Pasture brome *(Bromus valdivianus*) leaf growth physiology: a six-leaf grass species

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Abstract

Pasture brome (*Bromus valdivianus* Phil.) is a fast growing perennial grass, tolerant of water stress, with annual yield and herbage quality similar to perennial ryegrass (*Lolium perenne* L.). Its leaf stage (LS) development (expansion of sequential new leaves per tiller following defoliation), which impacts on grazing frequency, has not been adequately described. Pasture brome seeds were sown in pots (May 2016) under glasshouse conditions and continually defoliated at 2, 3, 4 and 5 LS, applying a randomised complete block design with six blocks. Tiller mass and number per plant, along with leaf number, appearance, elongation and senescence, lamina mass and area, and plant herbage mass above 5 cm defoliation height, were evaluated between August 2016 and January 2017. When pasture brome completed LS-5 for the third time, LS-2 had been completed seven times. When the oldest (first to emerge) leaf began senescing pasture brome tillers had three completely-expanded live leaves, along with three leaves still expanding. Pasture brome phyllochron corresponded to 20.1°Cd/leaf (thermal time; base t°=5°C) equivalent to 4.8 days/leaf; pasture brome lamina took 24.8 days for full expansion (14.8°Cd). Tiller weight (g dry matter) increased between LS-2 (0.81 g) and LS-5 (3.6 g) ($P<0.05$). Tiller number/plant was not affected by LS treatment ($P>0.05$). Leaf area per tiller increased ($P<0.001$) in the order LS-5 > LS-4 = LS-3 > LS-2. Thus LS-5 plants had 4.4 times greater leaf area than LS-2 plants. In conclusion, *B. valdivianus* is a six-leaf species, with three leaves concurrently expanding, and the oldest leaf senescing on appearance of the seventh leaf.

Additional keywords: leaf stage, tiller growth, lamina area, tiller senescence, defoliation frequency, thermal time

Introduction

Decreasing rainfall and increasing temperatures in summer result in soil water restriction for non-irrigated pastures, decreasing their growth rate. Such is the case for perennial ryegrass (*Lolium perenne* L.) and white clover (*Trifolium repens* L.), two species that are commonly sown as a pasture mix in New Zealand. This decreasing pasture growth rate is exacerbated by climate change. An alternative to help mitigate the decreased pasture production is the addition of drought-tolerant species to pastures, which also increases pasture diversity. Pasture brome (*Bromus valdivianus* Phil.) is more tolerant of water stress than perennial ryegrass probably due to a deeper root system (López *et al.*, 2013). Pasture brome is a perennial grass that can dominate pastures under soil conditions suitable for perennial ryegrass (López *et al.*, 1997) and its annual accumulated herbage mass and nutritive value are similar to perennial ryegrass (Balocchi and López, 2007). In non-irrigated fertile soils in temperate humid regions of Chile, conditions similar to many regions of NZ, perennial ryegrass and pasture brome often coexist naturally within a pasture. The presence of species such as pasture brome increases the stability of the pasture to environmental changes without decreasing herbage production and quality (Keim *et al.*, 2015). However, the defoliation management of a diverse pasture, such as one that includes pasture brome may differ from that of a perennial ryegrass-white clover pasture, especially when aiming for pasture production, quality, persistency and sustainability. Pasture brome plant growth and development differs to that of perennial ryegrass with pasture brome having 2.3 times heavier tillers, 3.6 times greater leaf area per tiller, 13% greater live leaf number per tiller and 1.5 times longer total lamina length per tiller. At the same time, the annual accumulated herbage mass of a pasture brome pasture is similar to that of a perennial ryegrass pasture, as perennial ryegrass produces 2.2 times more tillers than pasture brome (López *et al.*, 2013). Thus, it seems that there is a functional compatibility between perennial ryegrass and pasture brome which benefits the pasture, especially as pasture brome is able to continue growing under conditions of low soil moisture (Keim *et al.*, 2015). Perennial ryegrass physiology during regrowth has been studied, with defoliation (grazing) criterion developed for perennial ryegrass pastures based on leaf regrowth stage of plants, with the lower limit to grazing based on replenishment of the plant's carbohydrate stores, and the upper limit based on senescence of the oldest leaf (Fulkerson and Donaghy, 2001). However, there is a dearth of information regarding similar defoliation criteria for pastures that include pasture brome. This information is necessary to optimise the management of these pastures.

