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SHORT COMMUNICATION

Chloris gayana Kunth under different defoliation regimes. Morphogenesis, sward structure and leaf area index

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Abstract

Subtropical pastures are an important alternative to increase forage yields to fulfil cattle nutritional requirements. Despite the increasing expansion of these pastures in the semiarid subtropical region of Argentina, there is very little information about their responses to grazing management. The aim of this study was to evaluate the effect of different defoliation regimes on morphogenesis, sward structure and leaf area index of one of the most expanded forage species in this region, *Chloris gayana* Kunth. A combination of two defoliation frequencies (300 and 500 GDD) and two defoliation intensities (1 and 3 green stubble leaves) was compared by a controlled experiment that comprised 1,500 GDD. Defoliation frequency significantly affected leaf elongation rate (LER) and leaf area index (LAI). Under the high defoliation frequency, LER and LAI resulted almost half than under low defoliation frequency (0.34 ± 0.08 vs. 0.67 ± 0.08 mm·tiller^{-1}·GDD^{-1}; 8.31 ± 2.27 m^2/m^2 vs. 13.27 ± 1.59 m^2/m^2, at 300 or 500 GDD respectively), regardless of the intensity. Defoliation frequency or intensity did not affect leaf appearance rate, leaf lifespan, leaf size, number of green leaves per tiller nor tiller density at the end of the experiment. We conclude that to maintain high LER and LAI in *Chloris gayana* Kunth cv. Épica INTA-Pemán pastures, defoliation frequency could be of 500 GDD. Since leaf lifespan was 415 ± 110 GDD, under this defoliation frequency, a maximum accumulation of green leaf tissues with very little dead tissues may be achieved.

KEYWORDS
defoliation frequency, defoliation intensity, rhodes grass

1 | INTRODUCTION

Subtropical pastures are considered a main forage resource for cattle due to their high potential for dry-matter production in a wide variety of edaphoclimatic conditions, even in environments with abiotic restrictions such as low water availability and low temperatures (Da Silva, 2004; Fumagalli & Cornacchione, 2001; Humphreys, 1981; Tomás, Lacopini, Mattera, & Romero, 2013). Consequently, these pastures constitute a key resource to increase animal production (Kunst et al., 2003).

Although the introduction of these cultivated C_4 forage species is very recent in Argentina, their use has increased markedly over the last years (Jauregui, Zabala, Baudracco, Dimundo, & Lovino, 2012). One of the most extended subtropical species cultivated in the semiarid region is Rhodes grass (*Chloris gayana* Kunth), the tetraploid cultivar Épica INTA-Pemán being one of the most used. This cultivar is derived from Boma and has a photoperiodic response to short days, so flowering occurs at the end of summer, which allows extending the grazing period while maintaining a good nutritional value during spring and summer. In addition, its primary productivity is higher than that of diploid cultivars (Pérez, Taleisnik, Díaz, & Pemán, 2009). However, there is very little information about its response to grazing management.

Subtropical pasture management based on fixed parameters can produce large amounts of forage but, in many cases, of poor nutritional quality, thus diminishing animal performance and, consequently, the whole system productivity (Da Silva, 2004). Therefore, to fully exploit the high primary productivity of subtropical pastures, it is necessary to understand the functional relationship between plant and animal responses to different defoliation regimes (Nascimento, Da Silva, & Adese, 2004). Lemaire and Chapman (1996) established that individual plants in grazed communities are subject to sequential defoliations, the frequency and intensity of which mainly depend on the system of grazing management. They also mentioned that two types of response to defoliation can be distinguished at the individual plant level: (a) short-term physiological acclimatization to the restriction of carbohydrate supply for plant growth resulting from removal of photosynthetic tissues; and (b) longer-term morphological adaptation, constituting an important part of the avoidance mechanisms to grazing. In addition, Lemaire, Da Silva, Agnusdei, Wade, and Hodgson (2009) expressed that grazing frequency and intensity affect plants physiology and, therefore, the rate at which new leaf tissue is produced.

It is a well-known fact that morphogenetic variables depend on environmental factors such as temperature, nutrient supply and soil water status (Chapman & Lemaire, 1993) and that they allow to determine the best moment to start grazing, the optimal pasture rest period, and the defoliation intensity (Nascimento & Adese, 2004). In addition, Gastal and Lemaire (2015) mentioned that defoliation affects the morphogenetic variables, depending on its frequency and its intensity through several direct (reduction in light interception due to leaf area removal and subsequent decrease in plant photosynthesis rate) and indirect (impact on the spectral composition of light within the sward) physiological and environmental processes. The study of morphogenetic variables is then crucial to design grazing strategies to optimize forage production, cattle intake and to achieve pasture stability over time (Zanine, Santos, Oliveira, & Ferreira, 2005).

