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Research Article

Responses of Three Bromegrass (*Bromus*) Species to Defoliation under Different Growth Conditions

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Bromegrass species are important forage crops in temperate regions of world. This study compared responses of three bromegrass species to defoliation in the greenhouse and field to determine if the former could predict responses in the latter. Experiments were conducted in 2006 and 2007 in Saskatoon (52°07′ N, 106°38′ W), Canada on meadow bromegrass (*Bromus riparius* Rehm.), smooth bromegrass (*Bromus inermis* Leyss.), and hybrid bromegrass (*B. riparius* X B. *inermis*) following defoliation to 5 cm stubble height. When defoliated at the vegetative stage, above-ground biomass was similar among the three species in the field, but meadow bromegrass produced greater above-ground biomass than smooth bromegrass in the greenhouse. When defoliated at the stem elongation stage, meadow bromegrass produced greater above-ground biomass than smooth bromegrass in both environments. In the field, for all defoliation treatments, tiller number was greatest in meadow bromegrass, intermediate in hybrid bromegrass, and least in smooth bromegrass. In the greenhouse, however, the three species did not differ in tiller number. Similar results were found for below-ground biomass. Thus, testing the effect of defoliation in the greenhouse environment did not accurately predict the effect in the field environment.

1. Introduction

Smooth bromegrass and meadow bromegrass are perennial, cool-season grasses widely cultivated for pasture and hay in temperate regions of world. Meadow bromegrass is well adapted to grazing due to its rapid regrowth after defoliation [1], while smooth bromegrass is intolerant to frequent defoliation and generally used for hay [2]. The hybrid bromegrass cultivar "Knowles" was recently developed by hybridizing smooth and meadow bromegrass and has potential for both hay and pasture use [3]. A number of studies have been conducted in the field to understand morphological and physiological characteristics of the three bromegrass species in response to defoliation [1, 4–7]; however, little information is available on how these three species respond to defoliation under different growth environments.

In cool-season grasses, the optimum temperature for growth varies among species [8]. Leaf appearance and elongation rate are often reduced by low temperature and moisture level [9, 10]. High temperature inhibits tillering because of high respiration rates and lower soluble carbohydrate concentrations in the plant [8]. The ability of grasses to produce tillers is sensitive to changes in light intensity and quality. Tiller density increases with increasing light intensity [11] and high red: far-red ratio [12]. Resource competition also affects grass growth, and tiller development is stimulated by high nutrient concentration [13]. In addition to environmental factors, time of utilization for forage also causes differences in grass regrowth due to difference in available meristems among growth stages [14]. Generally, regrowth occurs faster from elongation of existing vegetative tillers than growth of axillary buds [14, 15]. The early spring grazing of bromegrasses occurs at the vegetative growth stage, while hay harvesting occurs after stem elongation [1]. The objective of this study was to compare the growth of three bromegrass species in field and greenhouse environments following defoliation at the vegetative or stem elongation stage to determine whether field response could be predicted by studies in controlled environments.

Table 1: Date of defoliation and the corresponding cumulative growing-degree-days (GDDs) between defoliation and measurement of above-ground biomass and tiller density for three bromegrasses during the summers of 2006 and 2007 in field studies at Saskatoon, Canada.

	Date of defoliation		Date of measurement		GDD	
	2006	2007	2006	2007	2006	2007
Vegetative stage						
All three bromegrasses	10 May	9 May	1 Aug	13 Jul	1465	964
Stem elongation stage						
Meadow bromegrass	19 May	25 May	28 Jul	24 Jul	1271	1049
Smooth bromegrass	22 May	31 May	1 Aug	27 Jul	1304	1045
Hybrid bromegrass	22 May	26 May	1 Aug	24 Jul	1304	1041

2. Materials and Methods

2.1. Field Study. Field plots were located at the Agriculture and Agri-Food Canada Research Farm (52°07′ N, 106°38′ W) in Saskatoon, Canada. The soil was a Dark Brown Chernozem [16]. Field studies were conducted from May to July of 2006 and 2007 in two trials consisting of meadow, smooth, and hybrid bromegrasses, which were established in 2004 and 2006, respectively. Each trial was established in a four replicate, randomized complete block design with each plot consisting of four, 6-m long rows, spaced 30 cm apart and seeded at a rate of 100 seeds m^{-1}. No fertilizer was applied during the growing season in the field. Plants were clipped to 5 cm stubble height at the vegetative (V1) or stem elongation stage (E1) [17]. An undefoliated control was also included in all plots. Rainfall during the experiments was 225 mm in 2006 and 147.5 mm in 2007. The 30-year long-term average rainfall from April–July at this site is 174 mm. Cumulative growing degree days (GDDs) during the study were calculated using equation GDD = $\sum$ (daily maximum temperature + daily minimum temperature)/2 [18] (Table 1). The base temperature of 5°C was used in the equation.

