Received: 19 January 2020 | Revised: 18 May 2020 | Accepted: 22 June 2020

DOI: 10.1111/grs.12302

ORIGINAL ARTICLE

GRASSLAND SCIENCE
Japanese Society of Grassland Science
WILEY

Variability of radiation use efficiency in mixed pastures under varying resource availability, defoliation and time scale

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Funding information
University of Buenos Aires; Foncyt

Abstract

Forage productivity is the product between incident radiation, the fraction of radiation absorbed by the canopy (fAPAR) and radiation use efficiency (RUE). The extent to which forage productivity may be estimated through remote sensing depends on the relative effects of stress and defoliation on fAPAR and RUE. In a mixed pasture, we determined the relative impact of resource availability and defoliation on forage productivity, fAPAR and RUE, and we evaluated the impact of time scale on fAPAR and RUE under stress conditions. We conducted a one-year experiment in a temperate-mixed pasture subjected to different resource availability treatments and defoliation management. We measured RUE and fAPAR with different temporal windows. RUE was less responsive than fAPAR to changes in resource availability and defoliation intensity. However, RUE slightly decreased under water stress and increased under severe defoliation. Additionally, RUE variability during regrowth and among treatments depended on the temporal scale of observation: RUE was more variable for 12-day periods than 45- or 90-day periods. Our results reinforce the value of fAPAR as an explanatory variable of the variations in forage productivity due to changes in resource availability and management. In addition, the temporal scale of observation affects RUE variability. Thus, most variations of forage productivity may be captured by monitoring systems based on remote sensing of fAPAR provided that the time scale is coarse enough. However, the contrasting response of RUE and fAPAR to defoliation indicates a potential weakness of such a system when situations with contrasting defoliation regime are compared.

KEYWORDS
forage productivity, mixed pastures, radiation use efficiency

1 | INTRODUCTION

In animal production systems, forage productivity (FP) is determined by the amount of photosynthetically active radiation absorbed by the canopy (APAR), and the efficiency with which that energy is converted into aerial biomass (RUE, Monteith, 1972):

$$\mathrm{FP}\,(\mathrm{kg\,ha^{-1}\,month^{-1}}) = \mathrm{APAR}\,(\mathrm{MJ\,ha^{-1}\,month^{-1}}) \times \mathrm{RUE}\,(\mathrm{kg/MJ})$$

APAR is the product of incident photosynthetically active radiation (PAR) and canopy fractional absorption (fAPAR), which depends on leaf area and canopy structure. FP may respond to stress or management through changes of fAPAR, RUE or both (Bondeau, Kicklighter, & Kaduk, 1999; Ojeda, Caviglia, Agnusdei, & Errecart, 2018; Russell, Jarvis, & Monteith, 1989). Changes of fAPAR may be readily monitored by vegetation indices derived from satellite images (Glenn, Huete, Nagler, & Nelson, 2008; Running et al., 2004; Running, Thornton, Nemani, & Glassy, 2000; Sinclair & Muchow, 1999), whereas estimating changes of RUE is more elusive. Thus, RUE of different conditions is often considered constant, a simplification of a more complex reality (Grigera, Oesterheld, & Pacín, 2007).

In a pasture, maximum RUE is set by the leaf-level photosynthetic rate under optimum environmental conditions (Turner et al., 2003). However, nutritional constraints, water stress, the amount of incident radiation and grazing, among other factors, prevent this value from being achieved under field conditions. Leaf nitrogen status is one of the factors that limit RUE (Hall, Connor, & Sadras, 1995; Sinclair & Horie, 1989). Several studies have shown that pasture RUE decreases under N deficiency (Agnusdei, Assuero, Lattanzi, & Marino, 2010; Bélanger, Gastal, & Warembourg, 1994; Cristiano, Posse, & Di Bella, 2015; Mills, Moot, & Jamieson, 2009). Water stress also reduces radiation interception and RUE, but it is unclear how severe the stress must be to have a significant impact on each of these variables (Collino, Dardanelli, De Luca, & Racca, 2005; Garcia et al., 1988; Gastal & Durand, 2000; Joel, Gamon, & Field, 1997; Muchow, 1985). Akmal and Janssens (2004) found that water stress had greater effect than N deficiency on RUE. Several studies concluded that modeling RUE requires to adjust a potential RUE according to different measures of soil water availability or atmospheric demand (Bat-Oyun, Shinoda, & Tsubo, 2012; Flanagan, Sharp, & Gamon, 2015; Rahman, Lamb, Stanley, & Trotter, 2014; Wang & Zhou, 2012). Finally, defoliation regime also alters RUE. Teixeira, Moot, and Brown (2008) observed, in alfalfa pastures, increases in RUE when shortening duration of the regrowth period in spring, but found no difference in summer. Conant, Brann, and Johnson (2003), meanwhile, found no effect of defoliation treatments on RUE of mixed grass-legume pastures. However, both studies focused on frequency and not intensity of defoliation.

The time scale at which fAPAR and RUE responses are analyzed (weekly, monthly, or yearly) adds an additional, less known dimension (Medlyn, Barrett, Landsberg, Sands, & Clement, 2003; Ruimy, Jarvis, Baldocchi, & Saugier, 1995; Running & Nemani, 1988). Evidence in forests, however, suggests that the plant response to stress in terms of decreasing fAPAR or RUE depends on the time period being considered (Medlyn, 1998; Medlyn et al., 2003). It is possible that short-term variations in RUE are undetectable at larger time scales, because leaf area tends to change rapidly to levels consistent with the availability of environmental resources, as predicted by the *resource balance* conceptual model, which states that the energy that plants invest in acquiring different resources is determined by the most limiting one (Chapin, Bloom, Field, & Waring, 1987; Field, 1991; Field, Randerson, & Malmstron, 1995).

