

Defoliation intensity and leaf area index recovery in defoliated swards: implications for forage accumulation

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ABSTRACT: This study evaluated the leaf area index (LAI) recovery mechanisms and forage accumulation rates on the regrowth of different grass species subjected to different defoliation intensities. For that purpose, plots of *Pennisetum clandestinum* (kikuyugrass), *Lolium multiflorum* (annual ryegrass), and *Avena strigosa* (black oats) were defoliated from 20 to 80 % of their initial heights (25, 20, and 25 cm, respectively). At different increments in height, forage samples were collected to ground level and used to estimate tiller population density (TPD), leaf area per tiller (L_n), and forage mass. From these data, we calculated the leaf area index (LAI), average leaf area index (aLAI), and average and instantaneous forage accumulation rate (FAR and IFAR, respectively). Data were plotted over time (days) to describe LAI recovery and forage accumulation rates. As the defoliation intensity increased, greater canopy heights were needed for pastures to achieve their maximum forage accumulation rates, which required longer regrowth intervals. The need for high tiller recruitment after defoliation, which delayed canopy LAI recovery, seemed to be one of the main cause. Thus, grazing management strategies that involve costly tiller recruitment could decrease both overall forage production and sward persistence over time. However, the plant ability to recover LAI after successive intense defoliations seems to be species-dependent and related to their phenotypic plasticity.

Keywords: grazing heights, grazing management, intermittent stocking, sward targets

Introduction

The critical leaf area index ([LAI]; Brougham, 1958) has been suggested as the upper limit to interrupt regrowth of pastures under intermittent stocking method (Korte et al., 1982; Carnevalli et al., 2006; Sbrissia et al., 2018). However, the effects of residual LAI on pasture productive capacity and its relationship with defoliation management heights are still unclear. Theoretical models developed by Parsons et al. (1988) indicate that heavily defoliated pastures reach maximum growth rates later than leniently defoliated pastures do. According to Chapman (2016), intense defoliations would result in longer regrowth intervals, which could reduce total forage production.

The LAI recovery after defoliation occurs through leaf growth from remaining tillers and/or the emergence of new tillers (Lemaire and Chapman, 1996). High defoliation intensities can stimulate initial LAI increments through the recruitment of new tillers due to the improved light quality reaching the plant base (Gautier et al., 1999) and apex meristem decapitation (McSteen, 2009). However, frequent recruitment of new tillers can affect forage accumulation; thus, an appropriate management strategy should minimize tillering dependence (Nelson and Zarrouh, 1981). Moreover, forage plants are incapable to maintain a high growth potential after defoliation, despite the possibility of mobilizing carbohydrate reserves and of changes in a specific leaf area (Irving, 2015; Chapman, 2016).

Research data regarding the effects of defoliation intensity on forage production do not always present

convergent findings. This is because defoliation intensities are frequently generated from different pre-defoliation targets, which tend to favor targets created with better criteria (e.g., critical LAI; Barbosa et al., 2007; Silva et al., 2009; Zanini et al., 2012). In addition, most studies did not assess possible interspecific variations in LAI recovery and in forage mass during pasture regrowth. Therefore, this study assessed LAI recovery mechanisms and forage accumulation rates throughout the regrowth of different grass species subjected to different defoliation intensities. The central hypothesis tested was that increasing the defoliation intensity reduces the productive potential of pastures and that it is a species-dependent response.

Materials and Methods

Three experiments (I, II, and III) were conducted using different grass species in Lages, Santa Catarina State, Brazil (27°47' S, 50°18' W, altitude of 913 m), between Jan 2014 and Sept 2015. According to the Köppen classification system, the region has a Cfb climate (humid subtropical under oceanic influences), with cold winters, mild summers, and well-distributed rainfall throughout the year (Alvares et al., 2013). Weather data from the experimental period are presented in Table 1. The soil in the experimental area is classified as Clayey Inceptisol (Soil Survey Staff, 1999). Before the beginning of each experiment, soil samples were collected from 0-20 cm depth and submitted to the chemical analysis. Liming and fertilization were performed in order to reach a baseline pH of about 6.0 and to supply adequate levels

Table 1 – Average monthly climatic conditions recorded during the experimental months of 2014 and 2015 in Lages, SC, Brazil.