2.2. Field Data Collection. The number of tillers was recorded in two 15×20 cm fixed quadrats which were randomly placed over rows in each plot before defoliation. In each year, tiller numbers were counted and regrowth harvested in these fixed quadrats after a similar number of GDD had accumulated following each defoliation (Table 1). Harvested above-ground biomass was dried at 60°C for 48 h and weighed. The areas harvested for above-ground biomass were trimmed to ground level before soil cores were taken to estimate below-ground biomass. Soil cores were 8 cm in diameter and 20 cm deep. Soil cores were washed with water under high pressure. Washed samples were dried in the oven at 80°C for 48 h and weighed.

2.3. Greenhouse Study. Sods of the three bromegrass species were transferred to the greenhouse from the field in early November of 2006 and 2007. Sods were planted in 20 cm pots. The experiment was a randomized-complete-block-design with four replicates. The space between individual pots was approximately 20 cm. Plants were defoliated to 5 cm stubble height at the vegetative (V1) or stem elongation stage (E1) [17]. An undefoliated control was also included in the experiment. Light was provided by Philips SON AGRO Lamps (Philips Lighting Co.) with a day length of 16 h at 21°C and a night period of 8 h at 16°C. Light intensity was 440 ± 150 Φmol s^{-1} m^{-2}. Sods were watered periodically when the soil surface became dry. No fertilizer was applied during the greenhouse study.

2.4. Greenhouse Data Collection. The number of initial tillers was counted in each pot before the experiment began. Final tiller number and regrowth biomass were determined in each pot after a similar number of GDD (1260) had accumulated following each defoliation. Harvested above-ground biomass was dried at 60°C for 48 h and weighed. Below-ground biomass was also determined for all samples at the end of experiment using the same procedure as for the field study.

2.5. Statistical Analysis. Above- and below-ground biomass and tiller densities were compared within each defoliation treatment by performing Proc Mixed as a one-way analysis of variance (ANOVA) using SAS 9.1.3 Proc Mixed Model [19]. Species was considered as a fixed effect, while year and block were considered random effects in the model. When ANOVA indicated significant differences ($P \leq .05$), means were separated using the least square means comparison. Initial tiller density had an interaction effect with final tiller density in the greenhouse study, but not in the field study. Analysis of Covariance was conducted to eliminate the effects of initial tiller differences among species in the greenhouse study.

3. Results and Discussion

3.1. Above-Ground Biomass. The three bromegrass species produced relatively greater regrowth biomass in the greenhouse than in field (Table 2). However, the ranking of species in above-ground biomass was not the same in field and greenhouse experiments. In undefoliated growth, hybrid bromegrass produced greater above-ground biomass than meadow and smooth bromegrass in the field study, but meadow bromegrass produced greater above-ground biomass than hybrid bromegrass in the greenhouse (Table 2). Above-ground biomass was not different between meadow and smooth bromegrass in both environments. When defoliated at the vegetative stage, there was again no consistency in

Table 2: Above-ground biomass (g m^{-2}) of three bromegrass species after 60 days of growth in undefoliated control or following defoliation to 5 cm in field or greenhouse studies conducted in 2006 and 2007 at Saskatoon, Canada.

Species	Undefoliated control		Defoliated at vegetative stage		Defoliated at stem elongation stage	
	Field	Greenhouse	Field	Greenhouse	Field	Greenhouse
Meadow bromegrass	1039 b†	1239 a	557 a	937 a	324 a	663 a
Smooth bromegrass	1072 b	1127 ab	493 a	775 b	217 b	561 b
Hybrid bromegrass	1224 a	954 b	512 a	822 ab	295 a	551 b
P	.03	.05	.48	.04	.01	.04
SEM‡	203	79	85	85	74	86

† Means within a column with the same letter (a-b) are not significantly different ($P > .05$).
‡Standard error of the mean.

above-ground biomass rankings of species in field and greenhouse experiments. Regrowth was not different among the three species in the field, but meadow bromegrass produced greater regrowth than smooth bromegrass in the greenhouse (Table 2). When defoliated at the stem elongation stage, however, meadow bromegrass consistently produced greater regrowth biomass than smooth bromegrass in both field and greenhouse, and more regrowth biomass than hybrid bromegrass in the greenhouse (Table 2). Meadow bromegrass is more suitable in moist, cool environment than smooth bromegrass [1]. The greenhouse plants were provided with more consistent soil moisture than those in the field, and regrowth of meadow bromegrass may have been favored by this moisture regime, relative to the other bromegrass species. In addition, meadow bromegrass has a greater number of unelongated tillers than smooth bromegrass when defoliated after stem elongation [1]. Differences in the number of unelongated tillers after the stem elongation stage may be related to the greater regrowth of meadow bromegrass under both environments, because elongated tillers die after defoliation, and regrowth comes from unelongated tillers or axillary buds [20].