The aim of the current study was to measure changes in leaves and tillers of pasture brome (*Bromus valdivianus* Phil.) with leaf stage (LS) development (expansion of sequential new leaves per tiller), in order to determine the impact of defoliation management based on plant regrowth.

Materials and Methods

The study was carried out under glasshouse conditions at the Plant Growth Unit, Massey University, Palmerston North, between August 2016 and January 2017.

Seeds of pasture brome (*Bromus valdivianus* cv. Bareno) were sown in 10 L pots (May 2016) at the rate of 16 seeds per pot in 8 equidistance positions; two of the positions were located in the centre of the pot. After the establishment, only one seedling was left in each position, such that two seedlings were located in the centre of the pot, surrounded by six seedlings closer to the pot edge, which were used as a border. Only the plants in the centre of the pots were evaluated.

The substrate used was a mix of 50% sand and 50% Manawatu silt loam soil. All the pots were individually irrigated daily by a spaghetti tubing automatic irrigation system. Fertiliser was added thus the short-term (short-term mix, 50 g/pot: 14% N, 6% P, 11.6% K, 1.4% Mg, 6.0% S, 2.0% Fe and 0.5% Mn) and long-term (long-term mix, 50 g/pot:15% N, 2.2% P, 8.3% K, 0.2% Mg, 1.4% S, 1.4% Fe, 0.3% Mn, 0.2% Zn) plants nutritional requirements were fulfilled.

When seedlings first reached an average of 15 cm height, they were cut to 5 cm, and this was repeated a further two times, to encourage tillering (Turner *et al.*, 2012). Treatments were imposed immediately after the third defoliation (28 August 2016); at that time all the plants were considered to be fully established.

At the beginning of the treatment period two individual tillers from each centre plant were marked by placing a paper clip at their base (Poff *et al.*, 2011). Every two days leaf appearance, leaf number, lamina elongation and senescence were recorded. A new leaf was considered as 'appeared' when its tip was visible within the sheath of the previous leaf (Wilhelm and McMaster, 1995). The length of a completely expanded leaf was measured as the distance from the lamina tip to its ligule. The length of an elongating lamina was measured from the tip of the lamina to the ligule of the previous completely expanded leaf (Poff *et al.*, 2011). The senescence of a lamina was determined as the distance from its ligule to the end of the green coloration in the lamina (Duru and Ducrocq, 2000). Since lamina length was recorded every two days for all the laminas, any variation in lamina length due to expansion or senescence was detected.

Four defoliation treatments were applied, being sequential defoliation on the full expansion of 2 leaves (LS-2), 3 leaves (LS-3), 4 leaves (LS-4) or 5 leaves (LS-5) per tiller and layout and performed according to a randomised complete block design with six blocks. All defoliations were to 5 cm height. The study ended when the LS-5 treatment was defoliated for a third time, after which each individual treatment was sequentially harvested when its corresponding LS was reached. As the temperature was continually recorded the thermal time was determined (Zhang *et al.*, 2013) and related to the progress of the different plant physiological stages.

At each defoliation event only the centre plants were evaluated. The marked tillers were cut first to 5 cm and individually evaluated for lamina area, number of leaves, leaf stage and lamina mass, sheath mass and tiller mass as dry weight. Also all the plants in each pot were individually cut to 5 cm, and the centre plants individually evaluated for tiller number and herbage mass as dry matter. The plant material produced by the other plants was discarded. Herbage dry matter (DM) was obtained by drying the plant material in an oven at 70°C for 48 hr.

