Defoliation impacts on *Festuca campestris* (Rydb.) plants exposed to wildfire

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Abstract

Wildfires commonly occur in the Fescue Prairie of Alberta, but little information exists to provide a basis for making grazing recommendations after burning. A wildfire in April 1999 provided an opportunity to study the effect of season and intensity of post-burn defoliation on foothills rough fescue (*F. campestris* Rydb.) in southwestern Alberta. A 3 (date of defoliation) x 2 (defoliation intensity) factorial experiment with 10 replicates (plants) was established in both a burned and a non-burned grassland and analyzed as a nested design. Plants were defoliated once during active vegetative growth (17 May), inflorescence development (2 July), or dormancy (30 September), at either 5 or 15-cm clipped stubble heights in the first growing season after fire. Burning increased tiller numbers by 54% compared to non-burned plants but reduced plant ANPP by 51% in the second growing season. While a single defoliation of burned plants, particularly early in the year, had little effect on growth, delaying defoliation into July decreased tillers 1 year later. Increasing defoliation intensity had the greatest impact on non-burned plants, reducing plant height (15%) as well as tiller (21%) and plant (32%) ANPP in the second year. May defoliation reduced etiolated growth 1 year later regardless of burn treatment. A single grazing event after wildfire does not necessarily appear to detrimentally affect rough fescue; however, the low herbage available immediately after fire may not justify the increased risk to the plant with subsequent grazing.

Key Words: defoliation intensity, deferment, etiolated growth, herbage yield, resilience, tillers

The Fescue Prairie of the Northern Great Plains is characterized by the occurrence of plains rough fescue [*Festuca hallii* (Vasey) Piper] and foothills rough fescue (*F. campestris* Rydb) in the prairie-parkland and foothill regions, respectively. Plains rough fescue is shorter than foothills rough fescue and produces short rhizomes compared with the strongly tufted habit of the latter (Pavlick and Looman 1984). Most fire ecology studies in the Fescue Prairie have been conducted in the Parkland (Bailey and Anderson 1978, Anderson and Bailey 1980, Redmann et al. 1993, Gerling et al. 1995). Although the foothills species of rough fes-

Resumen

Comúnmente ocurren fuegos naturales en las praderas de "Fescue" de Alberta, pero existe poca información en que basar las recomendaciones de apacentamiento después del fuego. Un fuego natural que ocurrió en Abril de 1999 brindó la oportunidad para estudiar el efecto de la época e intensidad de defoliación después del fuego en una pradera de "Foothills rough fescue" (*F. campestris* Rydb.) del sudeste de Alberta. Un experimento factorial 3 (fecha de defoliación) x 2 (intensidad de defoliación) con 10 repeticiones (plantas) se estableció en porciones de pastizal quemado y no quemado y se analizó como un diseño anidado. Las plantas fueron defoliadas una vez en las etapas de crecimiento vegetativo activo (17 de Mayo), desarrollo de la inflorescencia (2 de Julio) o dormancia (30 de Septiembre), la defoliación se efectuó a dos alturas del rastrojo, 5 o 15 cm, y se llevo a cabo en la primer estación de crecimiento después del fuego. El fuego aumento el número de hijuelos en 54% en comparación con las plantas no quemadas, pero redujo la ANNP de las plantas en 51% en la segunda estación de crecimiento. Mientras que una sola defoliación de las plantas quemadas, particularmente a inicio del año, tuvo poco efecto en el crecimiento, retasando la defoliación hasta Julio disminuyo el ahijamiento en el año siguiente. El aumento en la intensidad de defoliación tuvo el mayor impacto en las plantas no quemadas, reduciendo en el segundo año la altura de la planta (15%), el ahijamiento (21%) y la ANPP de la planta (32%). La defoliación en Mayo redujo el crecimiento etiolado al año siguiente, sin importar el tratamiento de quema. Un solo evento de apacentamiento después de un fuego natural no necesariamente parece tener un efecto detrimental en el "Rough fescue"; sin embargo, el poco forraje disponible inmediatamente después del fuego, puede no justificar el aumento en riesgo para la planta que se corre con el apacentamiento subsecuente.

cue might be expected to have a similar response to fire, this premise remains untested.

