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Temperature effects on regrowth of 3 rough fescue species

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Abstract

Three species of rough fescue, alpine rough fescue (*Festuca altaica* Trin.), mountain rough fescue (*F. campestris* Rydb.), and plains rough fescue (*F. hallii* (Vasey) Piper) were grown for 12 weeks under 5 temperature regimes - 7:3, 12:8, 17:13, 22:18, and 27:23° C - and defoliated 3 times to 3.5 cm at 4-weekly intervals in a growth cabinet study. Final plant dry mass and harvestable biomass production were greatest at 17:13° C for alpine rough fescue and plains rough fescue, and at 12:8° C for mountain rough fescue. Harvestable biomass plateaued or declined at the final harvest in all species for temperatures above 12:8 °C. Tiller numbers increased at successive harvests. Biomass per tiller declined markedly at the final harvest of alpine rough fescue at all temperatures. Regrowth in alpine rough fescue was markedly reduced at temperatures either above or below the optimum. The results indicate that mountain rough fescue and plains rough fescue are better able to regrow following defoliation at temperatures below or equal to their optima, than at temperatures above their optima. This provides greater understanding of field responses in both species where frequent defoliations are more deleterious after the April/May period when temperatures are above optimal.

Key Words: *Festuca hallii, Festuca campestris, Festuca altaica,* defoliation, management, persistence, biomass, tillering

The rough fescue complex consists of mountain rough fescue [*Festuca campestris* Rydb.], plains rough fescue [*F. hallii* (Vasey) Piper], and alpine rough fescue [*F. altaica* (Trin.)]. In Alberta, mountain rough fescue is found above 1,000 m elevation in southern and south western Alberta. Presently, about 450,000 ha remain uncultivated on hills east of the Rocky Mountains, the Cypress Hills, and on more fragmented areas in east-central Alberta. Plains rough fescue is distributed over about 1.54 M ha in the Alberta parklands while alpine rough fescue is found mostly in Alaska and the Yukon Territories in Montane and Subalpine regions and only in a few locations in Alberta. Although the species are all part of the rough fescue complex, genetic characteristics are clearly distinct with alpine rough fescue having the same number of chromosomes (n = 28) as plains rough fescue while mountain rough fescue has twice that number (2n = 56).

The overlapping but distinct distributions of the 3 species can be explained partly by differences in their physiological adaptation (Hill et al. 1995). Plains rough fescue and mountain rough fescue are thought to have evolved under the intermittent grazing pressure imposed by a nomadic buffalo herd (Moss and Campbell 1947). Both species are tufted although plains rough fescue is capable of producing short rhizomes (Pavlick and Looman 1984). Under similar growing conditions, alpine rough fescue produces fewer larger tillers with broader lamina (King et al. 1995). Plains and mountain rough fescue are sensitive to summer grazing (Johnston 1961, McLean and Wikeem 1985b). The response of alpine rough fescue to grazing has not been documented.

The objective of this study was to gain a better understanding of the regrowth response of 3 rough fescue species grown at a range of temperatures. Such information, while adding to our understanding of environmental factors that influence the distribution of the 3 species, could also help to elucidate the basis for the documented sensitivity of mountain and plains rough fescue to defoliation during their period of active growth (Willms 1991, Gerling et al. 1995).