At the end of the study the plant material between 0 and 5 cm also was evaluated for the marked tillers and the centre pot plants. The stubble of the marked tillers was evaluated for lamina area, number of leaves and lamina mass, sheath mass and tiller mass as dry weight. The stubble of the centre plants was evaluated for herbage mass. Tiller number per plant was also counted.

ANOVA, LSD test were performed on tiller number, lamina area, lamina weight, tiller weight, leaf area of individual tillers and plants at the final cut, and also on the accumulated leaf area per tiller, accumulated herbage mass per plant and accumulated leaf area per plant. Also canonical variate analysis was undertaken after standardising the data, thus each variable had average zero and standard deviation equal one (Marsh and Elliott, 2008).

Results

Pasture brome maintained six live leaves, with three expanding at any given time; when the seventh lamina appeared the oldest lamina (first to appear) began to senesce. As senescence began tillers had three completely-expanded leaves and three expanding leaves, which were at the following LS: the oldest expanding leaf was at about 0.75 LS (i.e. around three quarters of its final, fully-emerged size), the second oldest expanding leaf was at 0.5 LS and the youngest leaf was at 0.25 LS. Thus, senescence began at LS-4.5.

It took an average of 24.8±1.3 days (average ± sem) for full expansion of a pasture brome lamina, which in thermal time equated to 14.8±0.2°Cd (average ± sem; 5°C as base temperature). The average phyllochron was 96±1.9 GDD/leaf equivalent to 20.1±0.7°Cd/leaf and 4.8±0.3 days/leaf. The number of days required for pasture brome to reach each of the targeted LS varied due to the daily differences in temperature. However, when the results were standardised by thermal time, the results for each LS were consistent: 12.9±1.1 days to reach LS-2 (thermal time: 14.6±0.5°Cd; average ± sem; base t°=5°C), 19.2±1.4 days to LS-3 (14.8±0.6 °Cd), 26.5±2.1 days to LS-4 (14.7±0.6°Cd) and 35.7±0.9 days to LS-5 (14.7±0.8°Cd). When pasture brome completed LS-5 for the equivalent third time, LS-2 was completed seven times, LS-3 six times, and LS-4 four times.

At the end of the study plants under the different defoliation regimes did not differ in tiller number, but differed in herbage mass (Table 1). Plants harvested at LS-5 had 5.9 times greater herbage mass compared to those harvested at LS-2, 3.0 times greater herbage mass than LS-3 and 1.5 times greater herbage mass than LS-4. These differences were supported by LS-5 having bigger lamina area per tiller ($P<0.001$) and greater lamina mass per tiller ($P<0.001$) compared to all other LS treatments.

The accumulated growth over the whole experimental period is shown in Table 2. The accumulated lamina area per tiller was greater in LS-3 and LS-4, and LS-4 also had the greater lamina mass per tiller, tiller herbage mass and lamina area per plant. The greatest herbage mass per plant occurred under LS-4 and LS-5 treatments.

The canonical variate analysis (CVA) shows the relationships between the measured variables and the defoliation regimes. The first two canonical variates explained 96.3% of the differences between treatments (Wilk's Lambda: $P<0.001$). The first canonical variate (CAN 1; $P<0.001$) explained 87.8% of the differences between the treatments and the second canonical variate (CAN 2; $P<0.001$) explained 8.4% (Figure 1). Variables that were highly correlated to CAN 1, in the positive direction were lamina area per tiller, lamina mass per tiller, herbage mass per tiller and herbage mass per plant, being explained by increasing tiller mass and size. The variables that increased in the negative direction of CAN 1 were accumulated lamina area per tiller and accumulated lamina area per plant, which emphasise plant recovery and growth post-defoliation. CAN 2 was in the positive direction highly correlated to accumulated lamina mass per tiller, accumulated tiller mass and accumulated herbage mass per plant. These variables on CAN 2 explained also plant recovery and growth post-defoliation (Figure 2).