Month	2014									
	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct
Sunlight (h)	216.8	218.4	163.7	125.5	131.5	85.7	106.7	204.7	120.2	131.5
Precipitation (mm)	183.0	210.7	121.3	94.2	235.3	397.8	77.3	61.0	233.4	235.3
Maximum temp. (°C)	27.9	28.3	24.2	21.6	18.9	16.4	16.6	20.6	20.6	18.9
Average temp. (°C)	21.5	21	18.4	16.3	13.2	12.0	11.3	12.7	15.1	13.2
Minimum temp. (°C)	16.3	15.3	14.0	12.2	8.8	8.1	6.6	6.3	10.4	8.8
Month	2015									
	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct
Sunlight (h)	197.0	163.0	174.8	147.9	106.7	127.4	114.0	180.2	147.1	96.3
Precipitation (mm)	211.9	133.9	135.6	99.7	71.0	134.9	264.0	69.3	334.6	363.2
Maximum temp. (°C)	27.3	26.6	25.3	22.2	18.7	17.4	17.4	22.3	21.3	21.0
Average temp. (°C)	20.9	20.1	19.2	16.4	13.9	11.4	12.4	15.5	15.0	16.0
Minimum temp. (°C)	15.7	15.3	14.6	12.1	10.2	6.4	7.7	10.1	10.2	11.8

Source: National Institute of Meteorology (INMET, 2017).

of N, P, and K (Table 2), according to the soil analysis and the Fertilizing and Liming Manual for the states of Rio Grande do Sul and Santa Catarina (CQFS, 2004).

Experiment I (kikuyugrass)

This experiment was conducted in a well-established (~ 20-year-old) 1.8-ha kikuyugrass (*Pennisetum clandestinum* Hochst ex. Chiov) pasture. The experimental treatments consisted of four defoliation intensities (lowering 40, 50, 60, or 70 % of the initial height) applied from a recommended pre-cutting height of 25 cm (Sbrissia et al., 2018) and replicated three times in a randomized block design (12 plots of 1500 m²). The experimental treatments were established as follows: i) in early Dec 2013, the entire area was mowed to a residual height of 10 cm (to standardize the pre-experimental conditions), fertilized (Table 2), and plots were delimited; ii) when canopies reached 25 cm in height (from 14 Jan 2014 onward), grazing was performed by cattle to the intended residual heights (Table 3), defining the beginning of the data collection period. The canopy heights were measured with a sward stick (Barthram, 1985) at 50 points per plot after grazing and twice a week during the regrowth period.

Data were collected throughout two regrowth cycles (from 14 Jan 2014 to 20 Apr 2014). After each grazing event, three areas of 1 m² per plot were marked with wooden stakes. From these areas, forage samples were collected at five points throughout the regrowth period as follows: i) after grazing; ii) during regrowth (increments of 25, 50, and 75 % of height); and iii) at pre-grazing (25 cm). The heights of each sampling are presented in Table 3. On all occasions, clipping was performed to ground level, using quadrats of 0.0625 m² and scissors, and samples were taken to the laboratory for immediate processing.

Experiment II (annual ryegrass)

Annual ryegrass 'BRS Ponteio' (*Lolium multiflorum* Lam.) was broadcast-sown (90 kg seeds ha⁻¹) on 24 June

Table 2 – Application dates, fertilizer types, and amounts of phosphorus, potassium, calcium, and nitrogen applied during the three experiments.

Experiment	Date	Element	Fertilizer	Amount kg ha ⁻¹
I	16 Dec 2013	P	TSP	80 kg P ₂ O ₅
I	16 Dec 2013	K	KCl	80 kg K ₂ O
I	14 Jan 2014	N	Urea	90 kg N
I	10 Mar 2014	N	Urea	90 kg N
II	17 Apr 2014	Ca	CaL	20 kg CaO
II	25 May 2014	P	TSP	80 kg P ₂ O ₅
II	25 May 2014	K	KCl	80 kg K ₂ O
II	10 June 2014	N	Urea	200 kg N
II	09 Aug 2014	N	Urea	200 kg N
III	15 Feb 2015	Ca	CaL	30 kg CaO
III	08 Apr 2015	P	TSP	80 kg P ₂ O ₅
III	08 Apr 2015	K	KCl	80 kg K ₂ O
III	25 May 2015	N	Urea	150 kg N

TSP = triple superphosphate; KCl = potassium chloride; CaL = calcitic limestone (RTNP 98 %).