During the vegetative pasture growth period, morphogenesis is a function of three characteristics at tiller level: leaf appearance rate (LAR), leaf elongation rate (LER) and leaf lifespan (LLS). The combination of these morphogenetic variables determines the structural characteristics of the pasture: leaf size, tiller density and green (live) leaves per tiller, which, in turn, define the leaf area index (LAI). LAI is the main factor that determines light interception and, therefore, regrowth dynamics (Chapman & Lemaire, 1993). The phyllochron is the time interval between the appearance of two successive leaves outside the tube of sheaths; its inverse is the leaf appearance rate (Klepper, Rickman, & Peterson, 1982). The LLS is affected by temperature—like LAR—and determines the maximum green leaves number that a tiller can hold (Lemaire & Agnusdei, 2000). The LLS or the number of green leaves per tiller and the LAR are useful variables to determine the duration of the rest period, which should be the period after a complete defoliation in which an adult tiller can accumulate green tissues without senescence losses (Nascimento & Adese, 2004). Consequently, when the LLS is reached, the maximum green biomass per tiller is achieved and green tissue accumulation ceases unless tiller density increases (Lemaire & Agnusdei, 2000). Furthermore, forage harvesting efficiency is associated with the relationship between defoliation frequency and LLS (Lemaire & Chapman, 1996; Lemaire et al., 2009). LER depends on temperature changes in the shoot apex (Stoddart, Thomas, Lloyd, & Pollack, 1986) and on nitrogen supply (Cruz & Boval, 2000; Gastal & Nelson, 1994). Since the average LER of a leaf population reacts immediately to any change in temperature, the flow of leaf production copies seasonal variations. In a range of daily average temperatures between 12 and 20°C, LER response to temperature is approximately exponential in C_4 grasses (Lemaire & Agnusdei, 2000). Lemaire (2001) stated that shading (low red: far-red ratio) generated by a high leaf area index induces an increase in LER. Leaf size is positive compared with LER (Nelson, Asay, & Sleper, 1977) and negative compared with LAR (Cooper & Edwards, 1961), and in grass species, it depends mainly on its leaf length (Nelson et al., 1977). Tiller density is partially related to LAR, which determines the potential number of tiller appearance sites or *site filling* (Davies, 1974). Since LAI is the product of these three structural variables, they are affected by the same factors. Under this widely accepted conceptual framework, Agnusdei, Nenning, Marco, and Aello (2009) and Avila, Marco, Agnusdei, and Mayoral (2010) determined the LLS in a diploid cultivar (Finecut) of *C. gayana*. However, the response of this variable to different defoliation regimes was not considered in their study. Likewise, there is also little information about LAR or LER for this species.

The aim of this study was to evaluate the effect of different defoliation regimes, by a combination of two defoliation frequencies and two defoliation intensities on *C. gayana* cv. Épica INTA-Pemán morphogenetic variables, sward structure and leaf area index. We predicted that those defoliation regimes combining higher frequency and higher intensity would increase tillers density, reduce leaf size, LER and LAI.

2 | MATERIALS AND METHODS

2.1 | Plant material

The experiment was conducted in a greenhouse under controlled conditions (soil, irrigation and fertility) located at INTA Manfredi Research Station, Córdoba, Argentina (31°49′S, 63°46′W). *C. gayana* cv. Épica INTA-Pemán seeds were sown in 250 cm^3 plastic bags filled with Entic Haplustoll soil (organic matter: 7.41%, extractable phosphorus: 199 ppm, N-NO_3: 111 ppm, pH: 7.39, electric conductivity: 9.9 dS/m) in early October 2014. Two months later, ramets of equal size were extracted and planted in twenty containers of 0.9 m^3 filled with the same soil used in the plastic bags. In each container, a mini-sward of 1 m^2 was established by planting 40 ramets every 13 cm. Containers were fertilized with 90 kg P/ha and 92 kg N/ha before planting and were watered periodically to avoid drought stress.

2.2 | Experimental design

Four defoliation regimes resulting from the combination of two defoliation frequencies (300 and 500 growing degree days) and two defoliation intensities (1 and 3 green stubble leaves) were applied from December 2014 to May 2015. Treatments (300_1, 300_3, 500_1 and 500_3) were randomly assigned to the containers, which received a first homogeneous cut in December to create a uniform sward structure. Thus, a randomized complete block design with five replicates was performed.

Minimum and maximum daily air temperatures were recorded by a *datalogger* located inside the greenhouse, so as to estimate the growing degree days (GDD) considering a base temperature of 12°C (Agnusdei et al., 2009; Jones, 1985). The number of green stubble leaves was visually determined. Mini-swards were cut when the thermal sum of each treatment was achieved, at a stubble height of one or three green leaves according to the defoliation intensity of the treatment. Nitrogen fertilization (92 kg N/ha) was applied after each defoliation to maintain a high N content in soil.

The experiment lasted 1,500 GDD; consequently, three defoliations every 500 GDD (on 500, 1,000 and 1,500 GDD) and five defoliationsevery 300 GDD (on 300, 600, 900, 1,200 and 1,500 GDD) were performed.

2.3 | Morphogenesis and structural variables

Five tillers of different plants per container were labelled with coloured plastic-coated wire, and after each cut, five new tillers were selected and labelled. Leaf blade length was measured with a mechanical caliber in each labelled tiller. The appearance of new leaves and the number of green leaves per tiller was registered weekly when each experimental unit reached the defoliation criteria. Fully expanded leaf blades with 0%–50% of senescent tissue and expanding green leaves were considered as half green leaf. Before each defoliation, tiller density was measured in a 0.4 × 0.5 m frame.

Leaf appearance rate (leaves per GDD) was estimated considering the thermal sum elapsed between the appearance of the third and fourth leaf. Phyllochron (GDD per leaf) was estimated as the inverse of leaf appearance rate. Leaf lifespan (GDD) was considered as the product of the phyllochron and the maximum number of green leaves per tiller. Leaf elongation rate ($\text{mm}\cdot\text{tiller}^{-1}\cdot\text{GDD}^{-1}$) was estimated as the slope of a linear function across blade lengths sum per tiller and thermal time.