Table 1: Tiller number (per plant) and mass (g dry matter (DM) per tiller), leaf area (cm^2 per tiller and per plant) and mass (g DM per tiller) and herbage mass (g DM per plant) for pasture brome (*Bromus valdivianus*) in last defoliation (January 2017), following repeated defoliation at the 2, 3, 4 and 5 leaf stage.

Leaf stage defoliation treatment	Number of defoliations equivalent	Tiller number (/plant)	Tiller mass (g/tiller^{-1})	Lamina area (cm^2/tiller)	Leaf area (cm^2/plant)	Lamina mass (g/tiller)	Plant mass (g/plant)
LS-2	7	42.6	0.135d	12.5c	538.6b	0.094d	1.54c
LS-3	6	45.2	0.248c	23.6b	1099.1ab	0.171c	2.94c
LS-4	4	48.8	0.488b	28.3b	1421.1a	0.304b	6.20b
LS-5	3	39.0	0.605a	44.1a	1705.4a	0.403a	9.09a
Significance		n.s.	***	***	*	***	***

*P≤0.05; **P≤0.01; ***P≤0.001; n.s., non significant differences

Table 2: Accumulated lamina area (cm^2/tiller), leaf area (cm^2/plant), lamina mass (g DM/tiller), tiller mass (g DM/tiller) and plant mass (g DM/plant) for pasture brome (*Bromus valdivianus*) between August 2016, and January 2017, following repeated defoliation at the 2, 3, 4 and 5 leaf stage.

	Accumulated				
Leaf stage defoliation	Lamina area (cm^2/tiller)	Leaf area (cm^2/plant)	Lamina mass (g/tiller)	Tiller mass (g/tiller)	Plant mass (g/plant)
LS-2	179.3b	4884.2b	0.95 c	1.12 c	10.7c
LS-3	192.9ab	5110.9b	1.35 b	1.50 b	16.0bc
LS-4	213.5a	6611.6a	1.57 a	1.92 a	25.2a
LS-5	142.0c	4285.0b	1.91 b	1.46 b	21.5ab
Significance	***	*	***	***	***