Materials and Methods

Plains rough fescue seeds were collected at the University of Alberta ranch (53° 00' N, 111° 36' W), mountain rough fescue seeds were collected at Stavely, Alberta (50° 12' N, 113° 54' W), and alpine rough fescue seeds were collected near Mayo, Yukon (63° 35' N, 135° 54' W). Seeds of each species were germinated on moist sand in Petri plates at 20° C in the light and transplanted into pots when the first leaf was approximately 2-cm long. Three seedlings of the same species were established in each 15-cm diameter pot. The growing medium was a mix of equal parts loam, sand, and peat. The plants were maintained in a greenhouse at a temperature of 18° C and a 16-hour photoperiod for 10 weeks. The plants were then cut back to a height of 3.5-cm and 6 pots of each species were randomly assigned to each of 5 growing environments. The pots for this experiment formed a sub-set of a larger experiment described in King et al. (1995). The growth cabinets (Controlled Environments Ltd., Winnipeg, Man.) were set on an 18-hour photoperiod and temperature regimes of 7:3, 12:8,17:13, 22:18, and 27:23° C (light:dark). Photosynthetically active radiation (PAR, 400–700 nm), measured with a quantum sensor (Li-188SB, LI-COR Inc., Lincoln, Nebr.) at canopy level, averaged 330 μmol • m^2 • sec^{-1}. The pots were arranged randomly within each cabinet and watered daily. The assumption must be made that the environmental conditions (other than temperature) were similar. Cabinets were the same (size and lighting) and maintained to the same standards. Nitrogen, phosphorous and

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potassium were supplied through the irrigation system every 2 weeks.

The plants were harvested 3 times to a stubble height of 3.5-cm (harvestable biomass), at 4 week intervals. At the first 2 harvests tiller number per plant, dry mass of harvestable biomass, and leaf area were recorded. After the final harvest, plants were removed from the pots and the soil was washed from the roots. Tiller number per plant, leaf area (above 3.5 cm), harvestable dry mass, root dry mass, and crown mass (tiller base, below the 3.5-cm cutting height) were recorded. Shoot mass (crown plus harvestable biomass), percent harvestable biomass (harvestable biomass as a percent of total plant biomass) and harvestable biomass per tiller were calculated.

Harvestable biomass was measured from 6 replicates, for each species, for each of the 3 harvests. Roots were measured for the 6 replicates after the final harvest. For tiller number and biomass per tiller, 6 replicates were measured at the first 2 harvests but only 3 replicates were measured at the final harvest due to time constraints. Leaf area was measured at the first and final harvests for only 3 replicates, due to time constraints, and at the second harvest for 6 replicates. The 3 replicates measured at the first harvest were not the same as the 3 replicates measured at the final harvest.

Analysis of variance were made for data having a balanced design. Therefore, tiller number and harvest biomass tiller^{-1} were analysed by the first 2 harvests and the third harvest while leaf area was analysed by individual harvests.

Where harvest was a factor in the experimental design, the data were analysed across harvests as a split plot factorial design with temperatures split for species and harvests. The Box's Conservative Correction was applied according to Miliken and Johnson (1984) where harvest, a repeated measure, was a factor. Data were subject to analysis of variance and differences between means tested using Fischer's (protected) least significant difference ($P < 0.05$)

Results

Harvestable Biomass

There were significant temperature by harvest and harvest by species interactions for dry mass of harvested material (Table 1). Harvestable biomass was greater at the second and third harvests than at the first harvest for all species at all temperatures except at 27:23° C (Fig. 1). At growing temperatures below 17:13°C there was a further increase in harvestable biomass at the third harvest, while at 17:13° C or above the harvestable biomass was equal to or less than that at the second harvest. Harvestable biomass could be ranked: mountain = plains > alpine rough fescue at 12:8° C, plains > alpine > mountain rough fescue at 17:13° C and plains = mountain = alpine rough fescue at 22:13° C.

Harvestable Biomass Accumulation and Biomass Partitioning

At the end of the defoliation sequence, accumulated harvestable biomass was greatest at 17:13° C for alpine and plains rough fescue, and at 12:8° C for mountain rough fescue (Table 2). Harvestable biomass of alpine rough fescue was always less than that of the other 2 species. At 7:3° C, the dry mass of alpine rough fescue shoots was less than half that of mountain or plains rough fescue. Harvestable biomass at the third harvest, as a percentage of total harvest, was greatest at 17:13° C and least at 7:3° C in mountain and plains rough fescue, but more variable in alpine rough fescue. Overall, the percent biomass removed at the third harvest was significantly less in plains rough fescue than in mountain or alpine rough fescue (Table 2).