2014 into 16 plots of 1 m². The experimental treatments comprised four defoliation intensities (lowering 20, 40, 60, or 80 % of the initial height) applied from a recommended pre-cutting height of 20 cm (Santos et al., 2016) and replicated four times in a completely randomized design. Four weeks after sowing, canopies were approximately 20 cm tall. They were first lowered to 10-cm residual height to standardize the pre-experimental conditions and favor pasture establishment. On 09 Aug 2014, the canopies were 20 cm tall and were lowered to the intended residual heights by manual scissors trimming (Table 3), establishing the beginning of the data collection period. The canopy heights were measured with a sward stick (Barthram, 1985) at 15 points per plot twice a week during plot establishment, and daily during the data collection period.

Data were collected throughout a single regrowth cycle from 09 Aug 2014 until the canopies achieved

Table 3 – Cutting heights* (cm) from the residue in different defoliation intensity for kikuyugrass, annual ryegrass, and black oat pastures.

Experiment	I (kikuyugrass)				II (annual ryegrass)				III (black oat)		
	40 %	50 %	60 %	70 %	20 %	40 %	60 %	80 %	40 %	60 %	80 %
Cutting heights	-	-	-	7.5	-	-	-	4	-	-	5
	-	-	10	11.9	-	-	8	8	-	10	10
	-	12.5	13.8	16.3	-	12	12	12	15	15	15
	15	15.6	17.6	20.7	16	16	16	16	20	20	20
	17.5	18.7	21.2	25	20	20	20	20	25	25	25
	20.0	21.8	25	-	24	24	24	24	30	30	30
	22.5	25	-	-	28	28	28	28	35	35	35
	25	-	-	-	32	32	32	32	40	40	40
	-	-	-	-	36	36	36	36	-	-	-
	-	-	-	-	40	40	40	40	-	-	-

*Pre-cutting canopy height targets for each species are in bold.

40 cm in height. This procedure was performed in order to detect, at some point during regrowth, maximum forage accumulation rates (Parsons et al., 1988). Forage samplings were performed at every 4 cm increment in height throughout regrowth, from the residue until the canopy reached 40 cm (Table 3). Forage samples were collected to ground level using quadrats of 0.03 m² and scissors, and were taken to laboratory for immediate processing.

Experiment III (black oat)

Black oat 'IAPAR 61' (*Avena strigosa* Schreb.) was broadcast-sown (90 kg seeds ha⁻¹) on 15 Apr 2015 into nine plots of 2.8 m². The experimental treatments consisted of three defoliation intensities (lowering 40, 60, and 80 % of the initial height) applied from a recommended pre-cutting height of 25 cm (Guzatti et al., 2015; Duchini et al., 2014) and replicated three times in a complete randomized design. On 8 May 2015, canopies were trimmed to a residual height of 10 cm to standardize the pre-experimental conditions and favor pasture establishment. After reaching a height of 25 cm (25 May 2015), pastures were lowered for the first time to the intended residual heights (Table 3). From that point, as canopies reached 25 cm in height (from 06 June 2015 onward), another lowering to the intended residual heights was performed, starting a new data collection period. The canopy heights were measured with a sward stick (Barthram, 1985) at 15 points per plot, twice a week during the plots establishment, and daily during the data collection period.

Similar to Experiment II, data were collected throughout a single regrowth cycle from 06 June 2015 (residual heights) until the canopies achieved 40 cm in height (as mentioned above). Forage samplings were performed at every 4 cm increment in height throughout regrowth, from the residue until the canopy reached 40 cm in height (Table 3). Forage samples were collected to ground level using quadrats of 0.06 m² and scissors, and were taken to laboratory for immediate processing.