The evidence above indicates that it is necessary to better understand the effect of resource availability and management on fAPAR and RUE to increase the accuracy of FP estimations based on remote sensing. It has been shown both in alfalfa (Collino et al., 2005; Gosse, Chartier, & Lemaire, 1984; Khaiti & Lemaire, 1992; Thiébeau, Beaudoin, Justes, Allirand, & Lemaire, 2011) and tall fescue monocultures (Bélanger et al., 1994; Gastal & Durand, 2000) that N or water stress affected more fAPAR than RUE. These responses to environmental stresses have not been sufficiently studied in mixed pastures, where there are competitive relationships and different species responses. RUE variability in relation to measurement time scale is central for proper RUE characterization (Field et al., 1995; Joel et al., 1997; Medlyn et al., 2003; Ruimy et al., 1995).

The objectives of this paper are as follows: (a) to determine the relative impact of resource availability deficits and defoliation management on forage productivity and its two components: fAPAR and RUE; (b) to determine the impact of measurement time scale on RUE variations under stress conditions. Both objectives will be focused on a mixed pasture composed of alfalfa and tall fescue. The results are expected to improve current models of FP monitoring through remote sensing (Grigera et al., 2007).

2 | MATERIALS AND METHODS

2.1 | Site and pasture description

An experiment was carried out in Pergamino Agricultural Experimental Station (Instituto Nacional de Tecnología Agropecuaria, 33° 57 'S, 60° 34' W). The climate is temperate sub-humid. Mean annual rainfall is 975 mm, evenly distributed during spring, summer and autumn, and reduced by a half in winter. Mean monthly temperature ranges from 9.8°C in July to 23.3°C in January. The experiment was conducted on a typical Argiudoll (pH = 6.0–6.1; % organic matter = 3.89–3.95 and available p = 18–22 ppm), corresponding to the typical Pampean, agricultural, deep soils, with excellent structure and fertility.

The experiment was installed on a mixed grass-legume pasture: alfalfa (*Medicago sativa cv. Victoria INTA*, latency group 6, sown at 8.5 kg/ha) and tall fescue (*Festuca arundinacea*, Arrow cultivar, Mediterranean type, sown at 7.5 kg/ha). It was sown on May 3, 2004, under conventional tillage in alternating monospecific pure rows, 16 cm apart and fertilized with 50 kg/ha of diammonium phosphate (N:18–P:46–K:0). Until the installation of the experiment in 2005, the pasture was used for fattening steers under rotational grazing.

2.2 | Experimental design

The experiment was installed in June 2005 and lasted a year. Each season, the experiment occupied one of the four 15 × 45 m contiguous areas from which grazing had been excluded. Within each season, the experimental design was complete randomized block with a 2 × 4 factorial structure and three replicates per treatment. Thus, twenty-four 2 × 3 m plots were arranged in a grid of 3 columns by 10 rows with 1 m borders. The factorial treatments were as follows: Factor Defoliation, two levels, severe (Def 7) and less severe (Def 15). Factor Resource availability, four levels, irrigation (I, considered the control treatment), irrigation and P–N fertilization (IF), temporary drought (TD) and permanent drought (PD). Each treatment is described below:

2.2.1 | Defoliation

The defoliation treatment simulated two contrasting intensities of a rotational grazing management frequently found on this type of pastures. Each plot was mown with a helicoidal mower at either 7 (Def 7) or 15 cm (Def 15) height. Treatments were applied at the beginning and the middle of each season, approximately every 45 days (hereafter, we referred to the interval between defoliation treatments as a *regrowth period*). Thus, eight regrowth periods were evaluated across the four seasons.

2.2.2 | Irrigation

Water availability is the major source of stress for pastures in this region. Watering of irrigated plots was carried out so as to maintain the soil near field capacity.

2.2.3 | Irrigation and P–N Fertilization

Plots irrigated as those above received diammonium phosphate and urea (200 kg/ha N and 75 kg/ha P) at the beginning of each season and a further dose of urea (40 kg/ha of N) in mid-season.

2.2.4 | Temporary drought

Plots were not irrigated, and rainfall was suppressed during the first regrowth period of each season (first half of the season). During the second regrowth period, the plots were treated as irrigated plots.

2.2.5 | Permanent drought

Plots were not irrigated, and rainfall was suppressed throughout the season.

2.2.6 | Water management

Irrigation was done by an automated system with solenoid valves and drip tapes spaced at 40 cm with emitters every 20 cm. Ten to 20 mm of water was applied every 3–6 days according to pasture water consumption. Occasionally, particularly in the second regrowth period of summer, irrigation was greater than consumption plus deep drainage and lead to excess water in the irrigated plots. For drought plots, rainfall was suppressed by mobile rain-out shelters, located over each plot when a storm was imminent. The rain-out shelters were 2 × 3 m × 0.7 m high steel structures on wheels with a translucent sloping polycarbonate roof with a gutter that discharged the water outside the experiment through 1.5′′-diameter PVC pipes. A field worker, who lived near the experimental site, set on and off the shelters and recorded the time. We estimated the amount of rainfall received by the PD treatments when the worker could not place the rain shelters on time (automatic weather station VantagePro2, *Davis Instruments*, 10-min intervals). The PD treatments received 48% of a season's rainfall. Radiation and temperature in plots with and without shelters were also recorded. The polycarbonate absorbed on average 15% incident radiation and increased the temperature less than 0.8°C. During the year, shelters were placed 99 times for an equivalent of 108 days, 30% of the total duration of the experiment. Volumetric moisture sensors were installed in the soil (ECH_2O *Decagon Devices*) at 0–20 cm depths in plots with contrasting irrigation treatment and defoliation levels to characterize water treatment effect.