When defoliation criteria were achieved, ten representative green blades (subsamples) were cut, scanned and analysed with Image Tool software (Wilcox, Dove, McDavid, & Greer, 2002) to determine leaf size (cm^2 per leaf). Leaf area index (m^2 leaf per m^2 ground) was estimated as follows:

$$\text{LAI} = \text{leaf size} \times \text{green leaves per tiller} \times \text{tillers density} \tag{1}$$

2.4 | Statistical analyses

Analysis of variance using repeated measures option was carried out, since all variables were measured sequentially on the same experimental units throughout the experimental period. Contrast tests were carried out when it was necessary. Means were compared with the DGC method (Di Rienzo, Guzmán, & Casanoves, 2002) ($p < .05$), using InfoStat statistics software (Di Rienzo et al., 2008).

3 | RESULTS AND DISCUSSION

3.1 | Leaf appearance rate and phyllochron

It is not possible to asseverate that LAR evaluated in terms of thermal time and at individual leaf level was affected by defoliation regimes ($p = .1165$) and the same for phyllochron ($p = .358$) of *C. gayana* cv. Épica. The average values were 0.0138 ± 0.0048 leaves per GDD and 77.5 ± 18.5 GDD per leaf respectively. These results are consistent with those of numerous authors who found a similar response of LAR evaluated at tiller level, both in C_3 and C_4 grasses (Baker, Pinter, Reginato, & Kanemasu, 1986; Bauer, Frank, & Black, 1984; Berone, Lattanzi, Agnusdei, & Bertolotti, 2008; Chapman & Lemaire, 1993; Joya, Piccini, Ferri, & Sáenz, 2014; Lemaire & Agnusdei, 2000). However, other authors have studied LAR and phyllochron at individual leaf level but through the successive leaves of a whole tiller. They established that there is an ontogenic decrease in LAR during plant development due to an ontogenic increase in the sheath length of successive leaves, which would delay blades appearance (Duru & Ducrocq, 2000; Duru, Justes, Langlet, & Tirily, 1993; Kavanová, Grimoldi, Lattanzi, & Schnyder, 2006; Lemaire & Agnusdei, 2000; Skinner & Nelson, 1995). Hume (1991) studied six combinations of three defoliation frequencies and two intensities and found that LAR was reduced only in the most severe combination of frequency and intensity in C_3 grasses. This suggests that in our experiment, the most severe combination (300_1) would be within the tolerance range of *C. gayana* cv. Épica.

The average phyllochron of *C. gayana* cv. Épica (77.5 ± 18.5 GDD per leaf) showed intermediate values in relation to those values obtained for other C_4 grasses such as *Paspalum dilatatum* Poir. (100 GDD per leaf), *Cenchrus ciliaris* L. (57–74 GDD per leaf), *Megathyrsus maximus* (Jacq.) B. K. Simon & S. W. L. Jacobs (119 GDD per leaf), *Panicum coloratum* L. (98 GDD per leaf), *Digitaria californica* (Benth.) Henrard (57 GDD per leaf), *Trichloris crinita* (Lag.) Parodi (74 GDD per leaf) and *Pappophorum caespitosum* R. E. Fr. (158 GDD per leaf) (Lattanzi, 2011). These values suggest that phyllochron shows considerable variation across C_4 species.

3.2 | Leaf lifespan

Leaf lifespan was not affected by defoliation regimes ($p = .2368$) and achieved an average value of 414.8 ± 109.5 GDD. A constant LLS in terms of thermal time was also found for most C_3 and C_4 grasses (Agnusdei, 2013). LLS, expressed in GDD, varies substantially between species and cultivars (Lemaire et al., 2009). The average value that we determine for *C. gayana* cv. Épica, a tetraploid cultivar, was higher and more variable than those registered for the diploid cultivar Finecut (320 ± 13 GDD, Agnusdei et al., 2009 or 369 ± 5 GDD, Avila et al., 2010). It showed an intermediate value, with respect to other C_4 grasses, such as *Urochloa brizantha* (Hochst. ex A. Rich.) R. D. Webster cv. Marandu (417 GDD, Gonçalvez, 2002), *Sporobolus indicus* (L.) R. Br. (700 GDD, Agnusdei, 1999), *Cynodon* sp. (307 GDD, Pinto, 2000), *M. maximus* × *Megathyrsus infestus* (Andersson ex Peters) B. K. Simon & S. W. L. Jacobs (435 GDD, Martuscello et al., 2006) and *Cenchrus americanus* (L.) Morrone (339 GDD, Gonçalvez & Quadros, 2003). The LLS value is an indicator of the optimal pasture rest period when the aim of the production system is to maximize the cattle forage intake of green tissues (Nascimento & Adese, 2004).

3.3 | Leaf elongation rate

A significant effect of defoliation frequency within each defoliation intensity on LER was found (p = .0003 and p = .0235 at 1 and 3 green stubble leaves respectively) at the end of the experimental period (1,500 GDD), while defoliation intensity within each defoliation frequency did not affect LER (p = .0864 and p = .9019 at 500 and 300 GDD respectively). Tillers under the high defoliation frequency (300 GDD) showed a lower LER than under the low defoliation frequency (0.34 ± 0.08 vs. 0.67 ± 0.08 mm·tiller·GDD respectively) (Figure 1).

As will be mentioned later, leaf area index was also higher under the lower defoliation frequency than under the highest frequency at the end of the experimental period. These results are consistent with those found for *P. dilatatum* which in swards kept at higher LAI, showed a higher LER than in swards kept at a lower LAI (Agnusdei, 1999). Lemaire (2001) explained this response stating that shading (low red: far-red ratio) generated by a high leaf area index would induce an increase in LER. Berone et al. (2008) established that LER at tiller level increased 25% and 30% in treatments defoliated at one LLS (higher LAI) compared with those defoliated at half LLS (lower LAI) in *Bromus catharticus* Vahl. var. elata (E. Desv.) Planchuelo and *Lolium perenne* L. respectively. On the other hand, Davies (1974) indicated that LER did not usually change under lenient defoliation regimes (removal of two or three green leaves per tiller) in *L. perenne*, but it can decrease between 15%–20% when all leaves are removed.