Laboratory assessments

The laboratory assessments for experiments I, II, and III followed the same protocol. The number of tillers in each forage sample was counted to estimate the tiller population density (TPD; tillers m⁻²). Then, green leaf blades from 50 tillers chosen randomly per sample were detached and scanned in a leaf area meter. The results (cm²) were divided by 50 to estimate leaf area per tiller (L_A ; cm² per tiller). After TPD and L_A were estimated, each sample (i.e., 50 tillers + the remaining material) was separated into plant parts (green leaf blades, stems + sheath, and senescent material), and dried in a forced-air oven at 65 °C for 72 h. The dry weights of these fractions were used to calculate total forage mass (kg DM ha⁻¹).

From these data, the LAI, the average LAI (aLAI), average forage accumulation rate (FAR; kg DM ha⁻¹ d⁻¹), and instantaneous forage accumulation rate (IFAR; kg DM ha⁻¹ d⁻¹) were calculated as follows:

$$LAI = TPD \times L_A$$

$$aLAI = \left[\frac{LAI_i + LAI_0}{2} \right]$$

$$FAR = \left[\frac{FM_i - FM_0}{t} \right]$$

$$IFAR = \left[\frac{FM_i - FM_{i-t}}{t} \right]$$

where: LAI_i represents the leaf area index at some specific point during regrowth; LAI_0 is the leaf area index at the beginning of the regrowth period; FM_i is the forage mass (kg DM ha⁻¹) at some specific point during regrowth; FM_{i-1} is the forage mass (kg DM ha⁻¹) recorded before the FM_i ; FM_0 is the forage mass (kg DM ha⁻¹) at the beginning of the regrowth period; and t is the time interval (days) between FM assessments. Thus, ($FM_i - FM_0$) represents the net forage mass variation between the beginning and some specific point during regrowth, and ($FM_i - FM_{i-1}$) equals the net forage mass variation between subsequent increments in height (Table 3).

Finally, the values for maximum average forage accumulation rate (FAR_{max} , kg DM ha⁻¹ d⁻¹), maximum instantaneous forage accumulation rate ($IFAR_{max}$, kg DM ha⁻¹ d⁻¹), canopy height to reach FAR_{max} (CH_{FARmax} , cm), average forage accumulation rate (FAR_{CHT} , kg DM ha⁻¹ d⁻¹), and average LAI ($aLAI_{CHT}$) when pastures reached the canopy height target, and the time (in days) to reach $IFAR_{max}$ and FAR_{max} were determined for each species-defoliation intensity combinations by plotting the data against days at regrowth.

Statistical analyses

Data were analyzed separately for each experiment using the PROC GLM of SAS (SAS Institute, 2008). For Experiment I, data from regrowth cycles were averaged to compose a single mean per plot ($n = 12$), and analyzed using a model including the fixed effect of defoliation intensity and the random effect of blocks. Data from Experiment II ($n = 12$) and III ($n = 9$) were analyzed using a model including the fixed effect of defoliation intensity. Treatment means were estimated using LSMEANS and compared using the Tukey-Kramer test. The significance level was set at 5% ($p < 0.05$).

Results

In general, increments in defoliation intensity had negative effects on $aLAI_{CHT}$ and FAR_{CHT} (Table 4); however, kikuyugrass maintained similar levels when lowered by 40 or 50% of initial height. Similarly, canopies under greater defoliation intensities ($\geq 40\%$ for annual ryegrass and $> 50\%$ for black oats and kikuyugrass) had a lower FAR_{max} and reached that condition above the CHT (CH_{FARmax} ; Table 4). The time required for canopies to reach $IFAR_{max}$ and FAR_{max} rose as defoliation intensity increased (Figure 1A-F); however, kikuyugrass did not reach either FAR_{max} or $IFAR_{max}$ when defoliated at 70%, since the protocol used for this species comprised assessments of only up to 25 cm (Table 4).