Rough fescue loses vigor when grazed during the growing season (Looman 1969). Burning may reduce rough fescue abundance (Bailey and Anderson 1978, Antos et al. 1983) and productivity (Jourdonais and Bedunah 1990, Gerling et al. 1995). While considerable research has addressed the effects of grazing on Fescue Prairie (Barker and Erickson 1971, Wright 1974, Willms et al. 1985), no information is available on the cumulative effects of grazing following wildfire on foothills rough fescue plants. Previous research has shown that grazing can affect the subsequent recovery of native bunchgrasses such as Idaho fescue (*F. idahoensis* Elmer) and bluebunch wheatgrass [*Pseudoroegneria spicata* (Pursh) A. Löve subsp. *Spicata*] after wildfire (Bunting et

al. 1998). Recent increases in wildfire occurrence in the Fescue Prairie (Bork et al. 2002) indicate information specific to foothills rough fescue is needed to develop appropriate guidelines for grazing following fire.

In April 1999, a small wildfire in the Foothills region of Alberta provided an opportunity to study the effects of defoliation following burning on foothills rough fescue plants. The study was specifically designed to evaluate the resilience of plants subjected to variation in the season and intensity of defoliation over a 2 year period.

Materials and Methods

Site Description

The study was conducted in southwestern Alberta (50°11'30" N, 113°53'30" W; 1,366 m above sea level) within the Fescue Prairie ecoregion on the eastern slopes of the Porcupine Hills (Strong and Leggat 1992). The area was lightly grazed from 1949 until 1982 when it was fenced to exclude livestock. The plant community was a foothills rough fescue—Parry oat grass (*Danthonia parryi* Scribn.) type indicative of the modal range for the region (Wroe 1972, Strong and Leggat 1992).

The regional landform is rolling moraine upland. The local range site had a slope of approximately 8% with a southerly aspect and is well-drained on loamy parent material. Soils on the site have been classified as Orthic Black Chernozems (Udic Haploboral) developed on till over-lying sandstone (Dormaar and Willms 1990). The climate is dry subhumid with a mean annual precipitation of 444 mm (Table 1). In 1999 and 2000, annual precipitation was 399 and 264 mm, respectively. Growing season (April–August) precipitation during those same years was 123% (351 mm) and 60% (171 mm), respectively, of the long-term mean.

Wildfire Description

The study site was burned by a 1-ha wildfire around 2 pm on 7 April 1999. The average daily wind speed on the day of the fire was 30 km hour^{-1} (AAFC, unpublished climate data) and air temperatures averaged 6.7° C with a low of 0.9° C and a high of 13° C. Relative humidity in the morning was 50%, dropping to 30% at the time of the fire. The litter fuel load in the area was assessed at 6,372 kg ha^{-1} in 1999 (AAFRD-Public Lands Division, unpublished data). The fire occurred immediately following snowmelt but before the initiation of plant growth. Although only a small area was burned, the fire was intense and inflicted considerable visible damage (e.g., pitting) to rough fescue tussocks.

Although this study involved a single burn and is therefore unreplicated, variability in fuel loading and microclimatic conditions at the ground surface typically results in variable treatment exposure among individual plants, which was considered the experimental unit in this investigation. Immediate containment of the fire on the windward side ensured that rough fescue plants sampled on either side of the fire boundary were on the same range site.

Methodology

The effects of defoliation intensity following burning were evaluated in a 3 (season of defoliation) x 2 (defoliation intensity) factorial experiment using 10 replicates (plants) of each treatment combination within each of the burned and non-burned areas. Rough fescue plants (N = 120) having a diameter of 15 to 20 cm near the base were randomly selected from within the burned and adjacent non-burned areas following the fire and permanently marked.

Defoliation dates were 17 May (active vegetative growth), 2 July (inflorescence development), or 30 September (dormant). Defoliation intensities were 5 and 15-cm clipped stubble heights. All defoliation treatments were imposed only during

1999, the first growing season following fire, by clipping to the prescribed height. Harvested phytomass was oven-dried and weighed to determine defoliation intensity. An additional 10 plants were randomly selected in each of the burned and non-burned areas for measurement to serve as a check. These plants were added for qualitative comparisons only and were not part of the main design.

In spring 2000, 2 of 10 plants from each treatment were assessed for etiolated growth. Prior to spring green-up, all standing dead plant material was removed to a 5-cm stubble height. Cones were then placed over these plants down to soil around the outside base to exclude light and all etiolated growth clipped bi-weekly to ground level commencing 2 May until growth ceased. All harvested material was oven-dried and weighed.