*P≤0.05; **P≤0.01; ***P≤0.001; n.s., non significant differences

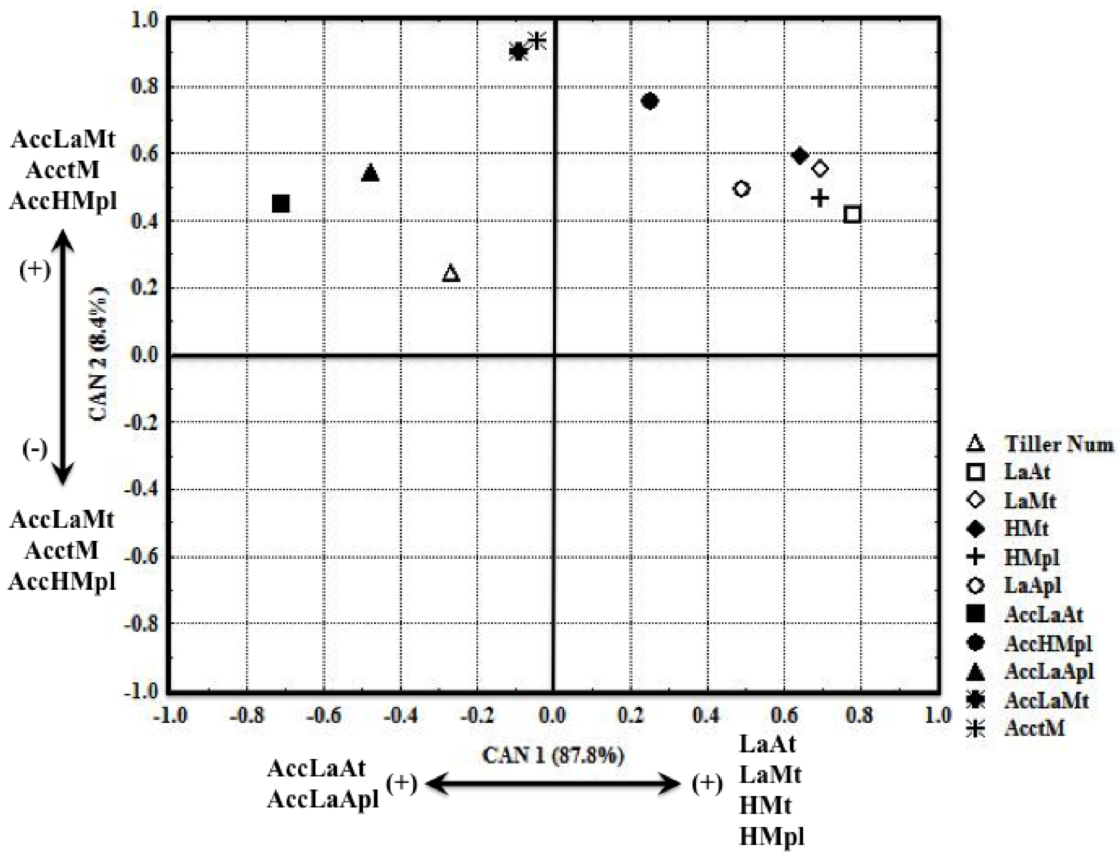

Figure 1: Seed Relationship between tiller and plant foliage components for pasture brome (*Bromus valdivianus*) following repeated defoliation at the 2, 3, 4 and 5 leaf stage. Tiller Num Tiller number; LaAt Lamina area per tiller; LaMt Lamina mass per tiller; HMt Herbage mass per tiller; HMpl Herbage mass per plant; LaApl Lamina area per plant; AccLaAt Accumulated lamina area per tiller; AccHMpl Accumulated herbage mass per plant; AccLaApl Accumulated lamina area per plant; AccLaMt Accumulated lamina mass per tiller; AcctM Accumulated tiller mass.

Discussion

Leaf regrowth stage reflects the physiological state of a plant, in terms of the progression of regrowth following defoliation (leaf regrowth before root regrowth before resumption of tillering) and the priority in use of carbohydrate stores for regrowth (Donaghy and Fulkerson, 1998). In perennial ryegrass the lower limit to grazing is based on replenishment of the plant's carbohydrate stores, and the upper limit is based on senescence of the oldest leaf (Fulkerson and Donaghy, 2001). Thus, LS is a precise, flexible and non-prescriptive method to determine pasture defoliation frequency (Rawnsley *et al.*, 2014). The present study measured changes in pasture brome leaves and tillers with LS development (expansion of sequential new leaves per tiller), in order to determine the impact of defoliation management based on plant regrowth.