The LAI recovery in canopies under intense defoliation ($> 50\%$) depended on TPD and L_A increments, mainly for kikuyugrass and annual ryegrass (Figures 2A-I). Black oat was less capable to recruit new tillers to recover LAI, even after intense defoliations (Figures 2G and 2I). Less-intense defoliations ($\leq 50\%$) resulted in LAI recovery through L_A increments for all of the studied species (Figures 2B, 2E and 2H). For kikuyugrass, lenient defoliations (40 and 50%) caused tiller mortality and L_A increases in the same proportions thus LAI was similar throughout the regrowth period (Figures 2A-C).

Discussion

Impact of defoliation intensity on the productive potential of pastures

Overall, decreases in FAR_{CHT} and $aLAI_{CHT}$ occurred with increasing defoliation intensity (Table 4). These decreases occurred due to a gradual reduction in

Table 4 – Variables related to canopy height and forage accumulation rate of kikuyugrass, annual ryegrass, and black oat pastures subjected to different defoliation intensities.

Variable	Experiment I (Kikuyugrass)				SEM	p-value
	Defoliation intensity					
	40 %	50 %	60 %	70 %		
CH_{FARmax}	20	22	21	+25*	-	-
$aLAI_{CHT}$	3.9 ^A	3.9 ^A	2.7 ^B	2.6 ^B	0.25	< 0.001
FAR_{CHT}	149 ^A	147 ^A	108 ^B	97 ^B	15.4	< 0.001
FAR_{max}	165 ^A	177 ^A	140 ^B	97 ^C	10.7	< 0.001
Days FAR_{max}	9 ^A	13 ^A	19 ^B	43 ^C	2	< 0.001
Variable	Experiment II (Annual ryegrass)				SEM	p-value
	Defoliation intensity					
	20 %	40 %	60 %	80 %		
CH_{FARmax}	24	20	24	32	-	-
$aLAI_{CHT}$	4.0 ^A	2.9 ^B	2.0 ^C	1.5 ^D	3.3	< 0.001
FAR_{CHT}	126 ^A	100 ^B	68 ^C	50 ^D	10.5	< 0.001
FAR_{max}	158 ^A	100 ^B	108 ^B	109 ^B	6.4	< 0.001
Days FAR_{max}	3 ^A	3 ^A	8 ^B	26 ^C	2	< 0.001
Variable	Experiment III (Black oat)			SEM	p-value	
	Defoliation intensity					
	40 %	60 %	80 %			
CH_{FARmax}	25	30	35	-	-	
$aLAI_{CHT}$	3.5 ^A	2.5 ^B	2.2 ^C	0.3	< 0.001	
FAR_{CHT}	149 ^A	57 ^B	45 ^C	9.8	< 0.001	
FAR_{max}	149 ^A	83 ^B	80 ^B	8.2	< 0.001	
Days FAR_{max}	9 ^A	21 ^B	39 ^C	3	< 0.001	

Means followed by the same upper case letter in rows are not different by the Tukey-Kramer test ($p > 0.05$). Abbreviations: $aLAI_{CHT}$ = average LAI when pastures reached the canopy height target; CH_{FARmax} = canopy height to reach maximum forage accumulation rate (cm); FAR_{CHT} = average forage accumulation rate when pastures reached the canopy height target (kg DM ha⁻¹ d⁻¹); FAR_{max} = maximum average forage accumulation rate (kg DM ha⁻¹ d⁻¹); Days FAR_{max} = days needed to reach maximum average forage accumulation rate; SEM = standard error of the mean. *Did not reach the CH_{FARmax} .

residual LAI, as residual LAI determines the amount of light intercepted by the canopy after defoliation and, consequently, the leaf area replacement and organic reserves usages during regrowth (Donaghy and Fulkerson, 1998). Another factor that might have contributed to these decreases was the initial LAI recovery pattern, since the initial TPD increase is associated to the emergence of new tillers, as they are light and have a low L_A , they have little contribution to the LAI and forage accumulation (Tainton, 1974). Thus, the increase in defoliation intensity triggered greater tissue renewal from low residual LAI (low pasture photosynthetic capacity), reducing FAR_{CHT} .

