Bromus-Poa response to defoliation intensity and frequency under three soil moisture levels

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Donkor, N. T., Bork, E. W. and Hudson, R. J. 2002. ***Bromus-Poa*** **response to defoliation intensity and frequency under three soil moisture levels.** Can. J. Plant Sci. **82**: 365–370. Smooth brome (*Bromus inermis* Leyss.) and Kentucky bluegrass (*Poa pratensis* L.) are important herbage for livestock and wildlife in Aspen-Boreal ecosystems in central Alberta, but there is paucity of information on the relationship between soil moisture and defoliation regimes on herbage production in these ecosystems. In a greenhouse experiment, we evaluated the effect of *Bromus-Poa* defoliation frequencies (2 or 4 wks) and intensities (2.5, 7.5, or 15 cm above the soil surface) under three soil moisture regimes [field capacity (wet), 50% field capacity (moist), 20% field capacity (dry)] on dry matter (DM) yield. Crude protein (CP) content, crude protein yield (CPY) and neutral detergent fiber (NDF) were also determined for herbage harvested. Total accumulated shoot DM decreased under defoliation compared to the undefoliated control, was higher if plants were clipped every 4 wks, rather than 2 wks, and increased with increasing soil moisture availability. Defoliation regimes decreased root DM Compared to the undefoliated control. Soil moisture regime did not significantly affect below-ground DM production, but root:shoot ratio increased significantly with decreasing moisture supply. The average CP content of grasses ranged from 12 to 23%, but was adequate to meet crude protein requirements of growing, pregnant or lactating grazing cattle (*Bos* spp.) The CPY decreased with increasing moisture stress, and was greatest when plants were clipped at a 7.5-cm height. Shoot NDF concentration increased with decreasing clipping frequency. These result indicate the need to investigate the relationship between soil moisture and management practices that affect the productivity of tame pastures in Aspen-Boreal ecosystems.

Key words: *Bromus inermis*, *Poa pratensis*, crude protein, neutral detergent fiber, water

Donkor, N. T., Bork, E. W. et Hudson, R. J. 2002. **Réaction de *Bromus-Poa* à l'intensité and à la fréquence de la défoliation dans trois régimes hydriques.** Can. J. Plant Sci. **82**: 365–370. Le brome inerme (*Bromus inermis* Leyss.) and le pâturin des prés (*Poa pratensis* L.) sont d'importantes sources d'herbages pour les animaux domestiques and sauvages dans les écosystèmes de type tremblaie-parc/forêt mixte boréale du centre de l'Alberta, mais on sait peu de choses sur les liens entre la teneur en eau du sol and les régimes de défoliation, d'une part, and la production d'herbages, d'autre part, dans les écosystèmes de ce genre. Dans le cadre d'une expérience effectuée en serre, les auteurs ont examiné quelle incidence la fréquence (2 ou 4 semaines) and l'intensité (2,5, 7,5 ou 15 cm au-dessus du sol) de la défoliation de *Bromus-Poa* avait sur le rendement en matière sèche (MS) dans trois régimes de teneur en eau (capacité maximale du sol (détrempé), 50 % de la capacité maximale (humide) and 20 % de la capacité maximale (sec)). Les auteurs ont aussi mesuré la concentration de protéines brutes (PB), le rendement en protéines brutes (RPB) and la concentration de fibres au détergent neutre (FDN) des herbages récoltés. La quantité totale de MS accumulée dans les pousses diminue avec la défoliation, comparativement aux plants témoins non défoliés, mais elle est plus grande chez les plants coupés à intervalles de 4 semaines que chez ceux tondus aux 2 semaines and elle augmente avec la quantité d'eau disponible dans le sol. La défoliation diminue la quantité de MS dans les racines, comparativement aux plants témoins. La teneur en eau du sol n'a pas d'incidence notable sur la production de MS dans les racines, mais le ratio entre les organes aériens and souterrains augmente significativement avec l'amenuisement des réserves hydriques. La concentration moyenne de PB dans les graminées varie de 12 % à 23 %, ce qui suffit aux besoins des bovins (*Bos* sp.) en croissance and des vaches gravides ou en lactation. Le RPB diminue quand le stress hydrique s'intensifie and atteint un maximum quand les plantes sont coupées à 7,5 cm de hauteur. La concentration de FDN dans les pousses augmente quand la défoliation est moins fréquente. Ces résultats laissent croire qu'il faudrait approfondir les liens entre la teneur en eau du sol and les pratiques d'élevage qui affectent la productivité des prairies artificielles dans les écosystèmes de type tremblaie-parc/forêt mixte boréale.

