Rough fescue (*Festuca campestris* Rydb.) response to heat injury

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Bogen, A. D., Bork, E. W. and Willms, W. D. 2002. **Rough fescue (*Festuca campestris* Rydb.) response to heat injury.** Can. J. Plant Sci. **82**: 721–729. Rough fescue (*Festuca campestris* Rydb.) is an ecologically and economically important native plant species within grasslands of southwest Alberta. This is also a region where wildfires have become prevalent over the past decade. While the risk of long-term damage from fire may be determined by the susceptibility of rough fescue to heat injury, understanding the additive stress imposed by defoliation may assist in the development of grazing strategies facilitating rangeland recovery. Three laboratory studies were conducted to assess rough fescue sensitivity to heat stress, including the added impact of subsequent defoliation. Results indicated that fescue tillers were capable of withstanding temperatures of 60°C, but only for short periods (i.e., 16 s or less). At lower temperatures, a distinct interaction between exposure time and temperature was evident, with shorter times at greater temperatures causing similar reductions in growth as long exposure times at low temperatures. Decreased plant vigour, as evidenced by lower tiller numbers, resulted from defoliation coinciding with active regrowth, reinforcing the notion that rough fescue is sensitive to defoliation following heat stress. The greatest detrimental impact occurred with relatively longer periods of deferment (8 wk) until defoliation following exposure to heat treatment. These results have implications for the recovery and conservation of burned rough fescue rangeland.

Key words: Defoliation, *Festuca campestris* Rydb., heat stress, mortality, tillers, water bath

Bogen, A. D., Bork, E. W. et Willms, W. D. 202. **Réaction de la fétuque scabre (*Festuca campestris* Rydb.) au stress thermique**. Can. J. Plant Sci. **82**: 721–729. La fétuque scabre (*Festuca campestris* Rydb.) est une espèce indigène d'importance tant écologique qu'économique dans les prairies du sud-ouest de l'Alberta. Durant la dernière décennie, cette région a souvent été dévastée par le feu. Même si l'on peut déterminer les risques de dommages à long terme dus au feu d'après la sensibilité de la fétuque scabre au stress thermique, comprendre les effets supplémentaires du stress venant de la défoliation faciliterait l'élaboration de stratégies de paissance qui concourront au rétablissement des grands parcours. Les auteurs ont effectué trois études en laboratoire afin d'évaluer la sensibilité de la fétuque scabre au stress thermique, y compris l'impact supplémentaire de la défoliation. Les résultats indiquent que les talles de fétuque résistent à une température de 60°C, mais uniquement pendant une brève période (à savoir, 16 secondes ou moins). À plus basse température, on note une autre interaction entre la durée d'exposition et la température, une période d'exposition plus courte à température élevée entraînant une baisse de croissance similaire à celle d'une longue période d'exposition à faible température. La perte de vigueur des plantes, comme le prouve le nombre réduit de talles, vient de la défoliation, qui coïncide avec la repousse, ce qui confirme la notion que la fétuque scabre est sensible à la défoliation après un stress thermique. Le pire impact survient quand la défoliation est relativement retardée (8 semaines) après l'exposition au stress thermique. Ces résultats ont des implications au niveau du rétablissement et de la conservation des prairies de fétuque scabre ravagées par le feu.

Mots clés: Défoliation, *Festuca campestris* Rydb., stress thermique, mortalité, talles, bain-marie

Within natural landscapes, fire is an important factor in maintaining diverse and productive ecosystems (Vogl 1974). The Fescue Prairie of southwestern Alberta is a fire maintained ecosystem with a historical fire frequency of 5–10 yr (Wright and Bailey 1982). Rough fescue (*Festuca campestris* Rydb.) is the dominant climax species of grasslands throughout this region (Moss and Campbell 1947, Looman 1969).

