once a week during the experiments to reduce the border effect.

Four treatments combining water and nitrogen availability were applied in each experiment: N1W1 (high availability of nitrogen and high availability of water), N1W0 (high availability of nitrogen and low availability of water), N0W1 (low availability of nitrogen and high availability of water) and N0W0 (low availability of nitrogen and low availability of water). In the W1 treatments, pots were watered up to field capacity every four days for winter species (C_3 species) and every three days for the summer species (C_4 species) because of the differences in atmospheric demand. In the W0 treatments, the irrigation frequency (times of irrigations during the experiment) and the irrigation intensity (amount of water per plant) were reduced to 50% of those of control plants (W1). For the N1 treatment, half of the pots were fertilized with a total of 4 g of ammonium nitrate (NO_3NH_4) in two applica-

Table 1. Details of the experimental design for the two experiments with different photosynthetic pathway species

Experiment	C_3	C_4
Species	*Lolium perenne*	*Cynodon dactylon*
	Dactylis glomerata	
Sowing date	22 May 2006	18 Jan 2007
Emergence	30 May 2006	23 Jan 2007
Dates of biomass harvests	61; 77; 99; 120; 141 and 161 DAE	98; 133; 127; 137; 148 and 157 DAE
Season	Fall–Winter	Spring–Summer
Beginning of water restriction	As from 73 DAE	As from 29 DAE
Dates of fertilization with NO_3NH_4	63 and 78 DAE	33 and 64 DAE

DAE, days after emergence; NO_3NH_4, ammonium nitrate.

tions of 2 g in each application. In the N0 treatment, plants were not fertilized. Analysis of soil samples from both the N1 and N0 treatments was carried out in every experiment, with a mean value of 0.29% and 0.13% N, respectively. The details of each experimental design are shown in Table 1.

The experimental unit was one canopy composed of four pots (2×2) covering 0.14 m². Three canopies were evaluated for each treatment and date (replicates). fPAR was measured every 10–15 days in a small darkroom ($1.5 \times 1.5 \times 1.5$ m) with artificial light to keep constant illumination conditions at each measurement. Four 150-W tungsten lamps (©Phillips Spot, R95) were mounted 1.5 m above the darkroom base. PAR (MJ m⁻²) was measured using a linear quantum sensor (©Cavadevices), which measures the photon flux between 400 and 700 nm and up to 3000 µmol m⁻² s⁻¹, over a linear 1 m surface. The fraction of intercepted PAR (fPAR) was estimated as follows:

$$fPAR \equiv (PAR_i - PAR_t)/PAR_i \qquad (2)$$

where PAR_i is the incident PAR measured locating the quantum linear sensor just above each experimental unit, and PAR_t is the transmitted PAR, recorded below each canopy. Two perpendicular measurements of PAR_i and PAR_t were made on each canopy and then averaged for fPAR calculation.

The PAR and air temperature across the day (mean hourly values) were taken from an automatic meteorological station located 1500 m away from the shelter. Using the linear quantum sensor, the incoming PAR was measured under the polycarbonate shelter in order to assess the differences between the radiation received by plants under the shelter and the data taken from the meteorological station. Using the relationship between the PAR under the shelter and the PAR recorded on the meteorological station, we corrected the incident radiation to calculate the absorbed PAR (APAR) values. The APAR was calculated by multiplying the average of the fPAR values from two consecutive measurement dates with the accumulated PAR in the same period, assuming as a simplification that all intercepted radiation has been absorbed (Ahl *et al.* 2004; Akmal & Janssens 2004; Lindquist *et al.* 2005).