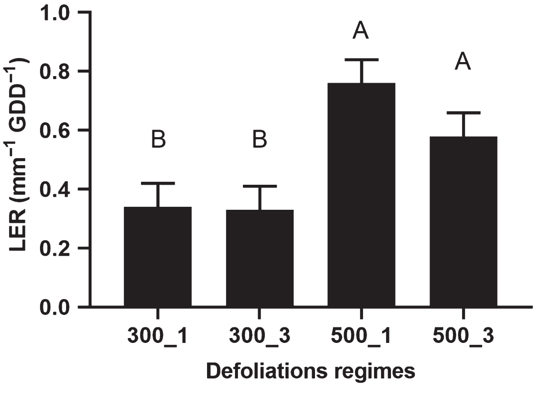

FIGURE 1 Leaf elongation rate (mm·tiller^{-1}·GDD^{-1}) of *C. gayana* cv. Épica INTA-Pemán subjected to the combinations of two defoliation frequencies (300 and 500 GGD) and two defoliation intensities (one and three green leaves). Data were obtained at the end of the experimental period (1,500 GDD). Vertical bars indicate 1 *SEM* of the means. Different letters indicate significant differences provided by the post hoc test (contrasts) among the combinations of defoliation intensity and frequency (300_1, 300_3, 500_1 and 500_3)

3.4 | Leaf size

Leaf size was significantly affected by defoliation regimes throughout the experimental period (p = .0001). Under the high defoliation frequency (300 GDD), leaf size was higher at the lenient intensity (three green leaves) than under the highest intensity (one green leaf) in the first and in the second cut and showed a pronounced fall between these cuts at both defoliation intensities. Under the lenient defoliation intensity, leaf size was similar from the second cut until the end of the experimental period, while under the highest intensity, leaf size increased at the third cut, reaching similar values to those in the first cut and to those of the lenient intensity through the end of the experimental period. Under the low defoliation frequency (500 GDD), this variable was similar for both intensities at the first cut and it was constant under the lenient intensity throughout the whole experimental period, while at the highest intensity, leaf size reached the highest value at the second cut. These results show that leaf size was highly variable across defoliation regimes throughout the experimental period (Figure 2). However, at the end of the experimental period (1,500 GDD), leaf size was similar across all defoliation regimes, reaching a value of 24.31 ± 2.29 cm^2 leaf per blade. In terms of absolute values, at the higher frequency and intensity regime, leaf size was lower than that at the lower frequency and lenient intensity regime. This response is consistent with numerous evidences which found that as the plant

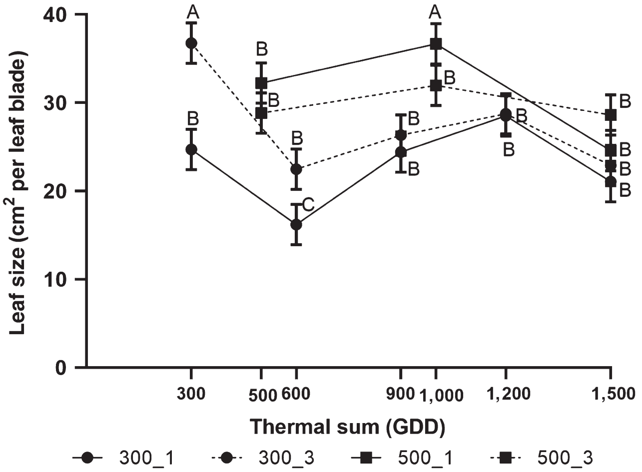

FIGURE 2 Evolution of leaf size (cm^2 leaf per blade) of *C. gayana* cv. Épica INTA-Pemán subjected to the combinations of two defoliation frequencies (300 and 500 GDD) and two defoliation intensities (one and three green leaves) throughout the experimental period, expressed as thermal sum (GDD). Vertical bars indicate 1 *SEM* of the means. Different letters indicate significant differences among means provided by the post hoc test (contrast) of the repeated measure analysis

grows the leaves are successively longer (Duru & Ducrocq, 2000; Duru et al., 1993; Kavanová et al., 2006; Lemaire & Agnusdei, 2000; Skinner & Nelson, 1995; Van Esbroeck, Hussey, & Sanderson, 1997). Consequently, under less frequent regimes, and a lenient intensity, plants have the possibility to grow for a longer period of thermal time and therefore, to achieve longer leaves. Considering that leaf growth is mainly unidirectional in grasses (Lemaire & Chapman, 1996; Nelson et al., 1977), longer leaves imply greater leaf size. Similarly, Carlson (1966) reported that the first leaf produced after a defoliation is small, and the successive ones increase in size until reaching the original equilibrium. Thus, if the defoliation frequency increases, the regrowth time may not be enough to allow for a total leaf recovery, and the size reached in such cases would be lower until a new equilibrium is achieved. Leaf length or leaf size depends on the ratio between LER and LAR, considering that for a given genotype, the leaf elongation duration is proportional to the LAR (Dale, 1982). The ontogenic increase in the length of successive leaves during tiller development is basically related to a longer leaf elongation duration rather than to an increase in LER (Gastal & Lemaire, 2015). In our experiment, we expected a greater leaf size at 1,500 GDD as LER was higher under the lower defoliation frequency. Lemaire and Chapman (1996) set that the potential maximum leaf size is genetically determined but, due to the morphological plasticity of grasses, it could be modified by defoliation regimes. Considering this aspect, our results suggest that the treatments applied were not different enough to generate a significant difference in leaf size.