2.3 | Forage production estimates

FP (gm^{-2} d^{-1}) for each plot was estimated from biomass harvested at ground level. Approximately every 12 days, accumulated standing biomass was harvested from subplots not previously used for these determinations (hereafter, we referred to the interval between these measurements as a 12–day period). Subplots consisted in eight rectangles (64 × 40 cm, 0.256 m^2) per plot, harvested sequentially at the end of each 12–day period within the season. Each subplot always included two rows of alfalfa and two rows of tall fescue, and was surrounded by 20 cm of unharvested border. In the laboratory, samples were separated into four components: green tall fescue, dead tall fescue, green alfalfa and dead alfalfa. They were oven-dried at 70°C until constant weight and weighed. FP was calculated as the positive difference in green dry matter between two successive harvests (Biondini, Lauenroth, & Sala, 1991; Sala & Austin, 2000).

2.4 | fAPAR estimates

The radiation absorbed by a pasture includes the absorption by both green and dead tissue. In the context of the RUE logic, we were interested in the fraction absorbed by green tissue (fAPAR), which is the photosynthetically active component that determines FP and may be estimated through remote sensing. In order to estimate fAPAR, we first measured $fAPAR_{green+dead}$ and derived the green component from estimates of green and dead biomass. The detailed procedure follows in the next paragraphs.

$fAPAR_{green+dead}$ was measured by recording incident radiation above and below the canopy (between 11 a.m. and 1 p.m.) in each subplot about to be harvested. A 50 cm long by 2 cm wide photosynthetic photon flux density integrating bar for pastures was used (Dual BAR-RAD, Cavadevices, Buenos Aires, Argentina). Three readings per subplot were done: under the canopy (reading 1), above the canopy (reading 2) and again under the canopy (reading 3). Two readings were taken under the canopy because they were more variable than the readings above the canopy. $fAPAR_{green+dead}$ was then calculated as:

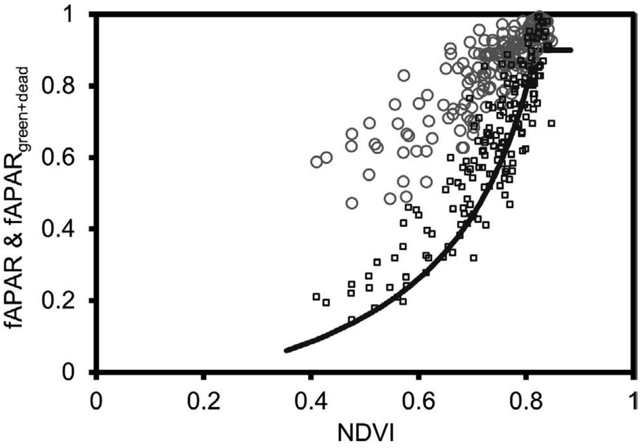

FIGURE 1 Relationship between different measures of absorbed radiation and Normalized Difference Vegetation Index (NDVI). The solid line, included as a reference, is an empirical model fit to field measurements of fAPAR in completely green wheat canopies and NDVI from the Moderate Resolution Imaging Spectroradiometer, MODIS (Grigera, 2011). The gray circles represent fAPAR$_{\text{green+dead}}$ measured in our experiment and NDVI estimated from reflectance measured with a handheld sensor (Skye). The black squares represent fAPAR estimates of the same data points after transformation by the correction factor

$$\text{fAPAR}_{\text{green+dead}} = \text{average}\,(\text{reading 1, reading 3})/\text{reading 2}$$

This equation is a commonly used simplification that captures the main components of the radiation flux, but does not account for the loss of reflected radiation (albedo) nor for the absorption of soil reflected radiation (Russell et al., 1989).

We transformed fAPAR$_{\text{green+dead}}$ into fAPAR through a correction factor based on the proportion of green and dead biomass weighed by an estimation of the vertical distribution of these two components in the canopy:

$$\text{fAPAR} = \text{fAPAR}_{\text{green+dead}} \times \text{Correction Factor}$$

$$\text{Correction Factor} = \text{P}_{\text{green}} + (\text{P}_{\text{dead}} \times \text{GVD})$$

The correction factor reflects the proportion of green and dead dry matter (P$_{\text{green}}$, P$_{\text{dead}}$) in the sample and its vertical distribution in the canopy (GVD for green vertical distribution). The first term (P$_{\text{green}}$) is straightforward because as P$_{\text{green}}$ increases a higher proportion of fAPAR$_{\text{green+dead}}$ is assigned to fAPAR. The second term (P$_{\text{dead}}$ * GVD) weighs the interference by dead tissue in the absorption by green tissue based on a relationship between the amount of green biomass (DM$_{\text{green}}$, g/m^2) and the vertical distribution in the canopy of green and dead tissue:

$$\text{GVD} = (\text{sample DM}_{\text{green}} - \mathit{min}\,\text{DM}_{\text{green}})/(\mathit{max}\,\text{DM}_{\text{green}} - \mathit{min}\,\text{DM}_{\text{green}})$$

where max and min indicate the 0.95 and 0.05 percentiles from the total observations of the experiment. GVD thus assumes that as DM$_{\text{green}}$ increases the dead biomass interferes less with fAPAR because it is in the lower strata of the canopy. This assumption is based on the systematic observation of this pattern in the field.