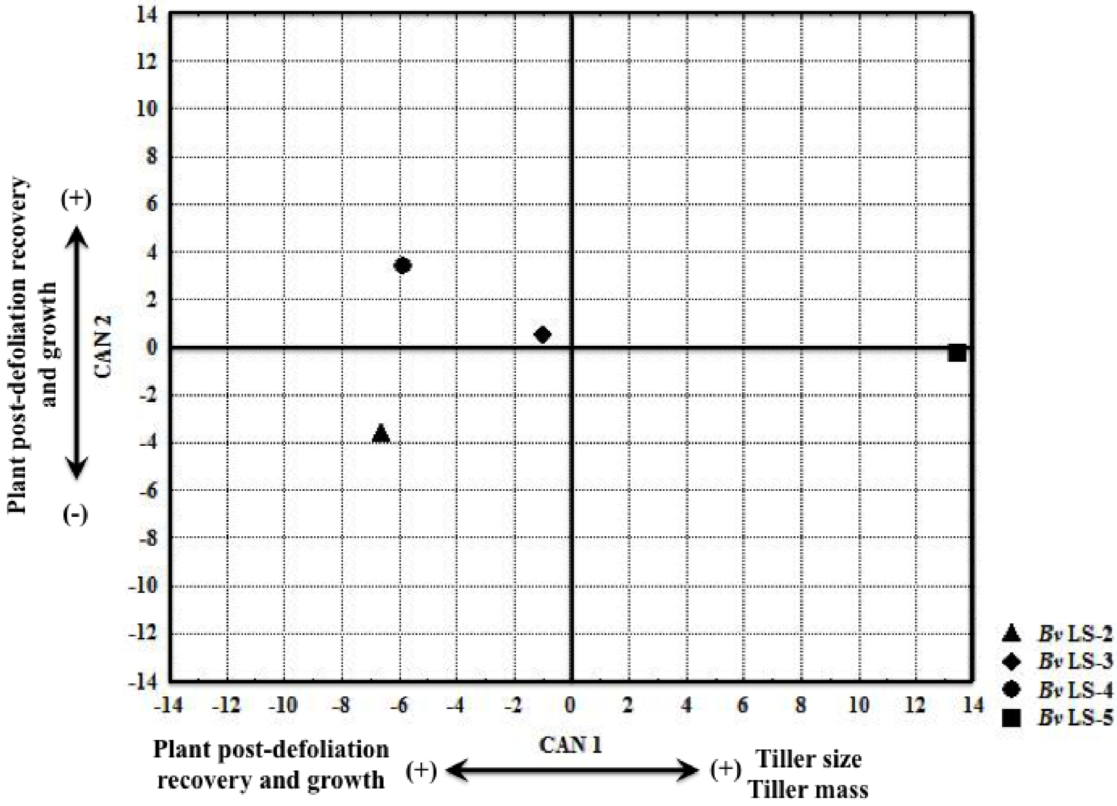

Figure 2: Pasture brome (*Bromus valdivianus* (*Bv*)) post-defoliation recovery and growth, and tiller size and mass following repeated defoliation at the 2, 3, 4 and 5 leaf stage (LS).

The results show that pasture brome is a six-leaved species, with the first (oldest) leaf beginning to senesce with the appearance of the seventh new leaf. Also, results found that three leaves were expanding at any given time. These attributes contrast with other species, for example perennial ryegrass maintains three live leaves with only one growing at a time (Fulkerson and Donaghy, 2001). In a previous study comparing pasture brome and perennial ryegrass, López *et al.* (2013) reported that pasture brome had 2.2 times more lamina mass and 3.6 times greater leaf area than perennial ryegrass, and pasture brome had 3.2 live leaves when perennial ryegrass had 2.8 live leaves. Less-frequent defoliation (LS-5) resulted in an almost six-fold increase in tiller mass, compared with more frequent defoliation (LS-2). Tiller mass and plant herbage mass of prairie grass (*Bromus willdenowii* Kunth.) showed similar results when defoliation frequency was extended from LS-2 towards LS-4 (Turner *et al.*, 2006). Based on these and similar results, it was recommended that defoliation interval for prairie grass coincide with LS-4 (Fulkerson *et al.*, 2000).

When prairie grass was less frequently defoliated (LS-4 versus LS-2), herbage mass per tiller increased by 43% (Slack *et al.*, 2000). Similar results were recorded for several cultivars of *Bromus* spp. and cocksfoot (*Dactylis glomerata* L.) (Turner *et al.*, 2007a). However, in the present study, increasing defoliation frequency within certain limits, generated an increase in the total accumulated herbage mass, with 17% greater herbage mass per plant when defoliation frequency increased from LS-5 to LS-4. Since tiller mass was greatest at LS-5 and declined with increasing defoliation frequency, this increase in accumulated herbage mass must have been due to compensatory processes. For example, there was an increase in both leaf area and mass, and although not significant, there were 25% more tillers per plant under LS-4 than LS-5.