Tiller counts were made on all plants in September 1999 at the time of the final defoliation treatments. These counts were subsequently repeated on all non-etiolated plants in the third week of May, second week of July, and last week of September 2000, in order to assess the residual treatment effects of burning and defoliation on tiller demography throughout the following growing season. Inflorescences were counted in July 1999 on all plants defoliated earlier in May and of all plants marked for defoliation in September. In addition, inflorescences were counted on all non-etiolated plants in July 2000. Plant heights were measured at the same time as tiller counts were undertaken on all undefoliated plants in 1999 (i.e., September) to assess the effect of burning alone, and of all plants in 2000. Plant height was measured as the average extended length of tillers. Maximum above-ground net primary production (ANPP) was harvested near ground level on 30 September, 2000, oven-dried, and weighed. Average tiller weights (mg tiller^{-1}) were determined for each plant using ANPP and tiller count data.

Table 1. Winter (January to March, November to December), monthly growing season, and 40-year average precipitation on the Fescue Prairie AAFC sub-station near Stavely, Alberta, from 1997 to 2000.

Year	Jan–Mar	April	May	June	July	Aug.	Sept.	Oct.	Nov–Dec	Total
					(mm)					
1997	21.9	21.4	138	73.1	28	77	34.9	0.2	4.9	399.4
1998	47.5	27.9	169.6	186.9	129.7	16.2	25.3	12.5	31.9	647.5
1999	10.9	66.2[1]	71.6	109	53.9	50.3	15.6	8.6	12.6	398.7
2000	23	27	16.6	66.2	13.1	48.1	59.9	1.6	8	263.5
40-yr average	76.2[2]	27.2[2]	61.8	84.1	56.1	56.8	40.8	22.6	44.8[2]	444.3[2]

[1]Indicates time of wildfire, 7 April 1999.
[2]Data from the Claresholm Meadows Creek, Alberta climate station, 1961–1990 (Environment Canada 1998).

Statistical Analyses

All data were analyzed using a split-plot design (Steel et al. 1997). Given the lack of replication of fire, burn treatment was considered the whole plot, with defoliation regimes nested within individual burn treatments. Analysis was done using ANOVA (Proc GLM, SAS Institute Inc. 1991), with an emphasis on defoliation and burn by defoliation effects. Where significant results were found, comparisons were made among seasons and/or intensities of defoliation within individual burned and non-burned treatments. Fescue plant responses examined included phytomass removed in 1999, ANPP levels and maximum plant height in 2000, as well as tiller and inflorescence numbers in 1999 and 2000. Probability values for the differences of the least-square-means were adjusted for multiple comparisons according to Tukey's procedure. Inflorescence numbers were analyzed as percent of total tillers to adjust for unequal tiller numbers per plant. Tiller count and weight data were normalized using a square root transformation to meet the conditions of normality based on the Shapiro-Wilk statistic and homogeneity of variance based on Levene's test (Steel et al. 1997).

To evaluate changes in tiller demographics, the percentage change in tiller numbers per plant was analyzed using a repeated measures multivariate analysis of variance (MANOVA, SAS Institute Inc. 1991). This procedure tested for the pattern of correlation between treatment effects and seasonal changes in rough fescue tiller numbers based on sequential sampling from September 1999 through May, July, and September of 2000. The process of evaluating percent changes in tiller numbers through time also circumvented the problem that initial, pre-wildfire tiller counts were not available for use as a covariate. Data on percent change in tillers per plant were also normalized using a square root transformation.

Results

First-Year Effects

Phytomass yields in the first growing season after burning (1999) were partly an artifact of the nature of the harvesting treatments and did not reflect a plant response to clipping (Tables 2 and 3). Nevertheless, the observations provide an opportunity to compare growth and associated opportunities for livestock grazing, as defined by the harvest date, between burned and non-burned plants when cut at

Table 2. Interactive effects of spring wildfire, season of clipping, and clipping height on plant and tiller characteristics of *Festuca campestris* plants (n = 10) in September 1999. Analysis of phytomass harvested and tiller numbers performed on square root transformed data.