Above-ground biomass was harvested every 2 or 3 weeks and dried at 70°C for 72 h in a drying oven. Five and six harvests were carried out along time to assess accumulated biomass in the experiments with the C₃ and C₄ plants, respectively. Each experiment lasted until the reproductive phase was finished and the spikes appeared. Therefore, time duration of each experiment was different as the processes were faster in summer than in winter and C₄ species required

less time to have spikes. Hence, the accumulated APAR values were lower in *C. dactylon* than in the other two species. The RUE for each treatment and species was computed as the slope of a simple linear regression between the mean of the three replicates per date of the accumulated APAR and the above-ground dry matter ($n = 6$ for the C₄ experiment and $n = 5$ for the C₃ experiments). The linear regression models used are shown as follows:

$$Y_i \equiv \beta_i \cdot APAR + \alpha + e \qquad (3)$$

where Y is the above-ground dry matter, β the slope of regression or RUE, α the y intercept and e the random error. The subindex i, with values from 1 to 12, corresponds to the applied treatments (combinations of nutrient and water availability and species). Some papers that deal with the estimation of RUE force the regression intercept to be zero (Sinclair & Muchow 1999; O'Connell *et al.* 2004) and others do not (Joel *et al.* 1997; Akmal & Janssens 2004). This different methodology has implications for the calculated RUE values. We tested whether the confidence interval of the intercept (α) contained the 0 value. If this was the case, we used $\alpha = 0$, whereas if not, we calculated the RUE with both options: forcing α to 0 and without forcing it to 0. Then, two null hypotheses were tested: $\beta = 0$ (linearity) and $\beta 1 = \beta 2 = \ldots = \beta 12$. The latter was tested for the different combinations of nutrient and water conditions and species by a multiple comparison test. This test is equivalent to making a test for equal slopes (Weber & Skillings 2000).

RESULTS

Monthly PAR values ranged between 372 MJ m⁻² (in December) and 97 MJ m⁻² (in June). The mean temperature was 21°C for the C₄ experiment (January to April) and 13.3°C for the C₃ experiment (June to October) and the monthly average showed the same pattern as historical data (1959–2010) (Fig. 1). All species presented the highest RUE values in the treatment with no restrictive growth conditions (N1W1) and ranged between 2.61 and 3.52 g MJ⁻¹. Significant differences were found between *C. dactylon* and *L. perenne*, while *D. glomerata* had intermediate values. All species also showed their lowest RUE value under water and nutrient stress (N0W0), ranging between 1.15 and 2.39 g MJ⁻¹ (Table 2). Under this stressed treatment, *C. dactylon* had significant higher RUE
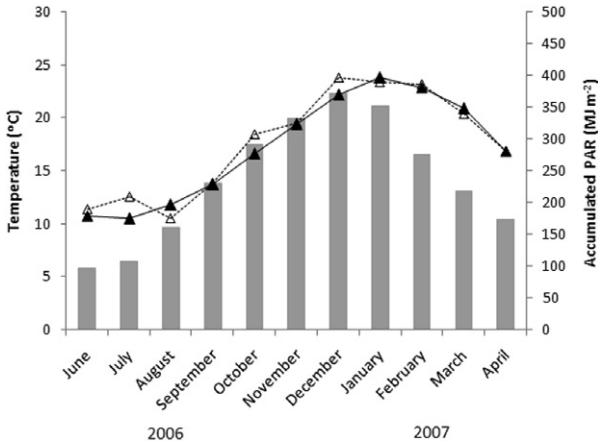
Fig. 1. Monthly accumulated photosynthetically active radiation (PAR, grey bars) and mean temperature (T°) of the studied period (-△-). The monthly historical mean temperature calculated from the 1959–2010 period is also presented (-▲-).

values than both C_3 species. The RUE values of both C3 species did not differ significantly. *Cynodon dactylon* was the only species that showed intercept values significantly different from zero. When forcing the intercept to zero, the RUE values were very different. Although the regressions were statistically significant in both cases, forcing the intercept to zero seemed to be too artificial and the mean square error increased (data no shown). Therefore, we used equations with intercept values different from zero (Table 3).