3.5 | Number of green leaves

The number of green leaves per tiller was not affected by the defoliation regimes (*p* = .5646) and achieved a mean of 5.31 ± 0.53 green leaves per tiller. This result was expected as the number of green leaves per tiller depends on LLS and LAR (Chapman & Lemaire, 1993; Lemaire & Agnusdei, 2000), and both variables were not affected by treatments. Yang, Matthew, and Rowland (1998) and Davies (1988) demonstrated that this structural variable is almost constant for C_3 grasses. Briske (1996) showed that the relationship between leaf initiation rate and senescence rate maintains a relatively constant number of green leaves per tiller. In C_4 grasses, Ferri, Brizuela, Cid, and Stritzler (2005) found that the number of green leaves per tiller in *P. coloratum* was constant (among 5 and 6). Other authors suggested that this variable also changes between cultivars (Borrajo & Alonso, 2014).

3.6 | Tiller density

At the end of the experimental period (1,500 GDD), tiller density was similar for both defoliation intensities at each defoliation frequency (*p* = .8104 and *p* = .9411 for 500 and 300 GDD respectively) and for both defoliation frequencies at each defoliation intensity (*p* = .1598 and *p* = .2133 for 1 and 3 green stubble leaves respectively). The mean tiller density was 807 ± 76 tillers/m^2. This value is highly lower than the average value (2,315 tillers m^2) found by Torres, Pérez, Pérez, Lara, and Martínez Calsina (2014) in *C. gayana*. These authors also reported that after two cycles of continuous grazing of *C. gayana* cv. Épica, tiller density increased at the highest stocking rate (5 heifers/ha) regarding the lower stocking rate (3 heifers/ha). In our experiment, it was expected that pastures defoliated more frequently would increase its tiller density due to a higher R:FR ratio, as they present a lower LAI. However, our results suggest that the duration of the experimental period and the number of cuts were not enough to promote tillering through the improvement of light quantity and quality (Agnusdei, 2013; Assuero & Tognetti, 2010; Evers, Vos, Andrieu, & Struik, 2006; Gautier, Varlet-Grancher, & Hazard, 1999) in the most frequent defoliation regimes.

3.7 | Leaf area index

Defoliation regimes significantly affected LAI throughout the experimental period (*p* = .0001). Under the lower defoliation frequency (500 GDD), at the lenient intensity (three green leaves) LAI was constant and higher than at the higher intensity (one green leaf) until the end of the experimental period, when LAI increased and achieved a similar value to that of the lenient intensity. Under the higher defoliation frequency (300 GDD) at both intensities, LAI increased throughout the experimental period and reached the maximum value at the fourth cut, and afterwards it dropped to even lower values than those of the lower defoliation frequency. At the end of the experimental period (1,500 GDD), the lower defoliation frequency (500 GDD) reached a higher average LAI of 13.27 ± 1.59 m^2/m^2 than that of the higher defoliation frequency, which was 8.31 ± 2.27 m^2/m^2 (Figure 3), although the number of green leaves per tiller, leaf area and tiller density, which are structural trait determinants of LAI, did not differ. However, in absolute values, leaf area and tiller density were higher in the less frequent regimes during almost all the

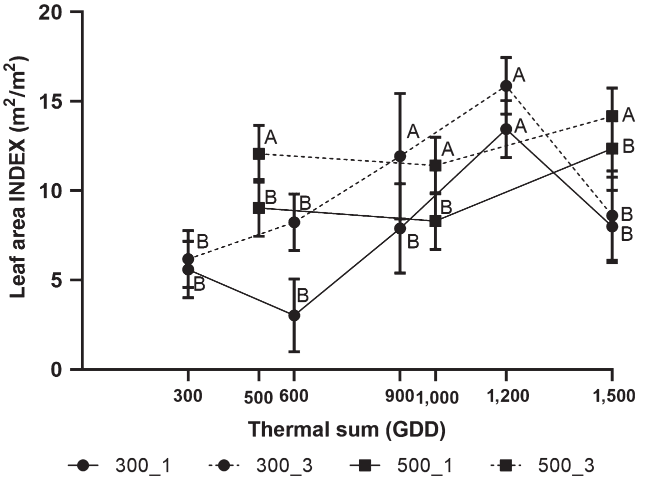

FIGURE 3 Evolution of leaf area index (m^2/m^2) of *C. gayana* cv. Épica INTA-Pemán subjected to the combinations of two defoliation frequencies (300 and 500 GDD) and two defoliation intensities (one and three green leaves) throughout the experimental period, expressed as thermal sum (GDD). Vertical bars indicate 1 *SEM* of the means. Different letters indicate significant differences among means provided by the post hoc test of the repeated measure analysis

experimental period, and since LAI is the product of these variables, this would explain the higher LAI values obtained under less frequent defoliations. Martínez Calsina, Agnusdei, Assuero, and Pérez (2012) also found a higher LAI in the less frequent defoliation treatments in *C. gayana* cv. Finecut.

Our results showed that LER and LAI of *C. gayana* cv. Épica was significant lower under the high defoliation frequency, irrespective of the defoliation intensity, and that tiller density and leaf size were not affected by defoliation frequency or intensity at the end of the experimental period. Therefore, our predictions were partially confirmed.