Then, if GVD is 1 (high DM$_{\text{green}}$), the correction factor is 1 and the resulting fAPAR equals the fAPAR$_{\text{green+dead}}$, that is, it is not corrected for dead material (as it is assumed that it is in the lower strata, so it does not interfere). If GVD is close to 0 (low DM$_{\text{green}}$), the correction factor is equal to the P$_{\text{green}}$ and fAPAR equals the one that would arise from a correction of multiplying fAPAR$_{\text{green+dead}}$ by P$_{\text{green}}$. This means that the minimum possible fAPAR value will be given by the product of fAPAR$_{\text{green+dead}}$ * P$_{\text{green}}$. Notice that if P$_{\text{green}}$ is high, the correction factor will be high, even when GVD is 0. fAPAR will be low in relation to the fAPAR$_{\text{green+dead}}$ when the P$_{\text{dead}}$ is high and the DM$_{\text{green}}$ (g/m^2) is low.

In order to validate this procedure, we measured reflectance with a handheld Skye sensor (SKR 1,800 2 channel sensor 660 nm and 730 nm) in 10 of the twenty-nine 12-day periods. Normalized Difference Vegetation Index (NDVI) was estimated for each measurement and converted into fAPAR through a previous calibration between fAPAR measured in canopies with no dead material and NDVI from the Moderate Resolution Imaging Spectroradiometer (MODIS, Vegetation Indices Product, MOD 13, Collection 4). The correction applied to the experimental data reduced the fAPAR$_{\text{green+dead}}$ to fAPAR values similar to those expected from the NDVI measured in the experiment (Figure 1, Grigera, 2011).

2.5 | Radiation use efficiency estimates

Radiation use efficiency was calculated for each plot and regrowth period as the slope of the linear regression between FP and APAR. Each regression included 4–5 data points that corresponded to 12-day periods with independent measurements of FP and APAR.

2.6 | Data analysis

For the first objective, impact of resource availability and defoliation on fAPAR and RUE, we compared, at seasonal scale, the changes in fAPAR and RUE among treatments of resource availability and defoliation management.

For the second objective, analysis of RUE variability at different measurement time scales, regressions between FP and APAR were built for each time scale. Then, the simple coefficient of determination (R^2) of the regression was used as an estimator of RUE variability at that particular scale; lower R^2 values indicate higher RUE variability. However, this logic presents some complexity that is explained below.

FP estimates for short time periods are associated with larger random error (Biondini et al., 1991; Sala & Austin, 2000). Thus, RUE variability may be influenced by time scale through a purely methodological effect. To distinguish this variability from the RUE variability per se that we wanted to test, we generated a "null model"