Mots clés: *Bromus inermis*, *Poa pratensis*, protéine brute, fibre au détergent neutre, stress hydrique

The Aspen Parkland and Low Boreal Mixedwood ecoregions of western Canada extend across central Alberta, and are important areas for agricultural land use, especially livestock and wildlife production (Strong 1992). Smooth brome (*Bromus inermis* Leyss.) and Kentucky bluegrass (*Poa pratensis* L.) are dominant cool-season grasses that are important herbage resources in these ecosystems (Looman 1976). Grazing or haying are common management practices that affect the productivity of these herbage species. The effect of defoliation regimes on the shoot DM production of these species may interact with soil moisture content, because soil moisture availability often limits growth in grasslands (Ogden and Loomis 1972). Williamson et al. (1989) stressed the need to investigate the interactive role of soil moisture content and defoliation for a better understanding of the relationship between grazing and herbage production.

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The timing, intensity, and frequency of defoliation interact in complex ways on production processes and herbage yield in rangeland ecosystems (Oesterheld and McNaughton 1988). In some plant species defoliation has reduced herbage DM production (Buwai and Trlica 1977), decreased root DM (Zhang and Romo 1994) and altered root:shoot ratios (Willms 1991). However, some species may also adapt to grazing or clipping by increasing aboveground plant growth (Barker and Kidar 1989). Such a stimulation is often referred to as overcompensation (Belsky 1986), which means that the production of defoliated plants exceeds the production of undefoliated plants. This phenomenon has led to herbivore optimization models, which predict that the level of overcompensation is dependent on the intensity of defoliation (Hik and Jefferies 1990).

The interactions of defoliation intensity and frequency with watering have received limited attention (Wallace et al. 1984). Most research in western Canada has focussed on the benefits of fertilizer and grazing regimes on pasture productivity (eg., Pearen and Baron 1996). Little information exists, however, on the interactive role of soil moisture and defoliation treatments on herbage production in western Canada. Research evaluating these effects is warranted because most prairie grasses grow in environments where water stress may influence herbage productivity and animal production (Bork et al. 2001). Better information on the relationship between soil moisture and defoliation regimes on herbage production would provide greater insight into the ecological response of these plant communities to climatic factors and harvest management. Ultimately, this information could improve the ability of rangeland managers to develop drought management during rangeland planning within the region, and would provide a database for modeling pasture growth and productivity. The objective of this study was to evaluate the effect of *Bromus-Poa* defoliation intensity and frequency under three soil water regimes on herbage production.

MATERIALS AND METHODS

Experimental Procedure

A hand-driven Uhland soil core sampler was used to collect 96 samples of Aspen Boreal grassland sods (14 cm diameter, 15 cm deep) from a Luvisolic loam soil at Ministik Wildlife Research Station near Edmonton, Alberta (53°18′N, 114°35′W), in June 1999. On average, the soil contained 25% clay, 33% silt and 42% sand. Organic matter content was 2.1%. Soil pH, determined using distilled water, was 5.5. Smooth brome (*Bromus inermis* Leyss.) and Kentucky bluegrass (*Poa pratensis* L.) dominated the vegetation. From field baseline studies, these two species comprised 42 and 22% of the cover, respectively. Each sod contained variable amounts of each of the two species. Forbs were removed because not all sods contained them.