Different defoliation frequencies induced changes in *C. gayana* Kunth cv. Épica INTA-Pemán swards through several direct and indirect physiological and environmental processes, mainly affecting LAI, factor that determines light interception and, consequently, regrowth dynamics. LAI is the product of the interaction between the three structural characteristics, which are determined by LER, LAR and LLS. Therefore, *C. gayana* Kunth cv. Épica INTA-Pemán shows a morphogenesis dynamic that responds largely to the model proposed by Gastal and Lemaire (2015).

4 | CONCLUSIONS

Our study suggests that to maintain high leaf elongation rate and leaf area index in *Chloris gayana* Kunth cv. Épica INTA-Pemán pastures, defoliation frequency could be low (500 GDD), irrespective of defoliation intensity. As the leaf lifespan was 415 ± 110 GDD and it determines the optimal pasture rest period to maximize cattle forage intake of green tissues, we can conclude that under a defoliation frequency of 500 GDD, a maximum accumulation of green leaf tissues, with very little dead tissues may be achieved. This result is relevant to design appropriate grazing management regimes for this widely expanded forage species in the semiarid subtropical region in Argentina and contributes to the knowledge of the morphogenetics and structural responses of this C_4 grass to defoliation regimes.

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REFERENCES

Agnusdei, M. G. (1999). Analyse de la dynamique de la morphogenèse foliaire et de la défoliation de plusieurs espèces de graminées soumises à un pâturage continu dans une communauté de la Pampa Humide (Argentine). *Thése de l´Institut Polytechnique de Lorraine*, France (108 pp).

Agnusdei, M. G. (2013). Rol de la ecofiosiología en el diseño de manejos especializados de pasturas. *Archivos Latinoamericanos De Producción Animal*, *21*(1), 63–78.

Agnusdei, M. G., Nenning, F. R., Di Marco, O. N., & Aello, M. S. (2009). Variaciones de calidad nutritiva durante el crecimiento vegetativo de gramíneas megatérmicas de diferente porte y longitud foliar (*Chloris gayana* y *Digitaria decumbens*). *Revista Argentina De Producción Animal*, *29*(1), 13–25.

Assuero, S. G., & Tognetti, J. A. (2010). Tillering regulation by endogenous and environmental factors and its agricultural management. *The American Journal of Plant Science and Biotechnology*, *4*(1), 35–48.

Avila, R. E., Di Marco, O. N., Agnusdei, M. G., & Mayoral, C. (2010). Digestibilidad de la fibra y materia seca de dos gramíneas megatérmicas (*Chloris gayana* y *Cenchrus ciliaris*) de diferente porte: relación con la edad y largo foliar. *Revista Argentina De Producción Animal*, *30*(1), 1–13.

Baker, J. T., Pinter, P. J., Reginato, R. J., & Kanemasu, E. T. (1986). Effect of temperature on leaf appearance rate in spring and winter wheat cultivars. *Agronomy Journal*, *78*, 605–613.

Bauer, A., Frank, A. B., & Black, A. L. (1984). Estimation of spring wheat leaf growth rates from air temperature. *Agronomy Journal*, *76*, 829–835.

Berone, G. D., Lattanzi, F. A., Agnusdei, M. G., & Bertolotti, N. (2008). Growth of individual tillers and tillering rate o *Lolium perenne* and *Bromus stamineus* subjected to two defoliation frequencies in winter in Argentina. *Grass and Forage Science*, *63*, 504–512.

Borrajo, C. I., & Alonso, S. I. (2014). Vida foliar y número de hojas por macollo en materiales de agropiro: Efecto de la fenología, temperatura y nitrógeno. *Revista Argentina De Producción Animal*, *34*(1), 133.

Briske, D. D. (1996). Strategies of plant survival in grazed systems: A functional interpretation. In J. Hodgson, & A. W. Illius (Eds.), *The ecology and management of grazing systems* (pp. 37–68). Wallingford, UK: CAB International.

Carlson, G. E. (1966). Growth of white clover leaves after leaf removal. *Proceedings of the X International Grassland Congress* (pp. 134–139).

Chapman, D. F., & Lemaire, G. (1993). Morphogenetic and structural determinants of plant regrowth after defoliation. *Proceedings of the XVII International Grassland Congress* (pp. 95–104).

Cooper, J. P., & Edwards, K. J. R. (1961 The genetic control of leaf development in *Lolium*. 1. Assessment of genetic variation. *Heredity*, *16*, 63–82. https://doi.org/10.1038/hdy.1961.5

Cruz, P., & Boval, M. (2000). Effect of nitrogen on some morphological traits of temperate and tropical perennial forage grasses. In G. Lemaire, J. Hodgson, H. Moraes, C. Nabinger, & P. Carvalho (Eds.), *Grassland ecophysiology and grazing ecology of natural grasslands* (pp. 151–168). Wallingford, UK: CAB International.

Da Silva, S. C. (2004). Understanding the dynamics of herbage accumulation in tropical grass species: The basis for planning efficient grazing management practices. In P. R. Curitiba (Ed.), *II Symposium on grassland ecophysiology and grazing ecology* (pp. 11–14). New York, NY: CABI Publishing.

Dale, J. E. (1982). Some effects of temperature and irradiance on growth of the first four leaves of wheat *Triticum aestivum*. *Annals of Botany*, *50*, 851–858. https://doi.org/10.1093/oxfordjournals.aob.a086428

Davies, A. (1974). Leaf tissue remaining after cutting and regrowth in perennial ryegrass. *Journal of Agricultural Science*, *82*, 165–172. https://doi.org/10.1017/S0021859600050334

Davies, A. (1988). The regrowth of grass swards. In M. B. Jones, & A. Lazenby (Eds.), *The grass crop* (pp. 85–127). London, UK: Chapman & Hall.