In grasslands, a uniformly and continuously distributed fuel load of 1000 kg ha^{-1} has been suggested as the minimum required to propagate fire (Bailey 1986). Maximum temperatures and their associated duration near the soil surface during fire vary among grasslands, and are influenced by many factors, including fuel loads, fuel moisture content and weather conditions. Accumulations of loosely packed litter and high winds created by fire generally result in greater air temperatures at the soil-air interface (Wright and Bailey 1982). High wind speeds may also increase the rate of fire spread, thereby increasing fire intensity (Byram 1959; Alexander 1982) but decreasing the duration of elevated temperature experienced by the plant along with subsequent injury (McDaniel et al. 1997; Morgan 1999).

Average temperatures ranging from 102 to 388°C have been reported for fires in the Great Plains (Stinson and Wright 1969), the Aspen Parkland (Bailey and Anderson 1980; Archibold et al. 1998), and other grassland systems (Bentley and Fenner 1958; Britton and Wright 1971). Greater fire temperatures in grasslands have been associated with increased fuel biomass (Stinson and Wright 1969;

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Bailey and Anderson 1980; McDaniel et al. 1997; Archibold et al. 1998; Morgan 1999), provided the fuel is readily available and combustible.

Exposure of plant tissue to fire can be lethal provided a sufficiently high temperature is maintained for a minimum period of time (Hare 1961; Yarwood 1961; Wright 1970). In general, a temperature of 60°C for a fixed period of 10 min has been reported as the lowest temperature required to kill plant tissue (Wright and Bailey 1982). Along with maximum temperature, the duration of elevated temperature may be equally important. Increased exposure times to elevated temperatures are directly correlated with fuel load as well (Morgan 1999; McDaniel et al. 1997), which in turn, influences plant mortality.

Interspecific differences may also exist with respect to fire tolerance. Effects of the time-temperature relationship on coniferous species have been extensively examined (Lorenz 1939; Kyall 1963; Shirley 1963; Nelson 1952), with significant variation among plant species as well as the type of vegetative material exposed to heating. In their examination of coniferous species, Brown and Davis (1973) found that many variables influence plant susceptibility to heat flux, such as the initial temperature of vegetation, size and morphology of the plant portion exposed to heat, growth habit and season of exposure. Fewer studies, however, have been conducted on perennial grasses. Wehner and Watschke (1981) found differences in heat tolerance among introduced grasses. Working with native grasses, Wright (1970) found a range of maximum temperature and exposure time combinations were equally capable of killing the meristems of squirreltail [*Sitanian hystrix* (Nutt.) J.G. Smith] or speargrass (*Stipa* spp.). In an examination of four grass species to lethal temperatures, Jameson (1961) reported that culm mortality varied between 60 and 75°C. Many attributes of plant morphology and phenology therefore influence how a plant responds to elevated temperatures and varied exposure periods.

Although rough fescue historically evolved under the influence of fire (Wright and Bailey 1982), its susceptibility to heat injury may be enhanced by its strongly tufted growth habit and location of meristems and perenating buds above the soil surface (Pavlick and Looman 1984). The potential for injury or mortality of rough fescue plants to burning may also increase if plant litter is allowed to accumulate because fire temperature is correlated to fuel load. Smoldering of fine fuels near or within the plant tussock at the soil surface during fire may extend the time plant tissue is exposed to heat stress.

In the early 1900s, wildfire in the Fescue Prairie was largely suppressed following settlement. More recently, there has been a noticeable increase in the number of wildfires impacting rangelands in the region. For example, from January of 1997 through August of 2000 a minimum of eight wildfires occurred affecting nearly 33 500 ha, leading to alterations in community composition and reductions in forage availability (e.g., Bork et al., in press). By quantifying and understanding temperature-exposure time relationships with injury to rough fescue plants, land managers may be better able to relate this information to management activities that affect rates of fuel accumulation and reduce the risk of mortality or damage to fescue rangeland.