Each sod core were placed carefully into a 15 cm-diameter PVC cylinder pot (15 cm deep) with as little disturbance as possible. To prevent channeling of water along the outer edge of the soil core after watering, the small space between the outer edge of the soil core and the walls of the pot was carefully filled with soil collected from the edges of the holes left by digging the sods. Caps with three holes were fitted at the bottom of the pots to allow free drainage. Samples were transported to a greenhouse on the University of Alberta campus in Edmonton. Moisture level treatments were applied by means of a gravimetric method described by Read and Bartlett (1972). The moisture content of the soil at field capacity was determined on 10 replicate samples. These pots were brought to field capacity by standing their bases in water until the waterfront reached the top of the pot. They were removed and left to stand on an elevated wire grid until freely draining water had passed through the basal draining holes. At this water content, the pots were weighed. Using this figure and the value of moisture content at field capacity, the weight at which any pot was to be maintained to provide a required water regime was determined. During the 3 wk acclimation period in the greenhouse prior to defoliation treatments, the sods were top-watered every 2–3 d with sufficient distilled water to bring the soil in the entire pot to field capacity after drainage. The greenhouse was maintained at an air temperature of 23°C, with an 18 h photoperiod.

Studies of plant response to defoliation in soils of different moisture regimes were subsequently conducted on the sods. A completely random design with four replicates of a factorial arrangement of treatments (moisture level, defoliation intensity and defoliation frequency) was used. Three moisture levels were imposed by adding water to the soil every 3 d after weighing: field capacity (wet), 50% field capacity (moist), 20% field capacity (dry).

Within a watering regime (soil moisture level), sods were randomly assigned to one of four defoliation intensities (height) by two defoliation frequencies, with four replications of each treatment combination. The four defoliation intensities were achieved by clipping sods at heights of 2.5, 7.5, or 15 cm above the soil or leaving them undefoliated (control) (ie., 90, 60, 30% or 0 shoot removal, respectively). Defoliation intensities were calibrated by clipping a sample of sods at estimated levels and comparing their weights with weights of plants clipped to the soil surface. After sods were initially defoliated on 1 July, they were defoliated again at frequencies of 2- or 4-wk for the 92 d duration of the experiment. Total accumulated shoot DM was calculated from the sum of dry weight of plant material collected at each clipping, plus material harvested to the soil surface at the termination to the experiment. Herbage samples were sorted into live and dead plant tissue, dried in a forced-air oven at 60°C for 72 h, cooled in a desiccator, and weighed. Dried samples were ground (live and dead together) in a Wiley mill to pass a 1-mm screen and stored in sealed containers for laboratory analysis.

Total root DM in the sods was measured at the end of the experiment. Below-ground material was separated from the soil by soaking each core in water for 12 h. These samples were hand washed over a set of three sieves of sizes – 6.3, 2.0 and 1.18 mm, and separated into roots and crowns. Samples were oven dried at 60°C for 72 h and weighed. The root:shoot ratios were calculated for each sod as the total below-ground DM over the total accumulated shoot DM (live and dead material).

Table 1. *F* values and their significance from the statistical analysis (ANOVA) for total accumulated shoot DM, end-of-trial below-ground DM and root:shoot ratios of *Bromus-Poa* sods

Source of variation	df	Shoot DM	Below-ground DM	Root:shoot ratio
Soil moisture (M)	2	4.96*	2.25	3.38*
Defoliation frequency (F)	1	4.55*	4.52*	1.23
Defoliation Intensity (I)	2	6.54**	1.35*	1.74
M × F	2	1.25	1.5	0.98
M × I	4	0.18	0.07	0.89
F × I	2	0.56	0.13	1.01
M × F × I	4	0.80	0.09	0.41

*, ** significant at $P \le 0.05$ and $P \le 0.01$, respectively.