Factor	df	Phytomass Harvested Tillers (mg • tiller^{-1})	Phytomass Harvested Plant (g • plant^{-1})	Tillers Total (no • plant^{-1})	Tillers Inflorescence[1] (% of total)
		-----	-----Probabilities-----	-----	-----
Burn (B)	1	N/a	N/a	N/a	N/a
Season of Clipping (S)	2	<0.001	<0.0001	0.03	0.25
Clipping Height (H)	1	<0.001	<0.0001	0.19	0.01
B x S	2	0.12	<0.001	0.08	0.74
B x H	1	0.88	0.15	0.81	0.01
S x H	2	0.02	0.03	0.43	–
B x S x H	2	0.18	0.70	0.59	–

[1]Analysis of % reproductive tillers per plant is based only on spring defoliated and non-defoliated plants due to interference of July clipping with inflorescence production (d.f. = 1 for all variables tested).

the same stubble height. Burned plants had tiller and plant phytomass levels that were 69 and 51% lower, respectively, than non-burned plants (Table 3). Burned plants also exhibited a marked reduction in spring growth leading to a burn by season interaction (P < 0.001), which was reflected in lower herbage yields throughout the year. For example, burned plants harvested in May and September yielded only 4 and 41% the phytomass of their non-burned counterparts, respectively (Table 3). As expected, defoliation later into the year increased harvested yields (P < 0.001), particularly at the 5-cm clipping height (Table 3).

The reduction of plant and tiller phytomass after burning was associated with a

reduction in plant height by September 1999, from an average of 54 (±5) to 25 (±4) cm. Although burning had little effect on tiller numbers at the end of the first growing season, tillering was significantly altered by the phenological stage when defoliation occurred (P = 0.03). Tiller counts taken in September indicated that plants harvested in May (active vegetative growth), July (inflorescence development), and September (dormancy) had an average of 120, 98, and 128 tillers, respectively, with burned and non-burned plants responding in a similar manner (P = 0.08).

In 1999, inflorescence production was also affected by a burn by clipping height interaction (P = 0.01). Burned plants produced few seedheads regardless of clip-

Table 3. Phytomass harvested at 3 dates and 2 stubble heights from burned and non-burned *Festuca campestris* plants (n = 10) during the first growing season (1999) after spring wildfire. Results of ANOVA are given in Table 2.

Treatment	Tiller Phytomass	Plant Phytomass
Burn x Season of Clipping	(mg • tiller^{-1})	(g • plant^{-1})
Burn		
May	6.4	0.4 c[1]
July	23.5	2.9 b
Sept	61.7	5.3 a
Pooled Mean	30.6	2.9
Non-burned		
May	99.1	9.0 b
July	82.4	10.7 ab
Sept	115.8	13.0 a
Pooled Mean	99.1	10.9
Interaction SE mean	10.2	0.9
Clipping Height x Season of Clipping		
5-cm		
May	67.1 b[2]	5.7 c[2]
July	67.2 b	8.8 b
Sept	128.1 a	12.9 a
15-cm		
May	38.4 a	3.7 b
July	38.6 a	4.8 a
Sept	49.4 a	5.4 a
Interaction SE mean	10.2	0.9

[1]Within a column and burn treatment, means followed by the same letter do not differ significantly (P > 0.05).
[2]Within a column and clipping height, means followed by the same letter do not differ significantly (P > 0.05)

Table 4. Interactive effects of burning, season of clipping, and clipping height on plant and tiller characteristics of *Festuca campestris* in September 2000 following exposure to spring wildfire and subsequent defoliation in 1999 (n = 8, except for etiolated growth, where n = 2). Analysis for tillers and ANPP performed on square root transformed data.

Factor (mg • tiller^{-1})	df	ANPP[1] Tiller (g • plant^{-1})	Plant (no • plant^{-1})	Height (cm)	Tillers Total (no. • plant^{-1})	Inflorescence (% of total)	Etiolated growth Tiller (mg • tiller^{-1})	Plant (g • plant^{-1})
		--Probabilities--						
Burn (B)	1	N/a	N/a	N/a	N/a	N/a	N/a	N/a
Season of Clipping (S)	2	0.89	0.31	0.65	0.15	<0.0001	0.02	<0.01
Clipping Height (H)	1	0.02	0.05	<0.001	0.47	0.97	0.62	0.78
B x S	2	0.18	0.05	0.13	0.05	0.04	0.16	0.70
B x H	1	0.01	0.02	0.04	0.36	0.70	0.93	0.43
S x H	2	0.24	0.69	0.84	0.74	0.27	0.31	0.42
B x S x H	2	0.91	0.38	0.40	0.17	0.17	0.13	0.55

[1]Aboveground net primary production.

ping height (< 0.11% of tillers), while plants not exposed to fire but clipped at 5 and 15-cm stubble heights had 0.43 and 1.76% of their tillers produce an inflorescence, respectively.