Root mass of alpine and plains rough fescue increased ($P < 0.05$) with increasing temperature to a maximum at 17:13° C and then declined at higher temperatures (Fig. 2). In contrast, root mass of mountain rough fescue was similar ($P > 0.05$) at temperatures of 7:3° C to 17:13° C but decreased at higher temperatures. Allocation of dry matter to roots was ranked: mountain > alpine =

Table 1. Analyses of variance on data for harvestable biomass, tiller number and harvestable biomass per tiller of *Festuca altaica*, *F. campestris* and *F. hallii* at 5 temperature regimes (7:3,12:8, 17:13, 22:18, and 27:23° C) and 3 harvests.

Source	Harvested biomass		Tiller number (H1, H2)		Harvested biomass per tiller (H1, H2)	Tiller number (H3)		Harvest biomass per tiller (H3)
	Df[1]	Mean square	Df	Means square	Mean square	Df	Means square	Mean square
Temp (T)	4	4,509,293***	4	5,106***	490***	4	5,404***	2,057**
Error	25	59,754	25	195	18.1	10	116	220
Harvest (H)	2(1)[2]	7,453,712***	1	21,293***	139			
T x H	8(4)	1,428,212***	4	1,036***	130			
Error	50(25)	33,200	25	29.4	5.7			
Species (S)	2	173,448	2	7,040***	787***	2	5,735***	1,506**
T x S	8	244,726	8	740	40.0	8	895*	197
Error	50	124,724	50	369	28.8	20	381	178
H x S	4(2)	78,949*	2	480**	47.4***			
T x H x S	16(8)	42,360	8	134*	7.6			
Error	99(49)	20,065	49	35.6	6.1			
CV[3] (T x H x S)		28.1(4.6)		14.7 (6.0)	24.7(8.7)		26.4(14.4)	33.9(10.5)
LSD[4] (P <0.05)								
T	25	96.9	25	6.8	2.1		11.3	15.6
H	25	56.0	25	1.7	0.7		na[5]	na
T x H	25	125.1	25	7.1	2.3		na	na
S	50	ns[6]	50	7.1	2.0		14.9	10
T x S	50	ns	50	ns	ns		31	ns
H x S	49	104.5	49	7.3	2.1		na	na
T x H x S	49	ns	49	15.2	ns		na	na

*, **, *** Significant F Test for $P < 0.05$; $P < 0.01$; $P < 0.001$.
[1]Box Correction applied.
[2]Degrees of freedom shown in 1 column also pertains to the next column where they are not given.
[3]CV for anaylsis of transformed data are given in brackets.
[4]LSD may be used for appropriate comparisons in the Figure; LSD's are not shown for all comparisons.
[5]Effect not tested.
[6]Effect not significant ($P > 0.05$).