Table 2. Accumulated shoot DM, end-of-trial below-ground DM and root:shoot ratios of *Bromus-Poa* sods as affected by defoliation intensity and defoliation frequency

	Defoliation intensity (cm)			Control	Defoliation frequency (weeks)	
Variable	2.5	7.5	15	Undefoliated	4	2
Shoot DM (g)						
Live	9.49*c*	13.36*b*	11.61*b*	15.39*aZ*	12.92*Y*	7.85*X*
Dead	5.01*c*	6.06*b*	6.12*b*	9.81*aY*	9.03*Y*	4.22*X*
Total	14.50*c*	19.40*b*	17.73*b*	25.2*aZ*	21.92*Y*	12.10*X*
Below-ground DM (g)						
Roots	7.58*c*[1]	9.90*b*	7.80*bc*	11.08*aZ*	9.23*Y*	6.01*X*
Crowns	5.72*b*	7.10*b*	6.40*b*	8.22*aY*	8.02*Y*	5.58*X*
Total	13.30*c*	17.0*b*	14.20*c*	19.30*aZ*	17.25*Y*	11.59*X*
Root:shoot ratio	0.92*a*	0.88*a*	0.80*a*	0.77*aX*	0.79*X*	0.96*X*

a–c, *x–z* Means for either defoliation intensity (*a*, *b* or *c*) or defoliation frequency (*X*, *Y*, *Z*) followed by the same letter are not significantly different ($P \le 0.05$). The same control was used for both sets of data.

Nitrogen content in aboveground accumulated DM was determined using a LECO FP-428 Nitrogen Determinator (Sweeney and Rexroad 1987). Nitrogen values were multiplied by 6.25 to obtain CP content. Neutral detergent fiber in shoots was determined using the ANKOM filter bag technique (Komarek 1993). Crude protein yield was calculated by multiplying the CP by the above-ground accumulated DM. Means of duplicated samples were used in the statistical analysis.

Statistical Analysis

The DM production and nutritive value data were analyzed by analysis of variance (ANOVA) using the PROC GLM of SAS (SAS Institute, Inc. 1989). Significance of main effects and interaction was determined with probability levels of 5 and 1%.

RESULT AND DISCUSSION

Herbage Yield Response

Soil moisture regime, defoliation frequency and defoliation intensity significantly affected shoot DM (Table 1). Shoot DM generally decreased with increasing defoliation intensity as compared to the non-defoliated control (Table 2). This was evident for both live and dead accumulated DM. This is in keeping with the work of Dovel (1996), who also found forage yields and regrowth following clipping of *Poa* spp. and *Trifolium* spp., *Poa* spp., *Deschampsia caespitosa*, and *Carex* spp., and *Carex* spp. associations decreased as clipping intensity increased. Defoliation may influence the dynamic interaction between plant growth rates and DM, as well as change the proportions of green herbage, standing dead, and fallen litter pools. Live shoot DM was greater when plants were clipped less frequently (e.g., every 4 wk rather than every 2 wk). As observed in previous studies (Buwai and Trlica 1977), repeated defoliation during growth reduced the accumulation of shoot DM. In Saskatchewan, when northern wheatgrass [(*Agropyron dasystachyum* (Hook) Scribn.)] was defoliated at 6-wk intervals, DM production was generally greater than when herbage was removed biweekly (Zhang and Romo 1994). Thus, longer recovery time is needed to maximize herbage yields.

Live shoot DM decreased with decreasing soil moisture availability (Table 3). This observation of reduced above-ground production with increasing water stress highlights the drought susceptibility of *Bromus-Poa* swards in central Alberta. There was little difference in above-ground standing dead DM between the dry and moist treatments. Therefore, most of the differences in total above-ground DM between the dry and moist treatments in response to moisture regimes are due to a greater live DM under moist conditions.

Defoliation frequency and intensity had a significant effect on below-ground DM, whereas soil moisture regime did not (Table 1). Similarly, Jacobs and Sheley (1997) found that watering regime had no effect on *Festuca idahoensis* root weight. Increasing defoliation reduced root and crown DM as compared to the control (Table 2). This is reflective of the botanical composition of the sods; Kentucky bluegrass (comprised one-fifth of cover) is tolerant of frequent defoliation, but smooth brome (comprised two-fifth of cover) is not. At the end of the trial, proportion of Kentucky

Table 3. Accumulated shoot DM, end-of-trial below-ground DM and root:shoot ratios of *Bromus-Poa* sods as affected by soil water regime