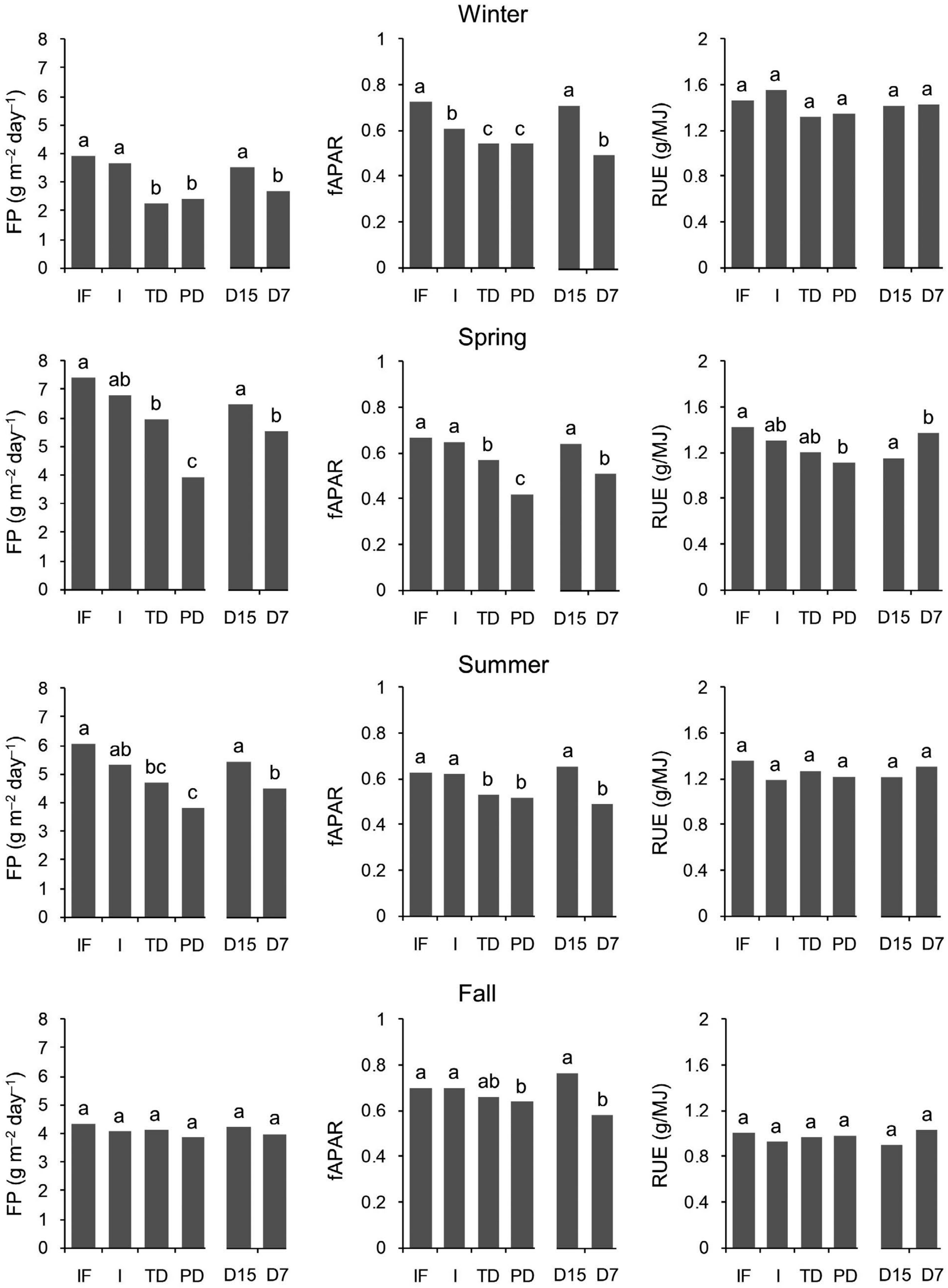

FIGURE 2 Seasonal forage productivity (FP, left), fractional absorbed photosynthetically active radiation (fAPAR, center), and radiation use efficiency (RUE, right) for resource availability and defoliation treatments for different seasons. Different letters indicate significant differences ($p \le .05$), based on two-way ANOVA performed with Infostat software (Di Rienzo, et al., 2018). IF: irrigated-fertilized, I: irrigated, TD: temporary drought, PD: permanent drought, D15: less severe defoliation (15 cm) and D7: severe defoliation (7 cm)

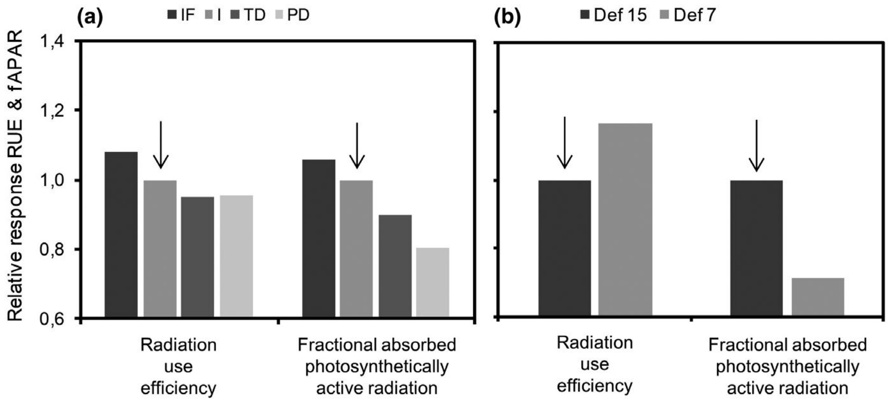

FIGURE 3 Relative responses of annual-average radiation use efficiency and fractional absorbed photosynthetically active radiation to (a) resource availability and (b) defoliation. Responses are relative to the treatment indicated by an arrow: irrigation in (a) and less severe defoliation in (b). Relative responses were calculated from mean values in Table 1. IF: irrigated-fertilized, I: irrigated, TD: temporary drought, PD: permanent drought, D15: less severe defoliation (15 cm) and D7: severe defoliation (7 cm)

that included the random error in the FP calculations at different time scales.

To generate the null model, FP as a function of APAR regressions were calculated using field data for the three time scales: season (90 days, 4 seasons, FP = 0.81 * APAR + 26.22, $R^2 = 0.86$, $n = 32$); regrowth (45 days, 8 regrowth periods, FP = 1.01 * APAR + 52.93, $R^2 = 0.77$, $n = 64$), and 12-day period (effective12 days, twenty-seven 12-day periods, FP = 0.92 * APAR + 141.52, $R^2 = 0.26$, $n = 232$). Data corresponded to a total of eight treatments and each point was the average of three replicates of the same treatment. We calculated the variances of the variables x (APAR) and y (FP) and identified 11 pairs of x–y points evenly distributed over the regression model. With the 11 FP and APAR values and their corresponding variances, normal distributions of 2000 values each were generated. Thus, for each time scale, we generated a set of 22,000 values. From this set, we randomly extracted pairs of points to generate new regressions, with n equal to the original regressions (season = 32, regrowth = 64, and 12-day period = 232). For each time scale, 15 regressions were generated. The mean R^2 of these regressions were 0.81, 0.80 and 0.59 for season, regrowth and 12-day period, respectively. In short, with the FP and APAR variation of the data from the different scales of analysis, similar R^2 for season and regrowth scales, and lower for the 12-day period scale could be expected. The difference between the observed and simulated values will be interpreted as an effect per se of the time scale of analysis on the FP-APAR relationship, that is, on the RUE.