It has previously been reported that tiller production is a sensitive variable that positively responds to increasing defoliation frequency. For example, prairie grass and cocksfoot increased their tiller number per plant with LS-2 and LS-3 defoliation frequency, but tiller number decreased when LS-1 and LS-4 defoliation frequency were applied (Turner *et al.*, 2007b). However, in relation to tiller number, this positive relationship has a 'tipping point' where from the results of Turner *et al.* (2007b) a defoliation frequency of LS-4 was 'too slow' but just as importantly, LS-1 was 'too fast'. In the present study, the increase of pasture brome tiller number per plant as a consequence of increasing defoliation frequency was not statistically significant, therefore the compensation of accumulated herbage mass produced was due to the leaf area and leaf mass production at tiller level through time (Figure 2; Table 2). It seems that there is a threshold to be reached by defoliation frequency to generate a significantly increase of tiller number. This assumption is based on the fact that increasing defoliation frequency (e.g. defoliated twice at LS-2 or once at LS-4) does not always result in an increase in tiller number per plant (Slack *et al.*, 2000); these results are in line with those of the present study.

The negative effect of defoliation frequency LS-2 on every variable measured in the present study indicates that this interval is too fast to allow recovery from the previous defoliation, most probably due to inadequate accumulation of carbohydrate reserves, as explained by Fulkerson and Donaghy (2001) for perennial ryegrass plants. This assumption is supported by the results of the CVA shown by CAN 2 (Figure 2) and would explain why plant recovery and growth post-defoliation diminished under the LS-2 treatment. Therefore it appears that LS-3 is the maximum defoliation frequency that pasture brome can tolerate without compromising herbage production and potentially persistence.

The other extreme of defoliation frequency in the present study was LS-5. Before pasture brome reached LS-5, leaf senescence was already occurring in the oldest leaf, thus the photosynthesis-respiration balance was losing efficiency, and the net growth rate would have been diminishing (Bircham and Hodgson, 1983; Rawnsley *et al.*, 2014).

The present study has highlighted the response of pasture brome to defoliation frequency based on its physiological state of development reflected by LS. The results indicated that there is a 'window of opportunity' for pasture brome defoliation between LS-3 and LS-4, to achieve optimal regrowth. Research performed on perennial ryegrass has shown that the ideal defoliation frequency is between LS-2 and LS-3 (Fulkerson and Donaghy, 2001).

Conclusion

Pasture brome is a six-leaf species, with three leaves totally expanded, three leaves concurrently expanding, and the oldest leaf senescing on appearance of the seventh leaf. The size of leaf and tiller components increase with longer defoliation frequency, however LS-5 is considered too long and LS-2 too short, in terms of their effects on all parameters measured. Leaf stage was a good physiological indicator to determine the appropriate defoliation frequency for pasture brome with results indicating that defoliation between LS-3 and LS-4 is optimal.

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References

Balocchi, O. and López, I. 2007. Improving naturalised pastures in the South of Chile. Pp. 13-21. *In*: Producción Ovina: Desde el Suelo a la Gestión. Ed Hervé, M. Ministerio de Agricultura, Gobierno de Chile, Chile.

Bircham, J.S. and Hodgson, J. 1983. The influence of sward condition on rates of herbage growth and senescence in mixed swards under continuous stocking management. *Grass and Forage Science* 38: 323-331.

Donaghy, D.J. and Fulkerson, W.J. 1998. Priority for allocation of water soluble carbohydrate reserves in *Lolium perenne* (L.). *Grass and Forage Science* 53: 211-218.

Duru, M. and Ducrocq, H. 2000. Growth and senescence of the successive leaves on a cocksfoot tiller. Effect of nitrogen and cutting regime. *Annals of Botany* 85: 645-653

Fulkerson, W.J. and Donaghy, D.J. 2001. Plant-soluble carbohydrate reserves and senesces – key criteria for developing an effective grazing management system for ryegrass based pastures: a review. *Australian Journal of Experimental Agriculture* 41: 261-275.