Second-Year Effects

Responses in 2000 represented residual effects of defoliation in 1999 (Table 4). In 2000, burned plants continued to have lower tiller and plant yields (i.e. ANPP) compared to non-burned plants, by 69 and 51%, respectively (Table 5). The observed reduction in plant ANPP in September of 2000 with burning coincided with a continued reduction in plant height (58% of non-burned; Table 5) and tillers that weighed 32% that of non-burned tillers (Table 5). Burned plants remained about 60% the height of non-burned plants throughout the summer of 2000 (data not shown).

In contrast to these results, burned fescue plants had greater tiller numbers (203 tillers plant^{-1}) compared to those not exposed to fire (132 tillers plant^{-1}). While the increase in tillers within burned plants occurred primarily before May 2000 (Fig. 1), tiller emergence in non-burned plants was most abundant between May and July of 2000.

Plants defoliated to a 5-cm height in 1999 had reduced tiller (P = 0.02) and plant ANPP (P = 0.05), as well as plant height (P < 0.001) in 2000. These effects, however, were confined to non-burned plants (P < 0.05, Table 5), suggesting burning reduced the impact of the intensive clipping treatment.

Variation in the response of plants to different seasons of clipping was also evident within the burn treatments (P = 0.05). Examination of these data indicated ANPP levels were stable among non-burned plants defoliated at different times the year before (Table 5). In contrast, defoliation of burned plants in July resulted in the lowest

plant ANPP the following year, although post-hoc mean comparisons revealed no significant difference (at P = 0.05). Year-end tiller numbers in 2000 also varied among the seasonal defoliation treatments within the burned and non-burned plants (P = 0.05). Defoliation of non-burned plants prior to September 1999 stimulated tillering the following year (140, 140, and 118 tillers plant^{-1}, with May, July, and September defoliation, respectively), but depressed tillering if applied in July to burned plants (234, 168, and 207 tillers plant^{-1}, with May, July, and September defoliation, respectively). Tiller numbers

within burned and non-burned plants defoliated in September were also similar to the non-defoliated controls for both burned (207 vs 195, respectively) and non-burned (118 vs 114, respectively) plants.

Additional effects were observed of burning and defoliation season on inflorescence production (P = 0.04) in 2000. Defoliation in July resulted in the greatest reduction of inflorescences (Fig. 2), but was most apparent within non-burned plants. Notably, inflorescence production also appeared to increase within the September defoliated plants in both burned and non-burned plants relative to the unde-

Table 5. Effects of different clipping heights and seasons of defoliation on the mean height and ANPP of burned and non-burned rough fescue plants (n = 8), as measured in September 2000 following spring wildfire and defoliation in 1999. ANOVA results are given in Table 4.

Treatment	Plant Height (cm)	Tiller ANPP[1] (mg • tiller^{-1})	Plant ANPP[1] (g • plant^{-1})
Burn x Clipping Height			
Burned			
5-cm	24 a[2]	44 a	9.6 a
15-cm	26 a	43 a	8.8 a
Undefoliated	23	46	9.7
Pooled Mean	25	44	9.3
Non-burned			
5-cm	39 b	122 b	15.3 b
15-cm	46 a	153 a	22.4 a
Undefoliated	46	172	20.1
Pooled Mean	43	143	19.0
Interaction SE	1	0.6	1.4
Burn x Season of Clipping			
Burned			
May	25	47	11.5 a
July	23	38	6.5 a[3]
September	22	45	9.6 a
Non-burned			
May	38	132	19.5 a
July	43	144	20.3 a
September	39	137	16.7 a
Interaction SE	1	0.8	1.7