3 | RESULTS

In relation to the first objective, FP changes due to defoliation management and environmental conditions were more closely related to changes in fAPAR than RUE (Figure 2). FP was reduced under severe defoliation in winter, spring and summer. Compared to the irrigated controls, FP increased with fertilization in winter and decreased with TD in winter and with PD in winter, spring and summer. In autumn, treatment effects on each species canceled each other out (data not shown), and as a result, total FP was not modified by any treatment. The interaction between resource availability and defoliation treatments was never significant. Seasonally, total FP was highest in spring, followed by summer, autumn and winter (Figure 2).

Variations of fAPAR in response to defoliation management and environmental conditions were very similar to those described for FP, while RUE was much more stable (Figure 2). fAPAR was reduced under severe defoliation in all four seasons. In relation to changes in resource availability, fAPAR mimicked very closely the general tendency of lower FP under resource scarcity: fAPAR increased with fertilization in winter and decreased with temporary drought in winter and spring, and with PD in all four seasons. RUE only showed significant responses to treatments in spring, when it increased by severe defoliation, and decreased under PD. The interaction between resource availability and defoliation treatments was never significant for either variable. fAPAR and RUE showed less variation than FP among seasons (Figure 2). Mean RUE for all treatments was 1.42 g/MJ in winter, 1.26 g/MJ in spring–summer and 1.38 g/MJ in autumn.

Summarized over the four seasons, the relative response of RUE to treatments was lower than the relative response of fAPAR (Figure 3, Table 1). In addition, the consistency of these variations between replicates of the same treatment was much lower for RUE than for fAPAR, so that similar relative differences were statistically more significant in the case of fAPAR than in the case of RUE (Table 1).

Regarding the second objective, to determine the impact of time scale on RUE variations, RUE variability considerably increased as time scale shortened from season (90 days, Figure 4a) to regrowth period (45 days, Figure 4b), to interval between visits (12-day period, Figure 4c). A lower R^2 of the FP–APAR relationship indicates a higher variability of RUE. Shortening the time scale from season (Figure 4a) to 12-day periods (Figure 4c) reduced R^2 from 0.93 to 0.41, a 56%

reduction. The R^2 reduction expected from the null model that accounted for the artifact of larger FP variability at shorter periods (see methods) was only 27% (R^2season = 0.81, $R^2$12-day period = 0.59). Thus, the observed increased of RUE variability with shorter time scale doubled the increase expected from our null model (actual 56% reduction of R^2 vs. 27% expected). Despite this strong influence of time scale on RUE variability, mean RUE was insensitive to the range of scales explored, as indicated by the lack of significant differences among regression parameters and the high overlapping of the three regression lines (Figure 4d).

TABLE 1 Comparison of means for annual-average radiation use efficiency (RUE) and fractional absorbed photosynthetically active radiation (fAPAR) for resource availability and defoliation treatments, based on two-way ANOVA performed with Infostat software (Di Rienzo, et al., 2018)

	Level	RUE (g/ MJ)	fAPAR	*N*
Resources	IF	1.42 a*	0.66 a	6
	I	1.34 a	0.63 b	6
	TD	1.27 a	0.56 c	6
	PD	1.26 a	0.51 d	6
Defoliation	Def 15	1.24 a	0.69 a	12
	Def 7	1.41 b	0.49 b	12

Note: The interaction between resources and defoliation was non-significant.

Abbreviations: Def15, less severe defoliation (15 cm); Def7, severe defoliation (7 cm); I, irrigated; IF, irrigated-fertilized; PD, permanent drought; TD, temporary drought.

*Different letters indicate significant differences ($p \le .05$) among levels of each factor (resources, defoliation).

4 | DISCUSSION

Both RUE and fAPAR were affected by changes in resource availability and defoliation intensity, but fAPAR was more variable than RUE. Furthermore, the influence of RUE versus fAPAR on FP depended on the time scale of observation. These two patterns may be used to improve the performance of models that estimate FP based on remote sensing and the RUE logic to be used in livestock production systems in temperate environments.

4.1 | fAPAR and RUE explaining changes in forage productivity

Severe defoliation at any season significantly reduced fAPAR and increased RUE. Average reduction of fAPAR was 29% and average increase of RUE was 17%, with stronger effect in spring (Figures 2 and 3). Usually defoliation reduces pasture productivity by reducing leaf area and, consequently, canopy photosynthetic capacity. But also, after severe defoliation the remaining canopy is structurally different: Shaded leaves are exposed to high light intensity, and canopy regrowth produces many new, young leaves (Soussana & Machado, 2000). It is not clear, from published results, how these changes alter RUE. Teixeira et al. (2008) found in a pure alfalfa pasture that RUE increased with increased defoliation frequency, while Conant et al. (2003) found no changes in RUE under continuous and rotational grazing in grass-legume mixed pastures. Compensatory growth, defined as an increase in the relative growth rate (Ferraro & Oesterheld, 2002; Oesterheld & McNaughton, 1991), often observed in studies at individual plant level, is an indication that RUE could increase under certain defoliation intensities. In this study, the relative growth rate increased by 42%