Di Rienzo, J. A., Casanoves, F., Balzarini, M. G., Gonzalez, L., Tablada, M., & Robledo, C. W. (2008). *InfoStat, versión 2008* (268 pp). Córdoba, Argentina: Grupo InfoStat, FCA, Universidad Nacional de Córdoba.

Di Rienzo, J. A., Guzmán, A. W., & Casanoves, F. (2002). A multiple comparisons method based on the distribution of the root node distance of a binary tree. *Journal of Agricultural, Biological and Environment Statistics*, *7*(2), 1–14. https://doi.org/10.1198/10857110260141193

Duru, M., & Ducrocq, H. (2000). Growth and senescence of the successive grass leaves on a tiller. Ontogenic development and effect of temperature. *Annals of Botany*, *85*(5), 635–643.

Duru, M., Justes, E., Langlet, A., & Tirily, V. (1993). Comparaison des dynamiques d'apparition et de mortalité des organs de fétuques élevée, dactyle et luzerne (feuilles, talles et tiges). *Agronomie*, *13*, 237–252.

Evers, J. B., Vos, J., Andrieu, B., & Struik, P. C. (2006). Cessation of tillering in spring wheat in relation to light interception and red: Far red ratio. *Annals of Botany*, *97*, 649–658. https://doi.org/10.1093/aob/mcl020

Ferri, C. M., Brizuela, M. A., Cid, M. S., & Stritzler, N. P. (2005). Estructura del forraje diferido de mijo perenne y dinámica de acumulación de hojas. *Boletín De Divulgación Técnica INTA EEA Anguil*, *88*, 19–27.

Fumagalli, A., & Cornacchione, M. (2001). Engorde de novillos sobre Gatton panic. Santiago del Estero, Argentina: Sitio Argentino de Producción Animal. Retrieved from http://www.produccion-animal.com.ar/informacion_tecnica/invernada_o_engorde_pastoril_o_a_campo/09-engorde_novillos_sobre_gatton_panic.pdf

Gastal, F., & Lemaire, G. (2015). Defoliation, shoot plasticity, sward structure and herbage utilization in pasture: Review of the underlying ecophysiological processes. *Agriculture*, *5*, 1146–1171. https://doi.org/10.3390/agriculture5041146

Gastal, F., & Nelson, C. J. (1994). Nitrogen use within the growing leaf blade of tall fescue. *Plant Physiology*, *105*(1), 191–197. https://doi.org/10.1104/pp.105.1.191

Gautier, H., Varlet-Grancher, C., & Hazard, L. (1999). Tillering responses to the light environment and to defoliation in populations of perennial ryegrass (*Lolium perenne* L.) selected for contrasting leaf length. *Annals of Botany*, *83*, 423–429. https://doi.org/10.1006/anbo.1998.0840

Gonçalvez, A. C. (2002). Morphogenetic characteristics and defoliation patterns in Marandu grass pastures submitted to continuous stocking regimes. M. Sc. Dissertation. Piracicaba, Brazil: University of Sao Paulo, ESALQ. Retrieved from http://www.teses.usp.br/teses/disponiveis/11/11139/tde-08082003-140411/en.php [accessed 01 April 2019]

Gonçalvez, E. N., & Quadros, F. L. F. (2003). Pearl millet (*Pennisetum americanum* (L.) Leeke) morphogenesis under grazing by heifers with or without supplementation. *Ciencia Rural*, *33*, 1123–1128.

Hume, D. E. (1991). Effect of cutting on production and tillering in prairie grass (*Bromus willdenowii* Kunth) compared with two ryegrass (*Lolium*) Species. 1. Vegetative plants. *Annals of Botany*, *67*(6), 533–541.

Humphreys, L. R. (1981). *Environmental adaptation of tropical pasture plants*, (p. 261). London, UK: MacMillan Publishers Ltd.

Jauregui, J. M., Zabala, J. M., Baudracco, J., Dimundo, C., & Lovino, D. (2012). Producción y valor nutritivo de gramíneas C4 en el primer año de crecimiento. *Comunicación. Revista Argentina De Producción Animal*, *32*(1), 354.

Jones, C. A. (1985). *C_4 grasses and cereals: Growth, development and stress response*. New York, NY, USA: Wiley & Sons. Inc.

Joya, M. R., Piccini, M., Ferri, C. M., & Sáenz, A. M. (2014). Tasa de aparición de hojas en cultivares de *Avena spp*. *Revista Argentina De Producción Animal*, *34*(1), 172.

Kavanová, M., Grimoldi, A. A., Lattanzi, F. A., & Schnyder, H. (2006). Phosphorus nutrition and mycorrhiza effects on grass leaf growth. P status and size-mediated effects on growth zone kinematics. *Plant, Cell & Environment*, *29*, 511–520. https://doi.org/10.1111/j.1365-3040.2005.01428.x

Klepper, B., Rickman, R. W., & Peterson, C. M. (1982). Quantitative characterization of vegetative development on small cereal grains. *Agronomy Journal*, *74*, 789–792.

Kunst, C., Ledesma, R., Basan, M., Angella, G., Prieto, D., & Godoy, J. (2003). Rolado de fachinales e infiltración de agua en el suelo en el Chaco occidental argentino. *Revista De Investigaciones Agropecuarias*, *32*, 105–122.