[1]Aboveground net primary production.
[2]Within a column and burn treatment, means followed by the same letter do not differ significantly (P > 0.05).
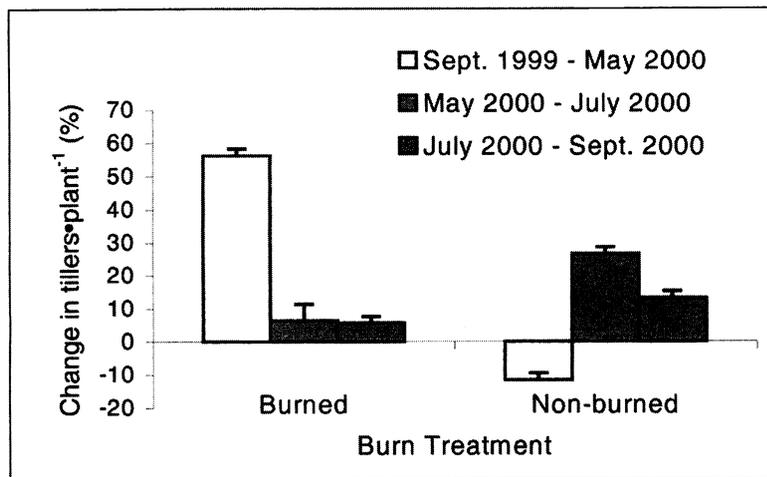[3]Burned July plant ANPP differs from May (0.05 < P < 0.10).

Fig. 1. Seasonal changes in tiller numbers (±SE) from September 1999 to September 2000 on burned and non-burned plants following a spring wildfire in 1999 (n = 8). Changes in tiller number were affected (P < 0.0001) by the measurement interval and the burning treatment as evaluated by multivariate analysis of variance for repeated measures.

foliated controls (Fig. 2). In contrast, clipping intensity had no effect (P > 0.05) on inflorescence production (Table 4).

Finally, burned plants had 44% less etiolated growth of tillers compared to non-burned plants (Table 6), and May defoliation the previous year resulted in significantly less (P < 0.05) etiolated growth at both the tiller and plant level (Table 6). The effect of defoliation intensity and season, however, were similar (P > 0.05) between burned and non-burned plants.

Discussion

Response to Burning

Foothills rough fescue plants had reduced yields the first and second growing seasons after spring burning, which is comparable to Redmann et al. (1993) and Gerling et al. (1995) for plains rough fescue. The yield reductions in the present study were related to burning resulting in shorter, lighter tillers, and occurred despite a 50% increase in tiller numbers in burned plants during the second year. These results indicate that tiller recruitment by burning could not compensate for depressed tiller weights over the 2 years of monitoring conducted here. This pattern may be related to re-allocation of limited plant resources such as carbohydrates to a greater number of tillers, particularly as they become larger with age throughout the growing season, post-burn conditions related to litter removal (Redmann 1978, Savage 1980) and precipitation.

Precipitation during the first growing season after fire was near average, however, precipitation to the end of the second growing season was only about 54% of the long-term average (Table 1). Reduced precipitation may have limited plant growth in the second year. Given the loss of litter with burning and its importance for growth (Willms et al. 1986), moisture deficits were also likely exacerbated by the fire.

Although burning decreased plant ANPP, height and inflorescence production, suggesting a negative response to burning, a more reliable indicator of plant response may be tiller numbers as it represents longer-term productive potential. Using tiller numbers as a standard, burning may have improved plant vigor by stimulating tillering, thereby supporting the notion that rough fescue is both adapted to, and the beneficiary of, fire. Coincident changes in etiolated growth, however, showed no effect (P > 0.05) of burning on the plant but a reduction for individual tillers (Table 6). Etiolated growth is positively correlated with carbohydrate levels in the roots and crowns of grasses (Raese and Decker 1966, Dorvat et al. 1972). The reduction in energy at the tiller level in burned plants suggests some susceptibility to further damage should tiller development be impeded. Burning foothills rough fescue has been shown to increase individual plant production 3 years after wildfire, but increased plant mortality of burned plants resulted in lower total fescue production compared to non-burned areas (Antos et al. 1983).

Therefore, enhanced tiller numbers following burning are likely to benefit future production only when plant mortality is limited. No mortality was documented in the current study.