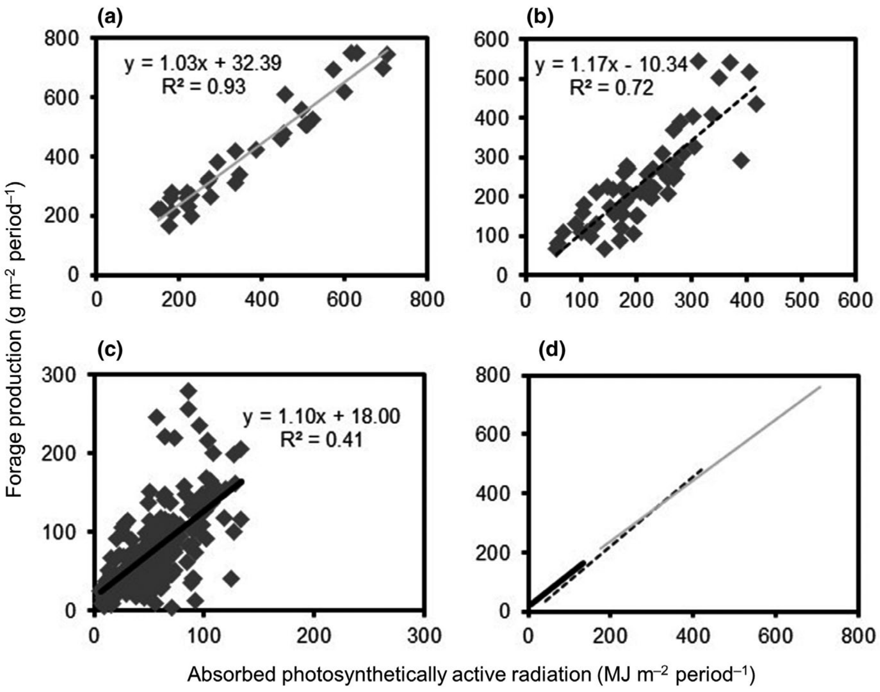

FIGURE 4 Forage production as a function of absorbed photosynthetically active radiation for resource availability and defoliation treatments at different time scales: (a) season (90 days), (b) regrowth period (45 days) and (c) 12-day interval between visits to the experiment (effectively 12 days). The functional relationship between forage productivity and absorbed photosynthetically active radiation represents radiation use efficiency, and the dispersion of the data around the fitted function (R^2) represents radiation use efficiency variability. Panel (d) shows the regression lines of each time scale showed in panels a, b and c. Statistical differences among time scale regressions were non-significant for both slope ($p = .2856$) and intercept ($p = .4548$) parameters, according to ANOVA

under severe defoliation. Under severe defoliation, alfalfa abundance in the mixture increased on average 20%, that is, RUE changes may respond not only to the discussed ecophysiological effect, but also to the species composition of the mixture. Considering that in general, legumes have lower RUE values (Faurie, Soussana, & Sinoquet, 1996; Sinoquet, Moulia, Gastal, Bonhomme, & Varlet-Grancher, 1990) and that in this experiment, plots with more alfalfa (severe defoliation) had higher RUE, and the ecophysiological effect of defoliation may have been greater than the overall effect observed.

At an annual scale, water stress significantly reduced fAPAR by 11 and 19% under TD and PD, respectively, but did not reduce RUE significantly (Figure 3, Table 1). In contrast, at more detailed temporal scales, the PD treatments decreased RUE in several growth intervals. Collino et al. (2005) working in alfalfa monoculture pastures subjected to water stress in Córdoba, Argentina, also found reductions in RUE only under very severe stress conditions. They concluded that the reduction of fAPAR was the main cause of FP reduction. At a daily scale, Gastal and Durand (2000) also concluded that the main effect through which water stress reduces photosynthesis of tall fescue pastures is the reduction of captured radiation because of a reduction of leaf area and increased leaf-rolling, which can reduce fAPAR by up to 50%. In that study, stomatal closure, which would be the mechanism by which RUE is reduced, played a minor role. Evaluation of these ecophysiological responses to stress is obviously more difficult in mixed systems such as the experiment of this study, where the components of the mixture may respond differently to a given stress.

The higher fertility generated by N and P addition increased fAPAR, but did not significantly change RUE (Figures 2 and 3, Table 1). Foliar N concentration depends on the state of the plant (demand) and available soil *N* (supply). With increased N availability, leaf elongation rate increases and, consequently, radiation interception and FP increase (Gastal & Durand, 2000). At individual leaf level, increases in N concentration increase photosynthesis at saturating light intensity, but at lower light intensities, such as the ones that most leaves of a closed canopy are exposed to, photosynthesis changes very little (Gastal & Durand, 2000). This is possibly one reason why there were no RUE differences in the fertilized treatment in agreement with experiments with tall fescue and alfalfa in the Southern Pampas (Ojeda et al., 2018). In addition, nutrient addition in our experiment was mild, as an attempt to mimic fertility differences that may occur among fields subjected to different natural fertility or management. The unfertilized treatment of the experiment was not deficient in nutrients as the plot was under livestock rotation, with acceptable levels of organic matter.

fAPAR and RUE remained relatively stable throughout the year at the seasonal scale (Figure 2). The fAPAR pattern contrasts with that of other systems, like the Flooding Pampa grasslands where fAPAR is much greater in spring than in winter (Aragon & Oesterheld, 2008; Posse, Oesterheld, & Di Bella, 2005). This difference may be due to two causes. First, our experiment took the canopy back to its initial condition every 45 days (simulating a variable stocking rate throughout the year that would always maintain the canopy in the same condition). This defoliation regime may have smoothed seasonal differences that could have been expressed under continuous grazing with a fixed stocking rate where consumption was greater than FP in winter and lower in spring, as is common in the grasslands of the Flooding Pampa mentioned above. The other cause may have been the shift of specific composition of the pasture throughout the year. In spring and summer, when alfalfa was dominant, defoliation left almost leafless stems with very low fAPAR. In autumn–winter, however, when tall fescue was dominant, defoliation resulted in a leafier canopy, with higher fAPAR.