Although the increase in defoliation intensity reduced the forage production capacity of all three species, some distinctions were observed (Table 4). The lack of difference between defoliations of 40 and 50% in the kikuyugrass was probably due to compensatory mechanisms between tiller size and tissue flows, as previously reported for this species under moderate defoliation intensity (50% of initial pre-grazing height; Sbrissia et al., 2018). On the other hand, the annual ryegrass and black oat growth habit (caespitose grasses) might have contributed, as small increments in defoliation

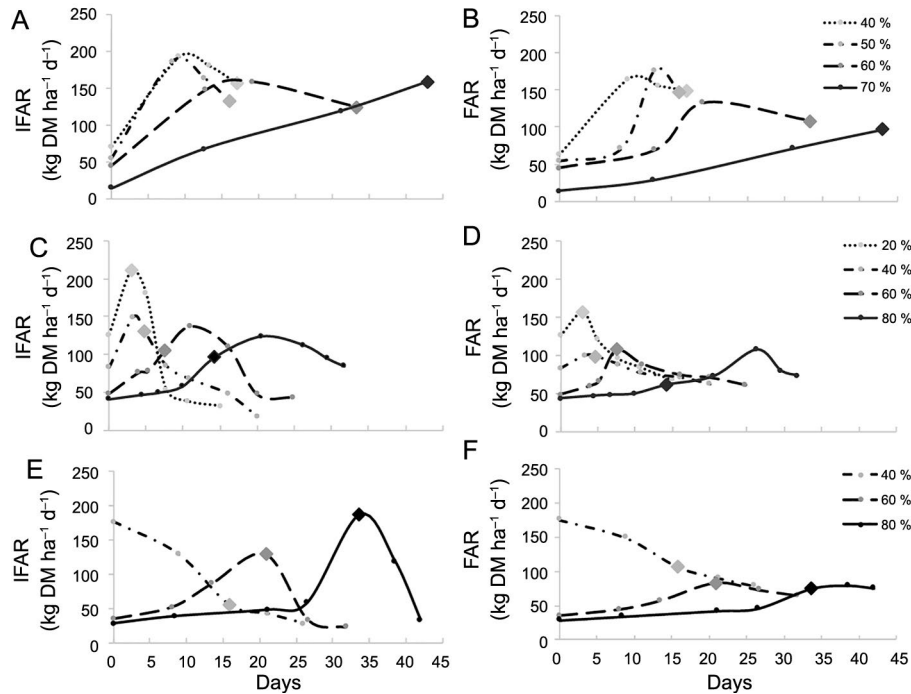


Figure 1 – Instantaneous (IFAR; A, C, and E) and average (FAR; B, D, and F) forage accumulation rates evolution in kikuyugrass (A and B), annual ryegrass (C and D), and black oat (E and F) pastures submitted to different defoliation intensities. Diamonds correspond to the moment when pastures reached their pre-cutting canopy height targets (CHT).