Although the results here focus on rough fescue plants, their response is not necessarily indicative of the entire grassland because the reproductive capacity of many plant species are uniquely adapted to filling ecological niches in the post-fire environment. Increased forb biomass after a late winter wildfire helped compensate for a reduction in grass production by the second year after burning in a grassland similar to the present study (Bork et al. 2002).

Response to Post-Burn Defoliation

Given that post-burn grazing of regrowth by wildlife was likely common prior to European settlement, the postulation might be made that rough fescue can tolerate this pattern of disturbance. However, the decision to graze with livestock in the year after burning might be based as much on the benefits to animals as on the effect to the plant. By May, the time when grazing normally begins on Fescue Prairie, burned plants had produced only 5% the biomass of non-burned plants, which subsequently increased to only 40% by September. Thus, available forage for grazing declined markedly with burning.

Results indicate that clipping of burned plants in early spring did not produce a cumulative negative effect on plant recovery. Burning appeared to increase plant resilience to post-burn harvesting by slowing growth and minimizing exposure of regrowth to defoliation. Nevertheless, plant energy reserves were lowest in

Table 6. Effects of spring wildfire and subsequent date of defoliation in 1999 on the ANPP[1] of etiolated tillers and plants in May 2000.

Plant	Treatment	Tiller
	(mg • tiller^{-1})	(g • plant^{-1})
Burn Treatment (n = 12)		
Burned	9.0	1.6
Non-burned	16.2	1.8
SE mean	1.8	0.23
Season of Clipping (n = 8)		
May	7.4 b[2]	1.2 b
July	14.0 ab	1.5 ab
September	16.3 a	2.5 a
SE mean	2.2	0.28
Undefoliated Control (n = 4)	16.3	1.5

[1] Aboveground net primary production.
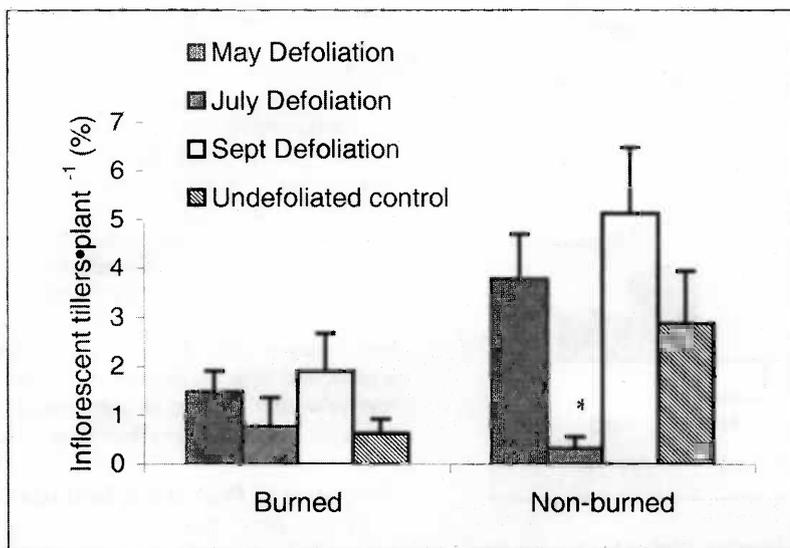[2] Within a column and burn treatment, means followed by the same letter do not differ significantly (P > 0.05).

Fig. 2. Changes in the proportion of inflorescences (±SE) in July, 2000 on burned and non-burned plants following a spring wildfire in 1999 and subsequent defoliation at 3 dates (n = 8). Within the unburned treatments, the July clipping (denoted with a *) differs from May and September (P < 0.05).

plants defoliated the previous year in May (Table 6), regardless of their burn status, which indicates vulnerability to spring grazing and supports the commonly held belief that grazing should be delayed in spring to benefit plant vigor. Burned plants of Idaho fescue had greater mortality when defoliated in early summer compared to early fall (Bunting et al. 1998). Although plants tend to become more vulnerable to defoliation at the time of inflorescence development (i.e., July) due to the re-allocation of energy to seed production (Branson 1953), rough fescue plants in this study produced very few inflorescences relative to the total number of tillers (Fig. 2). Inflorescence production in 2000, however, did exhibit a general reduction the following year within plants defoliated the previous July (Fig. 2). This observation, coupled with a marginal trend towards a decline in plant ANPP (Table 5) and a marked reduction in tiller numbers within burned plants defoliated during July, suggests deferral of grazing beyond inflorescence development is warranted, particularly if plant recruitment is desired.