The low variability of RUE among seasons contrasted with the positive response to temperature found in alfalfa pastures by Collino et al. (2005) in Argentina and Brown, Moot, and Teixeira (2006) in New Zealand. It also contrasts with alfalfa's physiological characteristic to allocate a significant portion of photoassimilates to roots and crowns in autumn, which should reduce RUE. In our study, the changing proportion of tall fescue and alfalfa in the pasture may have been the cause of the observed seasonal pattern. In general, higher RUE values have been found for grasses than for legumes (Faurie et al., 1996; Sinoquet et al., 1990). McCall and Bishop-Hurley (2003) propose values between 0.9 and 1.78 g/MJ for Lolium perenne, and Duru, Ducrocq, Fabre, and Feuillerac (2002) found in Dactylis glomerata pastures, average RUE of 1.1 g/MJ, with high RUE values in the winter months. Kiniry, Muscha, Petersen, Kilian, and Metz (2017) found a range of 0.27 (*Calamovilfa longifolia*) to 5.62 g/MJ (*Nassella viridula*) within a set of three grasses and one sedge near Miles City, USA (see other grass species within this range in Kiniry et al., 2007 and Kiniry, Johnson, Venuto, & Burson, 2013). Brown et al. (2006) and Teixeira et al. (2008) observed RUE between 0.29 and 1.6 g/MJ in alfalfa pastures. If grasses have somewhat higher RUE values than alfalfa, then it is to be expected that in late autumn–winter, when the pasture is dominated by tall fescue, RUE tends to be higher (Figure 2) and that species differences do not allow appreciation, at canopy scale, of the response of alfalfa RUE to temperature.

4.2 | Effect of measurement time scale on RUE variability

Our results support previous claims that RUE variability is lower at longer time scales. Numerous studies stressed the need to study RUE changes with changing time scales in other vegetation types (Field, 1991; Field et al., 1995; Joel et al., 1997; Medlyn et al., 2003; Ruimy et al., 1995; Ruimy, Saugier, & Dedieu, 1994). Our experiment analyzed RUE variability at varying scales, from less than two weeks to a whole season (90 days) in mixed pastures. At the scale of several weeks or months, pasture leaf area roughly matches the variation of resource availability, whereas RUE is close to the average for that type of vegetation (Chapin, Matson, & Vitousek, 2002). However, at a shorter scale, brief periods of either stressful or favorable conditions may trigger fast changes of RUE. For example, when water deficit becomes severely limiting, leaf expansion is reduced, leaf-rolling and leaf senescence increases, and RUE decreases, likely because of stomatal closure (Sinclair & Muchow, 1999). Similarly, short periods with various environmental conditions simultaneously in their optimum range may take place. For example, brief episodes of warm temperatures, high available soil water and a certain proportion of diffuse radiation will determine RUE values close to the maximum (Ruimy et al., 1995), a condition clearly unlikely when considering a whole season (90 days). Thus, there will be certain 7- to 12-day periods with very high or very low RUE. However, at regrowth period scale (e.g., 45 days), or at season scale (90 days), RUE will be more stable around a given average value.

Our results indicate that it is more difficult to estimate productivity of short periods assuming a constant RUE. In contrast, longer periods may reasonably assume a constant RUE and rely on tracking fAPAR variations. However, even at long time scales, the effect of environmental factors on RUE (in some cases detected in this experiment only as trends) should be included in FP estimates of systems as dynamic as temperate grasslands and pastures.

Several studies, mostly in forests, have analyzed the shape (linear vs. curvilinear) of the productivity-absorbed radiation relationship at variable temporal scales, trying to find the time limit in which the curvilinear model observed at minute and hour scales becomes linear. Ruimy et al. (1995) found that the curvilinear relationship between carbon exchange and irradiance at seconds or minutes scale becomes linear when it is integrated at a daily scale. In agreement with this, many simulation models use daily linear functions. Medlyn et al. (2003), however, suggest that at scales smaller than two weeks, linear models between productivity and APAR should not be used. That corresponds to the smallest scale used in this study, which proved to be linear (curvilinear models did not improve the fit) although some curvilinear tendency in the data can be seen. Another important aspect in the analysis of RUE at different time scales is its average value. In this experiment, the three scales evaluated are part of the same general model between FP and APAR, that is, calculated average RUE at these three different scales is relatively constant (Figure 4d).

5 | CONCLUSIONS

Our results reinforce the value of fAPAR as an explanatory variable of the variations in FP due to changes in resource availability and defoliation. However, RUE was increased by defoliation whereas fAPAR was reduced. The interaction between RUE variability and time scale was important: Variability was much greater at a scale of a few days. Extrapolating these experimental data to the variations observed among paddocks and seasons indicates, on the one hand, that most FP variations may be captured by a monitoring system based on remote sensing of APAR provided that the time scale is coarse enough. On the other hand, the contrasting response of RUE and APAR to defoliation indicates a potential weakness of such a system when situations with contrasting defoliation regime are compared.

ACKNOWLEDGMENTS

This research was supported by grants from the University of Buenos Aires and Foncyt. We thank Omar Scheneiter and the INTA Experimental Station at Pergamino for facilitating the experimental site.

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How to cite this article: Grigera G, Oesterheld M. Variability of radiation use efficiency in mixed pastures under varying resource availability, defoliation and time scale. *Grassl Sci*. 2021;67:156–166. https://doi.org/10.1111/grs.12302