Focusing on the differences between species, *C. dactylon* showed the greatest RUE values with respect to the other two species under all treatments, except with *D. glomerata* under no stress treatment (N1W1) and with *L. perenne* under water stress treatment (N1W0) (Table 2). As regards the response to the different treatments, no significant differences were found in the RUE values in *C. dactylon* (C_4), although the mean values diminished when restrictions were present. On the other hand, the RUE values of the C_3 species were

Table 2. Slope values (RUE) and coefficients of determination (R^2) of the regressions between accumulated absorbed PAR (APAR) and above-ground dry matter for four treatments (for each treatment and species, $n = 6$ for the C_4 experiment and $n = 5$ for the C_3 experiments)

Treatment	Species	RUE (g MJ^{-1})	R^2	Difference	
N1W1	*C. dactylon* (C_4)	3.52	0.99	–	a
	L. perenne (C_3)	2.61	0.98	–	bc
	D. glomerata (C_3)	2.92	0.98	–	ab
N1W0	*C. dactylon* (C_4)	2.86	0.96	24	abc
	L. perenne (C_3)	1.82	0.98	30	cdf
	D. glomerata (C_3)	1.74	0.98	41	def
N0W1	*C. dactylon* (C_4)	3.35	0.99	8	ab
	L. perenne (C_3)	1.70	0.95	35	cdef
	D. glomerata (C_3)	1.16	0.73	60	cdef
N0W0	*C. dactylon* (C_4)	2.39	0.95	35	acd
	L. perenne (C_3)	1.17	0.97	55	ef
	D. glomerata (C_3)	1.15	0.94	61	f

All regressions were significant for the null hypothesis RUE = 0 ($P < 0.05$). The 'Difference' column shows the percentage difference between the RUE values of each treatment and its corresponding N1W1. In the multiple comparisons (species and treatments), different letters indicate significant differences ($P < 0.05$). N1W1, high availability of nitrogen and water; N1W0, high nitrogen availability and water restriction; N0W1, nitrogen restriction and high water availability; N0W0, restriction on nitrogen and water availability.

Table 3. Slope values (RUE) and coefficients of determination (R^2) of the regressions between accumulated absorbed PAR (APAR) and above-ground dry matter for four treatments ($n = 6$) for *Cynodon dactylon* forcing the y-intercept to zero

Treatment	RUE (g MJ^{-1})	R^2	Difference	
N1W1	2.49	0.97	–	abc
N1W0	1.90	0.95	24	abcde
N0W1	2.30	0.96	8	abc
N0W0	1.63	0.96	35	cde

All regressions were significant for the null hypothesis RUE = 0 ($P < 0.05$). The 'Difference' column shows the percentage difference between the RUE values of each treatment respect to its corresponding N1W1. These RUE values can be compared with those of *Lolium perenne* and *Dactylis glomerata* in Table 2. Different letters indicate significant differences ($P < 0.05$). N1W1, high availability of nitrogen and water; N1W0, high nitrogen availability and water restriction; N0W1, nitrogen restriction and high water availability; N0W0, restriction on nitrogen and water availability.
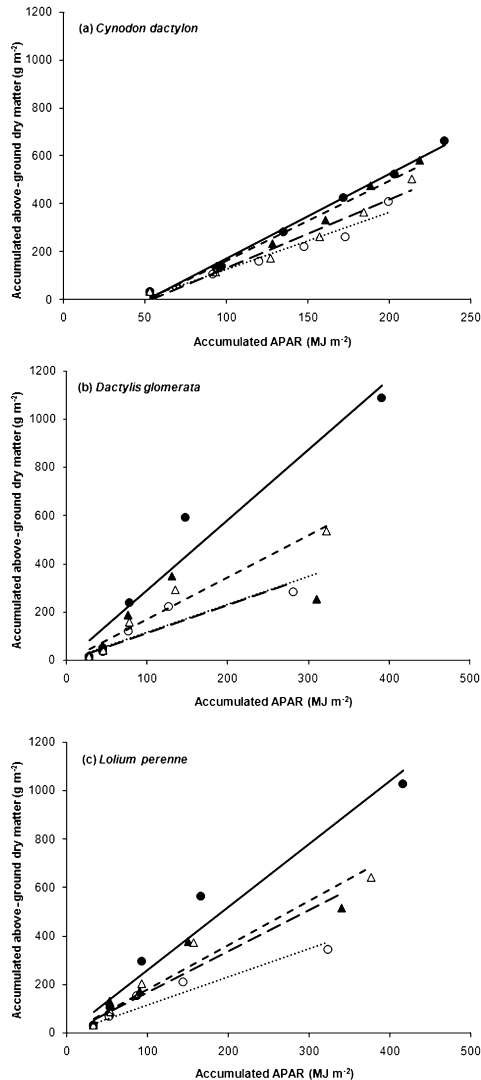
Fig. 2. Relationship between accumulated above-ground dry matter and accumulated absorbed photosynthetically active radiation (APAR) for one C_4 species (a – *C. dactylon*) and two C_3 species (b – *L. perenne* and c – *D. glomerata*) under four treatments combining contrasting availabilities of water and nutrients (for each treatment and species, $n = 6$ for the C_4 experiment and $n = 5$ for the C_3 experiments). The slope of each regression determined the RUE value. Note the different X scale between the two C_3 and the C_4 species. (●) N1W1, high availability of water and nitrogen; (△) N1W0, high nitrogen availability and water restrictions; (▲) N0W1, nitrogen restriction and high water availability; (○) N0W0, restrictions on nitrogen and water availability.