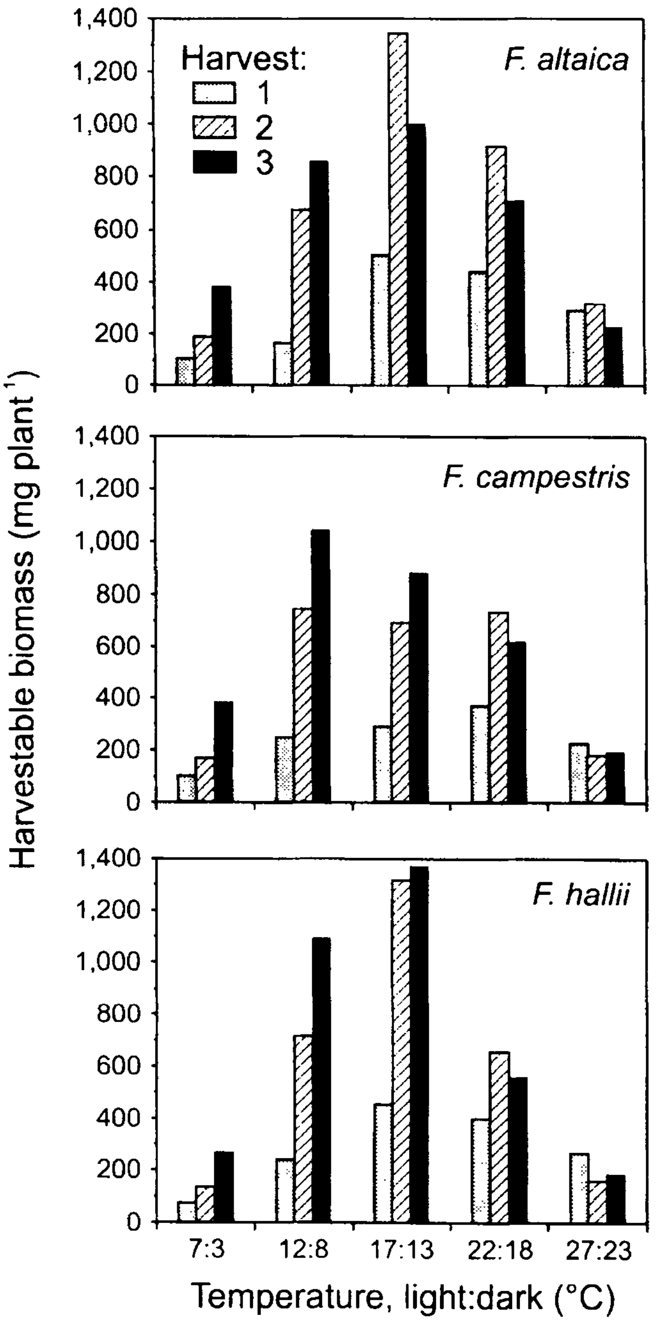

Fig. 1. Effects of temperature and harvests representing repeated regrowth periods on the harvestable biomass of 3 rough fescue species (*Festuca* spp). LSD's are given in Table 1.

plains rough fescue at 7:3° C; alpine > plains > mountain rough fescue at 17:13° C; and alpine = plains = mountain rough fescue at all other temperatures (all comparisons were based on P = 0.05). Percent of biomass allocated to roots at the final harvest was: 31.1% at 7:3° C, 31.1% at 12:8° C, 32.2% at 17:13° C, 20.6% at 22:18° C and 19.7% at 27:23° C averaged across species. Percent allocation was similar (P > 0.05) among the first 3 temperature regimes and between the last 2 temperature regimes, but differed (P < 0.05) between the 2 groups. Alpine

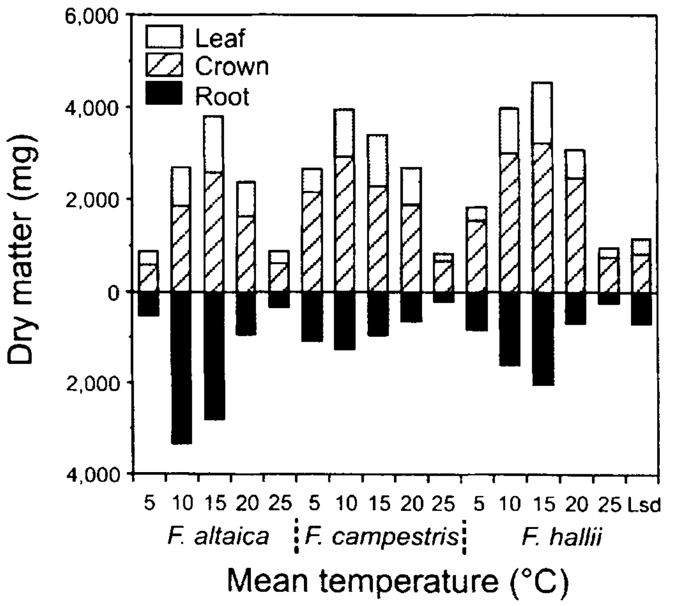

Fig. 2. Biomass partitioning between shoot and root for 3 rough fescue species (*Festuca* spp.) at the third harvest. The LSD's are for the temperature x species interaction which is significant (P < 0.05) for root and leaf weights but not crown weights (P > 0.05). The light:dark temperatures represented by the means are: 5 -7:3, 10 - 12:8, 15 - 17:13, 20 - 22:18, and 25 - 27:23° C.