Lattanzi, F. A. (2011). Crecimiento de plantas forrajeras. In C. A. Cangiano, & M. A. Brizuela (Eds.), *Producción Animal en Pastoreo* (pp.63–86). Argentina: Ediciones INTA.

Lemaire, G. (2001). Ecophysiology of grasslands: Dynamic aspects of forage plant populations in grazed swards. *International Grassland Congress, São Paulo*, *19*, 29–37.

Lemaire, G., & Agnusdei, M. (2000). Leaf tissue turnover and efficiency of herbage utilization. In G. Lemaire, J. Hodgson, A. Moraes, C. Nabinger, & P. Carvalho (Eds.), *Grassland ecophysiology and grazing ecology* (pp. 265–287). Wallingford, UK: CAB International.

Lemaire, G., & Chapman, D. (1996). Tissue flows in grazed plant communities. In J. Hodgson, & A. W. Illius (Eds.), *The ecology and management of grazing systems* (pp. 3–36). Wallingford, UK: CAB International.

Lemaire, G., Da Silva, S. C., Agnusdei, M., Wade, M., & Hodgson, J. (2009). Interactions between leaf lifespan and defoliation frequency in temperate and tropical pastures: A review. *Grass and Forage Science*, *64*(4), 341–353. https://doi.org/10.1111/j.1365-2494.2009.00707.x

Martínez Calsina, L., Agnusdei, M. G., Assuero, S. G., & Pérez, H. (2012). Size/density compensation in *Chloris gayana* Kunth cv. Fine cut subjected to different defoliation regimes. *Grass and Forage Science*, *67*(2), 255–262.

Martuscello, L. A., Fonseca, D. M., Nascimento, D. Jr, Santos, P. M., Cunha, D. N. F. V., & Moreira, L. M. (2006). Caracteristicas morfogênicas e estruturais de capim-massai submetido a adubação nitrogenada e desfolhação. *Revista Brasileira De Zootecnia*, *35*, 665–671.

Nascimento, D. Jr, & Adese, B. (2004). Acumulo de biomassa na pastagem. In O. G. Pereira, J. A. Obeid, D. M. Fonseca, & D. Nascimento Jr (org) *II Simpósio sobre manejo estratégico da pastagem. UFV Anais* (pp. 289–346). Viçosa, MG: Sociedade Brasileira de Zootecnia.

Nascimento, D. Jr, Da Silva, S. C., & Adese, B. (2004). Future perspectives for the use of grass species for grazing purposes. Proceeding of Annual Meeting of Brazilian Society of Animal Science, 41th, Campo Grande, Brazil (pp.130–141).

Nelson, C. J., Asay, K. H., & Sleper, D. A. (1977). Mechanisms of canopy development of tall fescue genotypes. *Crop Science*, *17*, 449–452.

Pérez, H. E., Taleisnik, E., Díaz, D., & Pemán, R. (2009). Development of a tetraploid salt-tolerant *Chloris gayana* cultivar. In E. G. Corte, (Ed.), *Simpósio Internacional sobre Melhoramento de Forrageiras*. Corte, Campo Grande, Brazil: Embrapa Gado de.

Pinto, L. F. M. (2000). Dynamics of dry matter accumulation in Cynodon spp. Swards under grazing. Sao Paulo, Brazil: Biblioteca digital: Tesses e Dissertações. Retrieved from: http://www.teses.usp.br/index.php?xml:lang=es

Skinner, R. H., & Nelson, C. J. (1995). Elongation of the grass leaf and its relationship to the phyllochron. *Crop Science*, *35*, 4–10. https://doi.org/10.2135/cropsci1995.0011183X003500010002x

Stoddart, J. L., Thomas, H., Lloyd, E. J., & Pollack, C. J. (1986). The use of a temperature-profiled position transducer for the study of low temperature growth in Graminae. *Planta*, *167*, 359–363.

Tomás, M. A., Lacopini, M. L., Mattera, J., & Romero, L. A. (2013). Producción inicial de Chloris gayana y Brachiaria sp. en la región central de Santa Fe. Jornada de Forrajeras Tropicales INTA EEA Rafaela, Argentina (pp. 34–35).

Torres, J. C., Pérez, P. G., Pérez, H. E., Lara, J. E., & Martínez Calsina, L. (2014). Evaluación de dos presiones de pastoreo en pasturas de *Chloris gayana* (Kunth) cv. Épica INTA-Pemán. *Revista Argentina De Producción Animal*, *34*(1), 203.

Van Esbroeck, G. A., Hussey, M. A., & Sanderson, M. A. (1997). Leaf appearance rate and final leaf number of Switchgrass cultivars. *Crop Science*, *37*, 864–870. https://doi.org/10.2135/cropsci1997.0011183X003700030028x

Wilcox, D., Dove, B., McDavid, D., & Greer, D. (2002). Image tool for windows, version 3.0. *Image Tool for Windows*, *version 3.0*. San Antonio, Texas, USA: The University of Texas, Health Science Center in San Antonio.

Yang, J. Z., Matthew, C., & Rowland, R. E. (1998). Tiller axis observations for perennial ryegrass (*Lolium perenne*) and tall fescue (*Festuca arundinacea*): Number of active phytomers, probability of tiller appearance, and frequency of root appearance per phytomer for three cutting heights. *New Zealand Journal of Agricultural Research*, *41*, 11–17.

Zanine, A. M., Santos, E. M., Oliveira, J. S., & Ferreira, D. J. (2005). Modernas estratégias no manejo do pastejo das gramíneas dos gêneros *Brachiaria* e *Cynodon*. *Revista Eletrônica De Medicina Veterinária*, *6*(11), 1–15.

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