affected by restrictions in either resource (water or nitrogen) and significant differences were species-specific (Fig. 2). Both C_3 species showed significant differences between the no-stress treatment (N1W1) and the water and nutrient stress treatment (N0W0). The RUE values of *L. perenne* were not significantly affected by the limitation on one resource (no differences between N1W1 *vs*. N1W0 and N0W1).

However, the RUE values of *D. glomerata* were significantly affected when water or nutrients were restricted compared with the no-stress condition, and no differences between both treatments were found.

One way to compare the effect of the resource constraints on the RUE for each species and between species is to calculate the percentage of decrease in the efficiency values. In the C_3 species, the difference between the control (N1W1) and the water-nutrient stress treatment (N0W0) represented a significant reduction ($P < 0.05$) of 55% in *L. perenne* and of 61% in *D. glomerata* (an average of 58%). In the C_4 species (*C. dactylon*), RUE decreased by 35%, although this value was not significant ($P > 0.05$) (Fig. 2 and Table 2). With water deficiency (N1W0), the plants reduced their RUE compared with N1W1 by 30% and 41% in *L. perenne* and *D. glomerata* respectively (i.e. an average value of 35%). In *C. dactylon* (C_4 species), the reduction was 24%, but not significant. Deficiencies in nitrogen (N0W1) decreased RUE by 35% in *L. perenne* and by 60% in *D. glomerata* (with an average decrease of 47%), while in *C. dactylon* RUE decreased only by 8% (Fig. 2 and Table 2).

DISCUSSION

In the treatments without stress, our results showed RUEs between 2.61 and 3.52 g MJ^{-1}. Under optimal growth conditions, similar values were found by Monteith (1977) who estimated for crop canopies an efficiency of 2.8 g MJ^{-1} and Joel *et al.* (1997) who reported values in sunflower between 1.66 and 2 g MJ^{-1}. Under experimental stressed conditions, the values of the C_3 species were significantly affected. When both stress factors were present, both C_3 species reduced their RUE values by 55–61%. The average percentage is close to the results reported by Field *et al.* (1995), who found that the RUE values estimated by the CASA model were 47% lower in the most stressful simulations. Under the same stressing conditions, Akmal and Janssens (2004) found that RUE decreased by 21–53% in ryegrass plants (*L. perenne*) when considering total biomass (shoot and root), while Joel *et al.* (1997) reported that aerial RUE decreased by 32–37% in sunflower. Some differences between the two C_3 species were found. In *L. perenne*, the decrease in RUE was significant only when both stress factors were present, whereas in *D. glomerata* the RUE values diminished significantly when at least one stress factor was present. This difference could be related to some characteristic that made *L. perenne* a more resistant species.