rough fescue allocated the greatest (P< 0.05) percentage of mass to roots (33.7%) followed by a similar (P > 0.05) proportion by plains (24.9%) and mountain rough fescue (22.4%). The response to temperature was not affected (P > 0.05) by species.

Maximum cumulative harvestable biomass for mountain rough fescue was at 12:8° C and at 17:13° C for the other species, giving a significant temperature by species interaction (Table 2). At 22:18° C and 27:23° C, the cumulative harvestable biomass of alpine rough fescue was significantly greater than mountain or plains rough fescue.

Tiller Number and Dry Mass per Tiller

Tiller number increased (P < 0.05) from the first to the second harvest for all species and temperatures (Table 1, Fig. 3); this trend appeared to persist to the third harvest (Fig. 3). Tiller numbers were always least in alpine rough fescue. Plains rough fescue had higher (P < 0.05) tiller numbers than mountain rough fescue at 17:13° C and 22:18° C. The tillering response to any variable was modified by another as shown by significant (P <0.05) interactions of temperature by harvest, harvest by species and temperature by harvest by species (Table 1).

Harvestable biomass per tiller of alpine rough fescue was greater (P < 0.05) at the second harvest than the first at all temperatures above 7:3° C and was always greater, within a harvest and temperature regime, than for the other species (Table 1, Fig. 4). However, at the third harvest it was similar to, or less than, that of the other species. There were significant temperature by harvest and harvest by species interactions for the first 2 harvests (Table 1). At 27:23° C, dry mass per tiller of mountain and plains rough fescue declined at each subsequent harvest.

Table 2. Harvestable biomass at third harvest (regrowth) as a percent of total plant biomass and total accumulated harvestable biomass from 3 harvests (n = 6).

	Temperature (light:dark)	Alpine rough fescue	Mountain rough fescue	Plains rough fescue	Mean
		(harvestable biomass - % of total)			
	7:3	19.7	12.4	9.3	13.8
	12:8	16.5	19.4	16.9	17.6
	17:13	18.1	23.9	20.3	20.8
	22:18	23.5	23.6	15.8	20.9
	27:23	22.4	15.5	13.7	17.2
Mean		20.3	18.9	15.2	
lsd (temperature)					2.9[1]
lsd (species)					2.9
lsd (t x s)					6.0
		(cumulative regrowth (mg)			
	7:3	661	630	470	587
	12:8	1,682	2,015	2,044	1,914
	17:13	2,830	1,841	3,135	2,602
	22:18	2,047	1,759	1,609	1,805
	27:23	818	605	576	
Mean		1,608	1,370	1,567	
lsd (temperature)					267
lsd (species)					ns[2]
lsd (t x s)					428

[1]Effect is significant ($P < 0.05$).
[2]Effect is not significant ($P > 0.05$).

Table 3. Effects of temperature on the leaf area of 3 rough fescue species at 3 harvests representing repeated regrowth periods.