Fulkerson, W.J., Fennell, J.F.M. and Slack, K. 2000. Production and forage quality of prairie grass (*Bromus willdenowii*) in comparison to perennial ryegrass (*Lolium perenne*) and tall fescue (*Festuca arundinacea*) in subtropical dairy pastures. *Australian Journal of Experimental Agriculture* 40: 1059-1067.

Keim, J.P., López, I.F. and Balocchi, O.A. 2015. Sward herbage accumulation and nutritive value as affected by pasture renovation strategy. *Grass and Forage Science* 70: 283–295

López, I.F., Kemp, P.D., Dörner, J., Descalzi, C.A., Balocchi, O.A. and García, S. 2013. Competitive strategies and growth of neighbouring *Bromus valdivianus* Phil. and *Lolium perenne* L. plants under water restriction. *Journal of Agronomy and Crop Science* 199: 449-459

López, I., Balocchi, O., Lailhacar, P. and Oyarzún, C. 1997. Characterization of the growing sites of six native and naturalized species in the Dominio Húmedo of Chile. *Agro Sur* 25: 62-80.

Marsh, C. and Elliot, J. 2008. Exploring data - An introduction to data analysis for social scientists. Polity Press, Cambridge, UK. 328 pp.

Poff, J.A., Balocchi, O.A. and López, I.F. 2011. Sward and tiller growth dynamics of *Lolium perenne* L. as affected by defoliation frequency during autumn. *Crop and Pasture Science* 62: 346-354.

Rawnsley, R.P., Langworthy, A.D., Pembleton, K.G., Turner, L.R., Corkrey, R. and Donaghy, D.J. 2014. Quantifying the interactions between grazing interval, grazing intensity, and nitrogen on the yield and growth rate of dryland and irrigated perennial ryegrass. *Crop and Pasture Science* 65: 735-746.

Slack, K., Fulkerson, W.J. and Scott, J.M. 2000. Regrowth of prairie grass (*Bromus willdenowii* Kunth) and perennial ryegrass (*Lolium perenne* L.) in response to temperature and defoliation. *Australian Journal of Agricultural Research* 51: 555-561.

Turner, L.R., Donaghy, D.J., Lane, P.A. and Rawnsley, R.P. 2006. Effect of defoliation management, based on leaf stage, on perennial ryegrass (*Lolium perenne* L.), prairie grass (*Bromus willdenowii* Kunth.) and cocksfoot (*Dactylis glomerata* L.) under dryland conditions. 1. Regrowth, tillering and water-soluble carbohydrate concentration. *Grass and Forage Science* 61: 164-174

Turner, L.R., Donaghy, D.J., Lane, P.A. and Rawnsley, R.P. 2007a. A comparison of the establishment, productivity, and feed quality of four cocksfoot (*Dactylis glomerata* L.) and four brome (*Bromus* spp.) cultivars, under leaf stage based defoliation management. *Australian Journal of Agricultural Research* 58: 900-906.

Turner, L.R., Donaghy, D.J., Lane, P.A. and Rawnsley, R.P. 2007b. Distribution of water-soluble carbohydrate reserves in the stubble of prairie grass and orchardgrass plants. *Agronomy Journal* 99: 591-594.

Turner, L.R., Holloway-Phillips, M.M., Rawnsley, R.P., Donaghy, D.J. and Pembleton, K.G. 2012. The morphological and physiological responses of perennial ryegrass (*Lolium perenne* L.), cocksfoot (*Dactylis glomerata* L.) and tall fescue (*Festuca arundinacea* Schreb.; syn. *Schedonorus phoenix* Scop.) to variable water availability. *Grass and Forage Science* 67: 507-518.

Wilhelm, W.W. and McMaster, G.S. 1995. Importance of the phyllochron in studying development and growth in grasses. *Crop Science* 35: 1-3.

Zhang, H., McGill, C.R., Irving, L.J., Kemp, P.D. and Zhou, D. 2013. A modified thermal time model to predict germination rate of ryegrass and tall fescue at constant temperatures. *Crop Science* 53: 240-249.