3.2. Below-Ground Biomass. In the field study, meadow bromegrass consistently produced greater below-ground biomass than smooth bromegrass in all treatments (Table 3). Below-ground biomass of meadow bromegrass was similar to hybrid bromegrass in the undefoliated and vegetative stage defoliation treatments but was greater than hybrid bromegrass after defoliation at the stem elongation stage. Below-ground biomass of hybrid bromegrass was greater than smooth bromegrass following defoliation at stem elongation but was similar in the other two treatments. In another field study [21], meadow bromegrass produced greater root dry matter than smooth bromegrass under low intensity grazing. In contrast to the field environment, below-ground biomass in the greenhouse was not different among the three species for any treatment (Table 3). In grass species, each tiller produces its own roots, and similar tiller density of these three species in the greenhouse (Table 4) may have resulted in similar below-ground biomass. Smooth bromegrass produces rapidly spreading rhizomes whereas meadow bromegrass and hybrid bromegrass have a more caespitose growth form with short rhizomes [1]. Rhizome spread of smooth bromegrass was limited by pot walls in the greenhouse, but there were no such restrictions in the field. This may result in more below-ground biomass for smooth bromegrass in a given area in the greenhouse and thus was similar to the other two species. In general, the restriction of pot walls in greenhouse may also have increased below-ground biomass of all three species compared to the field (Table 3).

3.3. Tiller Density. For all three species, there was a general trend of greater number of tillers in the greenhouse than in field (Table 4). For the field study, tiller density was the greatest for meadow bromegrass, intermediate for hybrid bromegrass, and least for smooth bromegrass in all treatments (Table 4). However, the final tiller density in the greenhouse was not significantly different among the three species within any treatment. Tiller development in grasses is strongly influenced by environmental conditions. In cool-season grasses, the optimum temperature for tillering is relatively low and varies among species [8]. The temperature was set to 21/16°C (day/night) in the greenhouse, while the temperature in the field fluctuated from −3.3 to 36.5°C during the studies. Light intensity and quality have a major influence on tillering [8, 11, 12], and self-shading within a dense canopy at the tiller base is associated with a decrease in tillering [22]. Light intensity in the greenhouse was $440 \pm 150\ \Phi\text{mol}\,s^{-1}\,m^{-2}$, which was lower than the light intensity of $1500\ \Phi\text{mol}\,s^{-1}\,m^{-2}$ or higher on a sunny day in a field environment in Saskatoon, Canada [Biligetu, unpublished data]. Relatively higher initial tiller numbers for meadow bromegrass are likely to cause shading under the low light conditions in the greenhouse, which may have restricted tillering of this species. In addition, grass tillering is associated with nutrient availability [13], and lateral buds can only elongate into tillers while the nutrient supply exceeds the requirement of existing tillers [23]. There may have been lower nutrient availability in the greenhouse due to the limitation of root proliferation in the pots [24].

4. Conclusions

The response of three bromegrass species to defoliation differed under field and greenhouse environments. Even though a greenhouse environment provides an opportunity

Table 3: Below-ground biomass (g m^{-3}) of three bromegrass species after 60 days growth in an undefoliated control or following defoliation to 5 cm in field and greenhouse studies conducted in 2006 and 2007 at Saskatoon, Canada.

Species	Undefoliated control		Defoliated at vegetative stage		Defoliated at stem elongation stage	
	Field	Greenhouse	Field	Greenhouse	Field	Greenhouse
Meadow bromegrass	7980 a†	18480 a	4560 a	14149 a	5650 a	10554 a
Smooth bromegrass	5610 b	16799 a	2740 b	10949 a	2870 c	8356 a
Hybrid bromegrass	6430 ab	17882 a	3660 ab	12280 a	4050 b	7840 a
P	.03	.93	.01	.51	< .01	.52
SEM‡	600	3748	720	2500	510	1589

† Means within a column with the same letter (a-b) are not significantly different ($P > .05$).
‡ Standard error of the mean.

Table 4: Final tiller density (tillers m^{-2}) of three bromegrass species after 60 days of growth in the field for undefoliated control or following defoliation to 5 cm at two stages of growth in 2006 and 2007 at Saskatoon, Canada.

Species	Undefoliated control		Defoliated at vegetative stage		Defoliated at stem elongation stage	
	Field	Greenhouse	Field	Greenhouse	Field	Greenhouse
Meadow bromegrass	2000 a†	6500 a	2107 a	6067 a	1320 a	3833 a
Smooth bromegrass	1200 c	5367 a	1093 c	5500 a	520 c	3500 a
Hybrid bromegrass	1520 b	5800 a	1547 b	5533 a	840 b	3467 a
P	< .01	.12	< .01	.40	< .01	.54
SEM‡	222	312	74	287	57	950

† Means within a column with the same letter (a-b) are not significantly different ($P > .05$).
‡ Standard error of the mean.
§ Final tiller number in the greenhouse was adjusted by analysis of covariance.

to study responses of bromegrasses to defoliation under controlled environmental conditions, it was not predictive of responses to defoliation in the field. This may be due to low light intensities in the greenhouse and restrictions in lateral growth imposed by the walls of the greenhouse pots. The latter would likely have a greater effect on grass species that produce long rhizomes.

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