Harvest	Temperature (light:dark)	Alpine rough fescue	Mountain rough fescue	Plains rough fescue	Mean
1 (n=3)		($cm^2 \cdot plant^{-1}$)			
	7:3	10.6	5.5	7.5	7.9
	12:8	12.3	23.1	20.9	18.8
	17:13	53.0	22.0	44.2	39.8
	22:18	43.1	30.8	37.0	37.0
	27:23	30.1	18.2	23.8	24.0
	Mean	29.8	19.9	26.7	
	lsd (temperature)				10.6[1]
	lsd (species)				9.2
	lsd (t x s)				ns[2]
2 (n=6)		($cm^2 \cdot plant^{-1}$)			
	7:3	19.7	16.0	14.4	16.7
	12:8	75.5	88.5	85.0	83.0
	17:13	146.3	76.7	160.7	127.9
	22:18	92.0	69.5	74.2	78.6
	27:23	38.4	17.6	15.0	23.7
	Mean	74.4	53.7	69.9	
	lsd (temperature)				17.5
	lsd (species)				17.0
	lsd (t x s)				ns
3 (n=3)		($cm^2 \cdot plant^{-1}$)			
	7:3	22.5	27.8	21.7	27.4
	12:8	141.6	98.6	87.6	109.3
	17:13	177.0	158.5	168.2	167.9
	22:18	85.6	54.9	44.9	61.8
	27:23	20.9	11.3	11.1	14.4
	Mean	89.5	72.2	66.7	
	lsd (temperature)				31.5
	lsd (species)				13.6
	lsd (t x s)				ns

[1]Effect is significant ($P < 0.05$).
[2]Effect is not significant ($P > 0.05$).

Leaf Area

Leaf area per plant was greatest at 17:13° C in all species except at the first harvest when maximum leaf area occurred from 17:13 to 22:18° C (Table 3). Alpine rough fescue had a similar (P < 0.05) leaf area to plains rough fescue at the first and second harvests. At the third harvest, alpine rough fescue had a greater (P < 0.05) leaf area than either mountain or plains rough fescue. The leaf areas of mountain and plains rough fescue tended to be similar (P > 0.05) at all harvests (Table 3).

Discussion

Species differentiation

The 3 rough fescue species exhibited differences in growth and morphology that may reflect an adaptation to their environment. The lower optimal temperature for biomass production exhibited by mountain rough fescue, than either plains or alpine rough fescue, may be in response to conditions in the eastern foothills of Alberta where soils warm slowly and soil moisture availability is greatest in the spring (Strong 1991). For alpine rough fescue, a slow growth rate at cool growing temperatures is an advantage in northern environments where spring frosts and snow storms are common and moisture availability remains limited until the soil thaws. The faster tillering rate, at high temperatures, by plains rough fescue can result from rhizome development and may represent an adaptation to opportunistic growth following summer storms.

Plains and alpine rough fescue allocated more biomass to roots under optimal growing conditions than did mountain rough fescue. The proportion of total plant biomass allocated to roots, and total root mass was considerably less under defoliation (20–30%) than was observed in undefoliated plants (30–50%; King et al. 1995). These different allocation patterns may partially explain the decline in persistence of mountain rough fescue plants when defoliated repeatedly during the season when compared with a single defoliation at the end of the growing season (McLean and Wikeem 1985b; Willms 1991). Frequent defoliation may lead to "grazing induced drought" caused partly by reduced rooting depth (Johnston 1961).

The presence of fewer but larger tillers and leaves of alpine rough fescue allows the plant to develop leaf canopy rapidly in spring to optimize photosynthesis during the short growing season. Since carbon stored in tillers is used for regrowth (Briske and Richards 1995), an investment in tiller mass would provide a storage buffer that could be used to support rapid redevelopment of the canopy following removal. However, this strategy makes the plant vulnerable to frequent defoliation since residual leaf area following defoliation is generally low and redevelopment of the canopy depletes carbohydrate reserves in tiller bases. Such species are usually intolerant of continuous grazing or frequent defoliation regimes. The greater investment in individual tiller mass in alpine rough fescue may be positively related to flower development, since alpine fescue produces seed annually (King, unpublished data) while seed production in plains and mountain fescue is infrequent and unpredictable (Johnston and McDonald 1967).