In contrast to the season of defoliation, severity of defoliation had no effect (P > 0.05) on any plant response variable measured within burned plants. Burned plants had a linear pattern of growth from May to September, which may indicate that sufficient photosynthetic tissue remained after severe defoliation to restore the plant energy requirements under conditions favorable for growth in the first year.

More severe defoliation of non-burned plants, particularly those defoliated at 5 cm, resulted in declines in height as well as tiller and plant ANPP 1 year after defoliation. The different response to clipping between burned and non-burned plants may be partly related to the relative proportion of herbage removed from plants and the photosynthetic area remaining after clipping. Clipping at a fixed height will remove a greater proportion of total herbage from tall, rapidly growing non-burned plants compared with shorter, burned plants, and likely accounts for the differing phytomass levels harvested in 1999. This resulted in clipped, non-burned plants having greater treatment differences than burned plants. Similar mechanisms have been suggested for the effect of water stress on subsequent defoliation in grasses (Simone and Baruch 1991), and highlights a limitation of the common practice of using fixed clipping heights as a replacement for actual grazing.

Morphological differences in burned and non-burned plants may also be important. Unlike burned plants, tiller sheaths in non-burned plants remained intact below the height of defoliation, shielding the enclosed leaf tissue. Clipping at 15 cm, however, may still leave some photosynthetic surface exposed. Additionally, the clipping height of 5 cm used in this investigation represents a relatively severe defoliation, which livestock grazing may only achieve when stubble had previously been removed by burning or severe grazing.

It should be noted that the single defoliation treatment we applied more closely simulates the effect of short duration or high intensity-low frequency grazing rather than season-long grazing. Multiple harvests during the growing season, as might occur under season-long grazing, has been shown to severely reduce yields of rough fescue plants and increase mortality (Willms and Fraser 1992). However, the results found here do support the findings of Willms (1991) suggesting that the effects of defoliation on plant yield may only be fully evident in the second year after treatment.

Plant responses to burning or defoliation are also dependent on previous disturbances. In our study, individual fescue plants had a long history of protection from grazing, which was likely to produce stability within plant vigor and its local environment. Although tiller demographics have not been documented for rough fescue, it appears that individual tillers can be several years old prior to producing an inflorescence. In our study, very few plants produced inflorescences in either year and tillers became more robust over time. Therefore, it is likely that initial disturbances have the greatest impact in upsetting the energy dynamics within fescue plants, while the effect of subsequent disturbance is dependent on factors such as recovery time. In our study, clipping represented the initial disturbance of non-burned plants and could be expected to have a greater effect than in slower growing burned plants.

Tillering is perhaps the most important response to disturbance as it determines the future potential productivity within the plant (Murphy and Briske 1992). Both burning and clipping increased overall tiller numbers, which implies enhanced productive potential. However, this trend also coincided with a decline in the potential for sexual reproduction, as evidenced by a decrease in the proportion of inflorescent tillers. July defoliation appeared to be particularly detrimental, reducing the proportion of seedheads 1 year later from about 5% to less than 1% of all tillers, indicating longer-term impacts due to defoliation can occur on sexual recruitment within rough fescue.

Management Implications

Although burning may impede various aspects of development in foothills rough fescue plants, it also represents a potential mechanism for plant renewal through

enhanced tiller production. Its also appears that spring burned fescue plants can be safely grazed in a single defoliation event during the early part of the first growing season if the environmental conditions are favorable for recovery. This tolerance is probably linked to slow plant growth limiting the impact of subsequent defoliation. Despite this, limited available forage from burned plants may not warrant the potential risk to the plant under most grazing systems as burning could facilitate grazing close to the crown and lead to a loss of plant vigor. In addition, burned plants appear to increase in sensitivity to July defoliation during the post-burn recovery growing season, potentially due to a delay in plant growth coinciding with burn-induced stress. In conclusion, both plant physiological (carbohydrate) and morphological (height, ANPP, tillers, and inflorescence) characteristics exhibited marked responses into the second year following burning and defoliation, suggesting that the risk associated with grazing burned fescue plants may be greater than any potential benefits in the short-term. Finally, these results also highlight the importance of longer-term monitoring and management to maximize the recovery of foothills rough fescue plants exposed to defoliation or fire.

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