	Soil moisture regime (g kg^{-1})[z]		
Variable	Wet	Moist	Dry
Shoot DM (g)			
Live	13.05*c*	11.31*b*	6.28*c*
Dead	9.25*a*	7.25*b*	7.48*b*
Total	22.30*c*	18.56*b*	13.76*c*
Below-ground DM (g)			
Roots	9.55*a*	9.70*a*	9.50*a*
Crowns	8.10*a*	7.80*a*	7.50*a*
Total	17.66*a*	17.5*a*	17.0*a*
Root:shoot ratio	0.79*b*	0.94*b*	1.24*a*

[z]Wet, moist and dry represent field capacity, 50 and 20% field capacity, respectively.
a–c Means in a row followed by the same letter are not significantly different ($P \le 0.05$).

bluegrass in the sods had increased slightly from 22 to 30%, whereas smooth brome had changed little, remaining at about 40%. Wedin and Huff (1996) reported that due to its growth habit, Kentucky bluegrass resists grazing injury and often becomes dominant in pasture stands where it is associated with tall grasses. Previous studies on prairie grasses are in general agreement that clipping of the shoots inhibited root production: e.g., Zhang and Romo (1994), Li and Redmann (1992) (*Agropyron dasystachyum*); Smoliak et al. 1972 (*Stipa-Bouteloua*); Harrison (1931) (*Poa pratensis*), and may be a mechanism by which species preferentially allocate carbon resources to above-ground growth (Richards 1984).

Plant response to clipping or grazing has often resulted in increased root:shoot ratios (Oesterheld and McNaughton 1988). However, in our study, the root:shoot ratio did not significantly increase with clipping intensity and frequency (Table 2). The root:shoot ratio of the dry treatment was significantly greater than those of plants maintained at field capacity (wet) and 50% field capacity (moist) (Table 3). This has been observed in many pastures: eg., Brar and Palazzo (1995) (*Festuca* spp.) and *Festuca ovina*) where the root:shoot ratio of vegetation increased under drought. To obtain maximum DM production, a relatively small root system might be an advantage if it could supply adequate water and nutrients. However, a large root system increases the survivability of plants because it allows the large root system to obtain water for a smaller shoot.

No interactions were observed between defoliation intensity, frequency and soil moisture regimes for herbage production. However, the lack of statistical interaction in this study between clipping management and soil moisture content does not address the hypothesis that the two factors may interact in an ecophysiological sense. Bork et al. (2001) reported that Boreal grassland production is heavily dependent on summer precipitation and remains prone to variations in herbage production with summer drought.

The levels of water supply used in these sod experiments would commonly occur in the field at some times during the growing season. However, it would be rare for each level to remain constant in the field for prolonged period. It remains

Table 4. *F* values and their significance from the statistical analysis (ANOVA) for CP content, NDF, and CPY of accumulated shoot of *Bromus-Poa* sods

Source of variation	CP	NDF	CPY
Soil moisture (M)	0.76	0.40	4.67**
Defoliation frequency (F)	4.00*	6.28**	3.33*
Defoliation Intensity (I)	3.11*	0.48	6.55**
M × F	0.40	0.69	0.99
M × I	0.42	0.69	0.20
F × I	0.94	0.06	0.71
M × F × I	1.96	0.70	0.17

*, ** significant at $P \le 0.05$ and $P \le 0.01$, respectively.

to be seen whether or not plant community responses to defoliation and soil moisture condition will interact under field conditions in tame pastures.

Nutritive Value Response

The CP content of the accumulated shoot DM ranged from 120 to 230 g kg^{-1} DM. The average CP content observed in plants in this study was greater than the 90 g kg^{-1} DM observed by Kilcher and Troelsen (1973) for irrigated smooth brome, indicating an earlier maturing or earlier termination of the growth cycle in the latter. The CP content of *Bromus-Poa* plants falls well within the National Research Council (1984, 1989) range of values considered adequate to meet protein requirement of all classes of grazing cattle: cows nursing calves and dry pregnant mature cows require a total protein level in rations of 92 g kg^{-1} DM and 59g kg^{-1} DM, respectively. In addition, grazing animals are selective, and generally consume herbage of higher nutritive value than animals fed clipped herbage.