In this study, the optimum temperature for regrowth of alpine rough fescue of 17:13° C was more marked than that for undefoliated primary growth (King et al. 1995). Allocation of biomass to roots was similar in regrowth and primary growth at this temperature, but was reduced in regrowth compared with primary growth for temperatures on either side of the optimum (King et

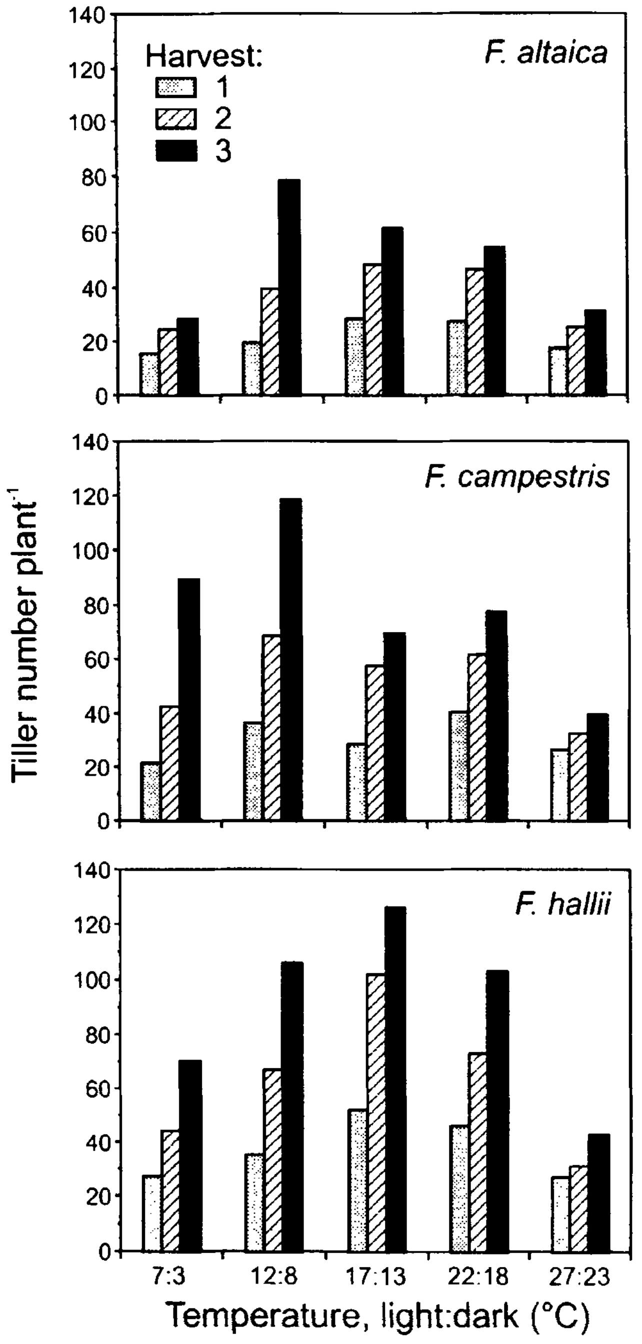

Fig. 3. Effects of temperature and harvests representing repeated regrowth periods on the tiller number of 3 rough fescue species (*Festuca* spp). LSD's are given in Table 1.