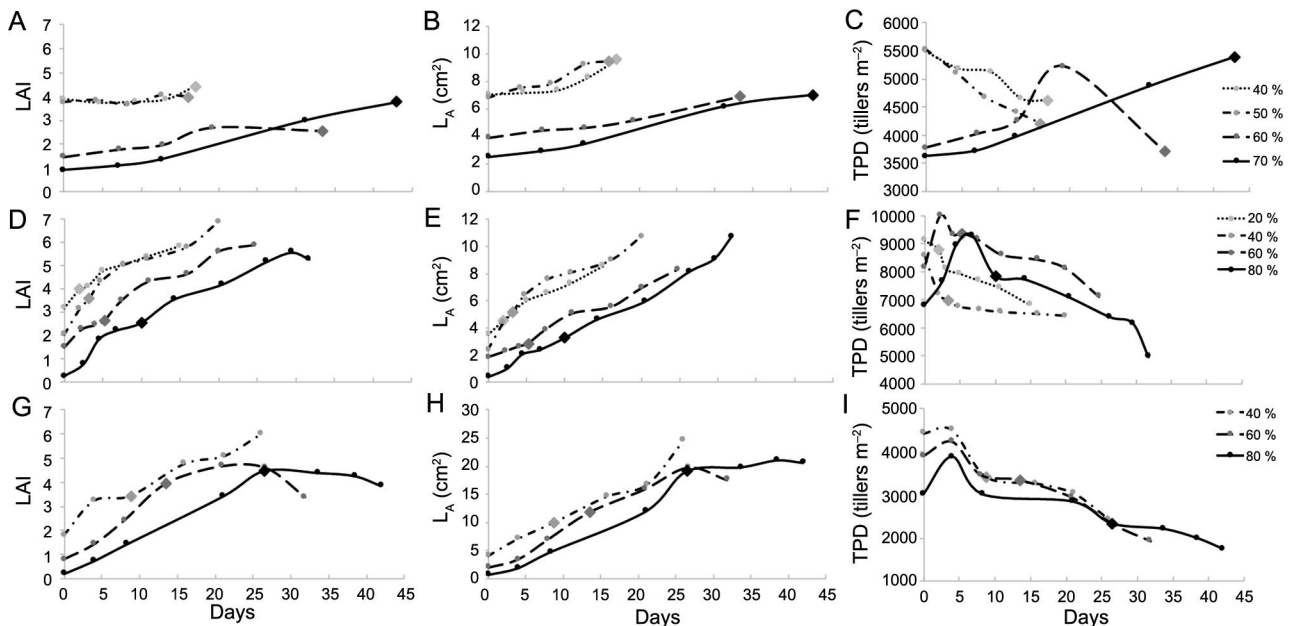


Figure 2 – Tiller population density (TPD) and average leaf area per tiller (L_A) contribution in LAI recovery for kikuyugrass (A, B, and C), annual ryegrass (D, E, and F), and black oat (G, H, and I) pastures submitted to different defoliation intensities. Diamonds correspond to the moment when pastures reached their pre-cutting canopy height targets (CHT).

intensity significantly decreased the residual LAIs and consequently their productive potentials (Figures 1B and 1C). Such responses suggest that these forage species

exhibit mechanisms of adaptation to defoliation that are different from those observed in kikuyugrass, even under moderate defoliation intensities.

According to Parsons et al. (1988), young leaves and/or those that grow under full light conditions (e.g., pastures managed at shorter heights) exhibit greater photosynthetic capacity as compared to old leaves and/or those grown under shadowy conditions (e.g., pastures managed at taller heights), which could, in theory, explain some productive equivalencies of pastures managed under different conditions (e.g., different heights or residual LAI). However, in our study, this advantage does not seem to have been enough to compensate for the differences in residual LAI when the pastures were defoliated more than 50 %. This probably occurred because once pasture regrowth, it partially depends on tiller recruitment, a process that involves a concomitant investment on tissues that do not contribute to LAI and aerial biomass increment (e.g., roots) (Tainton, 1974), which extend the period to reach the maximum growth rates. Therefore, Nelson and Zarrouh (1981) showed that tiller growth is more important than TPD to determine forage accumulation rate in established swards. Additionally, greater LAIs (observed in the less-intense defoliations; Figures 2A, 2D and 2G) usually results in greater leaf elongation rates (Berone et al., 2007; Sbrissia et al., 2018), which, associated with the greater TPD (Figures 2C, 2F and 2I), allowed fast initial increments of average and instantaneous forage accumulation rates in the canopies that were defoliated less intensively (Figures 1A-F). Therefore, apparently, the intense tissue renewal *per se* cannot be considered a factor that justifies the use of defoliation intensities above 50 % of initial height, particularly when the objective is to maximize forage accumulation.

Defoliation intensity influence on LAI recovery

The greater defoliation intensities resulted in lower residual LAI due to lower TPD and L_A ; thus, canopies used different means to recover the LAI after defoliation (Figures 2A-I). Canopies that were lowered by more than half of their canopy height target invested in increasing both L_A and TPD at the initial regrowth, while those lowered up to 50 % recovered their LAI mainly through L_A increments (Figures 2A-I).