On the contrary, RUE values of *Cynodon dactylon* (C_4 species) were not affected by our resource deficiency treatments. This may be either because its metabolic pathway presents higher water use efficiency or because *C. dactylon* is an r-strategist species (Grime 1979) able

to colonize disturbed environments. Despite the strategy of this grass, the study of this species is important because of its high frequency in grazed lands, as denoted by the numerous studies analysing its behaviour in different situations (Ellis *et al.* 1997; Agnusdei & Mazzanti 2001; De Abelleyra *et al.* 2008; Du *et al.* 2011; Simmons *et al.* 2011). On the other hand, the minimum RUE values for each species correspond to the treatments under both stresses, with values between 1.15 and 2.3 g MJ^{-1}. These values are similar to those found by Kiniry *et al.* (2007) whose efficiencies ranged between 1.01 and 2 g MJ^{-1} under similar stress conditions.

In accordance with the assertion that C_4 species are more efficient than C_3 species, in converting solar radiation into biomass (Lambers *et al.* 1998; Chapin *et al.* 2002) greater RUE values were found in *C. dactylon* in comparison to both C_3 species, when intercept values were not forced to zero. However, no significant differences were observed with *D. glomerata* without stress and with *L. perenne* with only water restrictions. It is necessary to study in more detail the physiological response to stress factors of these species to understand this issue. Our prediction was not fully confirmed because, on the one hand, the C_4 showed no significantly higher efficiencies than the C_3 in all treatments. On the other hand, neither water nor nutrient stress affected the RUE of C_4 and both affected the efficiency in C_3 by similar percentages. It must be remembered that *C. dactylon* was the only species that showed intercept values significantly different from zero. When forcing the intercept to zero, the RUE values change a lot and the resulting values seemed to us to be unrealistic to *C. dactylon*, so we left the intercept value different to zero. Verón *et al.* (2005) pointed out that RUE could be estimated from the slope of this regression only when the *y* intercept is zero. The negative intercept of *C. dactylon* in all treatments means that the RUE changes with time, first increasing and then decreasing its values as the plants grow. In these cases, the calculated slope represents the value at which the efficiencies gradually converge as the accumulated APAR increases (Verón *et al.* 2005).

Discrepancies in the published RUE values are important when experimental versus field estimations are considered. For instance, in the report by Piñeiro *et al.* (2006), above-ground RUE estimated by biomass harvests for pastures and grasslands located in the Flooding Pampa in South America varied seasonally between 0.2 and 1.2 g MJ^{-1}. Ruimy *et al.* (1994) reported three values of RUE from a bibliography for temperate grasslands with a mean of 0.84 g MJ^{-1}. Paruelo *et al.* (1997) found values of 0.48 g MJ^{-1} for a wide range of grasslands across the US Great Plains when estimating ANPP from NDVI data. Moreover, the RUE values generated from different models – such as CASA and Miami NPP/GCM – range between 0.27

and 0.49 g MJ^{-1} (Field *et al.* 1995). Therefore, the RUE values seem to decrease when measurements are carried out in the field (lesser scales). These differences might be due to the interaction of multiple factors, such as lack of competition when the experiments were carried out in pots, temporal resolution, different stress factors acting together, the floristic composition with a mixture of species with different pathways and growing strategies, the presence of livestock or new emergent properties characteristic of large scales. So, the absolute RUE values found in these experiments are not appropriate to be used at a regional scale to estimate PP. However, the diminished percentage due to stress factors could be applied to grassland RUE values estimated from a regional scale. Understanding regional scale processes that impact over the efficiency to convert solar radiation into biomass remains a major challenge to obtain accurate predictions of regional ANPP.

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