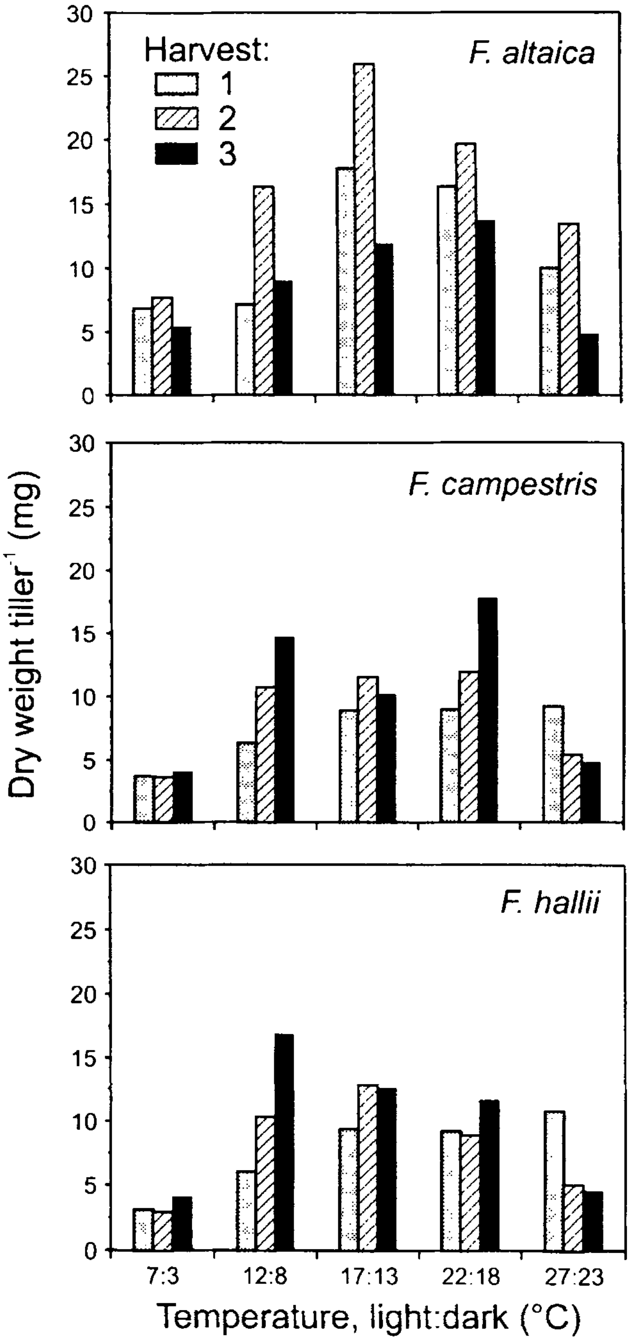

Fig. 4. Effects of temperature and harvests representing repeated regrowth periods on the dry weight per tiller of 3 rough fescue species (*Festuca* spp). LSD's are given in Table 1.

al. 1995). This suggests that alpine rough fescue is more tolerant to defoliation under optimum growing conditions in an early alpine/boreal summer, but less tolerant when defoliated in early spring or at higher temperatures in late summer.

Increased tolerance to defoliation through rapid tillering (Richards et al. 1988) does not seem to favor plains and mountain rough fescue over alpine rough fescue. Plains and mountain rough fescue are thought to have evolved under infrequent dormant season grazing by bison (Adams et al. 1993), and such grazing pressure would not necessarily favor a rapid tillering rate. The rapid tillering rate in these species, coupled with narrow involute leaf blades, may result more from a need to increase canopy size while controlling transpirational losses in environments with frequent summer droughts, rather than a response strategy to tolerate grazing.

Response to temperature

Regrowth of the 3 rough fescue species appear to be less affected by temperatures at, or below, their optimum temperature.

Carbon loss by respiration increases dramatically with temperature (Coyne et al. 1995) leading to an amplified stress when harvesting is imposed. On the other hand, as temperatures decrease more carbon remains available for regrowth thereby reducing stress due to defoliation. Under field conditions the stress due to high temperature responses may then interact with the onset of summer moisture deficits to increase plant mortality and reduce sward condition (McLean and Wikeem 1985a).

All 3 species had lower vigor as indicated by reduced harvestable biomass, tillering rate, and root biomass when defoliated more than twice at temperatures above 17:13° C. The current management recommendation for mountain and plains rough fescue in Alberta is to defer grazing until July when the plants have completed their growth and entered summer dormancy which avoids stressing the plants during the spring when growing conditions are optimum. Summer dormancy appears to be triggered by moisture stress since in this experiment, where water was non-limiting, none of the plants entered dormancy, even at 27:23° C.

While the results from this study clearly indicate that the species are less resilient to defoliation at above-optimal temperatures, it is probably a complex interaction between temperature sensitive plant growth processes, reduced root production, and the development of moisture deficits in mid-summer which combine to reduce vigor and persistence in all species when frequently defoliated under field conditions.

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