Defoliation frequency and intensity had significant effects on shoot CP content (Table 4), which increased in the plants clipped more frequently (Table 5). More frequent defoliation increased CP due to constant defoliation of regrowth on these plants. Defoliation intensity had a nonlinear effect on CP, with a maximum CP at 7.5 cm defoliation (Table 5). Similar results were obtained from studies in Kentucky bluegrass/white clover pastures (Dovel 1996) and may be due to reduced levels of crude fibre and lignin in the regrowth of plants with lower defoliation intensity.

Soil water regime and defoliation frequency and intensity significantly affected CPY of the plants (Table 4). Crude protein yield of plants clipped at the 15-cm height was not significantly different from that of controls, while CPY of plants clipped at the 7.5-cm height was significantly greater than all other treatments (Table 5). Since shoot DM generally decreased with increasing defoliation intensity, the increased CPY of plants clipped at 7.5-cm is due to a greater CP content at that defoliation intensity compared to all other treatments. Therefore, optimum defoliation intensity for this vegetation is 7.5 cm above ground level. Crude protein yield of herbage was also greater when plants were clipped every 4 wk rather than every 2 wk (Table 5). Through soil moisture regime did not significantly affect percentage crude protein (Table 4), CPY decrease with decreasing moisture supply (Table 6).

Table 5. Crude protein content, NDF and CPY in total accumulated shoot DM of *Bromus-Poa* sods as affected by defoliation intensity and defoliation frequency

	Defoliation intensity (cm)			Control	Defoliation frequency (weeks)	
Variable	2.5	7.5	15	Undefoliated	4	2
CP (g kg^{-1} DM)	152.5*b*	179.1*a*	132.7*c*	100.0*dZ*	131.9*Y*	164.9*X*
NDF (g kg^{-1} DM)	589.5*a*	594.9*a*	596.1*a*	600.0*aZ*	550.0*Y*	550.0*X*
CPY (g)	2.21*c*	3.47*a*	2.35*c*	2.52*bZ*	2.89*Y*	1.99*X*

a–d, x–z Means for either defoliation intensity (*a, b* or *c*) or defoliation frequency (*X, Y, Z*) followed by the same letter are not significantly different ($P \le 0.05$). The same control was used for both sets of data.

Table 6. Crude protein content, NDF and CPY of *Bromus-Poa* sods as affected by soil water regime

	Soil moisture regime (g kg^{-1})[z]		
Variable	Wet	Moist	Dry
CP (g kg^{-1} DM)	173*a*	170*a*	168*a*
NDF (g kg^{-1} DM)	560*a*	562*a*	165*a*
CPY (g)	3.35*a*	2.60*b*	1.92*c*

[z]Wet, moist and dry represent field capacity, 50 and 20% field capacity, respectively.
a–c Means in a row followed by the same letter are not significantly different ($P \le 0.05$).

The NDF content of harvested shoots ranged from 500 to 600 g kg^{-1} DM (Table 5). Increasing the clipping frequency from 4 to 2 wk decreased NDF contents (Table 5). The NDF contents in herbage are consistent with previous results obtained for average whole-herbage NDF of smooth brome and Kentucky bluegrass: 537 and 557 g kg^{-1} DM, respectively (Hockensmith et al. 1997).

CONCLUSIONS

Defoliation intensity and frequency affected both above-ground and below-ground DM yield and herbage nutritive value. Long rest (4 wk frequency) and moderate defoliation intensity (7.5 cm height) result in maximum DM production and CPY in this vegetation. Both defoliation intensity and frequency affected CP and CPY, while only defoliation frequency affected NDF via maturity.

The *Bromus-Poa* sod is drought-susceptible with impacts observed mostly above-ground, not below-ground. Soil moisture regime affected above-ground DM and root:shoot ratios but not below-ground DM. Shoot DM increased with increasing soil moisture, whereas root:shoot ratio increased under drought. Soil moisture regime affected CPY, which decreased with increasing moisture stress.

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