Although every species exhibited TPD reduction after a period of regrowth, this occurred at different intensities and LAI for the three species, which could be a result of their different tillering and TPD maintenance abilities (Duchini et al., 2014; Sbrissia et al., 2018). Therefore, LAI recovery after defoliation depends not only on the defoliation intensity, but also on interspecific factors. In this sense, kikuyugrass submitted to moderate defoliation exhibited lower LAI variations, maintaining a high L_A and adjusting TPD; however, when submitted to intense defoliation, this species resorted to L_A and TPD adjustments (Figures 2A-C). Annual ryegrass showed adjustments in TPD and increments in L_A to recover its LAI in all defoliation intensities (Figures 2D-F), whereas black oat regulated its LAI throughout the regrowth primarily through adjustments in L_A , regardless of the

defoliation intensity (Figures 2G-I). These results are in line with those reported in the literature, as annual ryegrass and kikuyugrass have higher tillering capacity while black oat has difficulty to maintain its TPD over time and depends on quick L_A increments to recompose its LAI (Duchini et al., 2014; Sbrissia et al., 2018). It is worth noting that the deviations from these trends in specific moments of regrowth are due to the emergence of small and low L_A tillers and/or tiller size/density compensation mechanisms (Matthew et al., 1995).

Defoliation intensity effect on average and instantaneous forage accumulation rate

Parsons et al. (1988) used mathematical models to show the LAI recovery pattern of perennial ryegrass (*Lolium perenne* L.) submitted to different defoliation intensities to dissent about the rates of gross photosynthesis (P_{gross}), net photosynthesis (P_{net} ; i.e., gross tissue production), senescence, and average and instantaneous growth rates. In their study, pastures that were intensively defoliated had lower initial P_{net} and senescence rates, which led to a delay in reaching the maximum growth rates, while lenient defoliations had little effect on P_{net} and senescence, allowing those pastures to quickly obtain the maximum growth rates. Similarly, our results showed that increasing defoliation intensity promoted delays to obtain the $IFAR_{max}$ and FAR_{max} rates in kikuyugrass, annual ryegrass, and black oat pastures (Table 4; Figures 1A-F). An important difference compared to Parsons et al. (1988) is that, while they found different intervals to reach the FAR_{max} , our results show that, over time, increasing height is needed to reach this condition in highly defoliated swards.

Therefore, based on various studies suggesting a period for pastures to be defoliated to maximize forage production, for instance, the FAR_{max} (Parsons et al., 1988) and $IFAR_{max}$ (Morley, 1968; Maeda and Yonetani, 1978), or when both of these are equivalently high (Parsons et al., 2011), our findings show that the productive response of management based on presumed *ideal* pre-defoliation heights are dependent on the defoliation intensity to which the pasture will be submitted. Generally, in canopies submitted to defoliations up to 60 %, the maximum growth rates were obtained at heights close to the pre-defined targets for our study (Table 4; Figures 1A-F). On the other hand, for defoliation intensities of 70 % and 80 %, the maximum forage accumulation rates were reached at greater heights as compared to the pre-determined ones (Table 4; Figures 1A-F). This lack of synchrony may be due to the average LAI reduction and to the delay in LAI recovery caused by greater defoliation intensity. Thus, for intensively defoliated pastures, the delay in reaching their maximum forage accumulation rates reflects not only the low initial growth rates (Chapman, 2016), but also their need to reach greater heights to minimize the negative effects of low residual LAIs. The use of heights greater than those defined in this study as the pre-defoliation target could

favor the accumulation of stem and dead material (Da Silva et al., 2015), structures that reduce the nutritional value of the material offered to the animals and impose physical restrictions on the foraging process (Stobbs, 1973; Benvenuti et al., 2006).

Implications

The findings reported here highlight the mechanisms of LAI recovery and forage accumulation rates in defoliated swards. As the defoliation intensity increases, greater canopy heights are needed for pastures to achieve their maximum forage accumulation rates, requiring longer regrowth intervals. The need for high tiller appearance after defoliation, which delays canopy LAI recovery, seems to be one of the main causes; thus, grazing management strategies that involve costly tiller recruitment could decrease both overall forage production and sward persistence over time. However, the plant ability to recover LAI after successive intense defoliations seems to be species-dependent and related to their phenotypic plasticity.

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Authors' Contributions

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