A secondary concern associated with the recovery of heat-stressed rough fescue is the potential for additive stress effects from defoliation. Fescue rangeland provides an economical and practical source of fall and winter grazing for commercial ranches (Willms et al. 1993). It has also been well documented, however, that rough fescue responds negatively to defoliation during the growing season (e.g., Looman 1969; Willms 1988; Willms 1991; Willms and Fraser 1992). The stress imposed by repeated removal of actively growing vegetative tissue causes reduced root mass, smaller bunch size, lower yields and even mortality of rough fescue plants in subsequent years (Johnston 1961; McLean and Wikeem 1985; Willms 1991; Willms and Fraser 1992). It has been postulated that July is a critical period for fescue development and that defoliation at this time may be particularly detrimental, likely due to the carbohydrate demands of inflorescence production or vegetative growth before carbohydrates are replenished (McLean and Wikeem 1985; Willms 1991). During the growing season, defoliation shortly after temperature stress may have an additive negative impact on the long-term survival of fescue plants.

In an attempt to determine the survival and growth response of rough fescue to a range of temperature stresses and associated exposure times, as well as the additive effect of defoliation following temperature stress, we conducted several controlled laboratory studies. Specific objectives were (1) to evaluate the effects of temperature, exposure time, and their interaction, on the survival and leaf extension of rough fescue tillers, and (2) to evaluate the combined effects of temperature and subsequent defoliation on the number of tillers, tiller survival, and phytomass of fescue plants.

MATERIALS AND METHODS

Experimental Approach and Treatments

Four dormant rough fescue plants, 20–25 cm in diameter, were removed to a depth of 15 cm below the soil surface in December 1998 from an ungrazed exclosure on native *Festuca-Danthonia* grassland. The exclosure was located on the Agriculture and Agri-Food Canada (AAFC) research substation (50°11′N; 113°58′W) west of Stavely in southwestern Alberta. Due to the absence of herbivory, all plants were considered to be in excellent condition at the time of removal, and were stored in the dark at –10°C until used several weeks later.

Fescue plants were thawed and individual tillers were separated from the tussock. Tillers were trimmed to a uniform length of 7 cm above the crown (i.e., root-shoot interface) and root mass was removed without exposing the root-culm interface or damaging the sheath. Tillers from all four fescue plants were combined, from which a random sample of 300 tillers was taken to provide 10 replicates for each of 30 treatments within two subsequent experiments.

Many methods have been used to determine the susceptibility of plant tissue to heat stress, which may contribute to the wide variation in plant responses reported (Brown and Davis 1973). For example, Shirley (1936) found that for conifer seedlings, killing temperatures were greater in air than water, and greater in dry than moist air. Immersing plant material in heated water prevents heat dissipation, whereas heated air applied to a restricted portion of the plant material does not (Kyall 1963). Treating tissues in a water bath has been used in other studies (e.g., Shirley 1936; Kyall 1963; Wehner and Watschke 1981) and has the added benefit of ensuring rapid, uniform transfer of heat to individual tillers. Furthermore, moisture is generally available from thermal degradation and combustion of fuel because hydrogen is mostly released as water (Pyne 1996). Consequently, moist heat may simulate fire conditions more closely than dry heat (Martin et al. 1975), while heated air without combustion would likely over-estimate lethal temperatures for plant tissue during fire.

In this investigation, temperatures were varied using a hot water bath, with treated tillers submersed for varying durations. Tiller heating (e.g., heat flux) therefore provided a controlled measure of the susceptibility of tillers to heat stress, which is assumed to reflect, at least in part, the effects of exposure to fire. All temperature trials were conducted in the laboratory using a hot plate to heat a 1-L beaker of distilled water. Water was continuously stirred and monitored throughout each experiment to maintain a constant temperature. Detailed methods can be found in Bogen (2001).

Initial Temperature and Exposure Time Experiment

In the first experiment, hot water treatments were applied to 10 randomly selected rough fescue tillers at temperatures of 23, 40, 50, and 60°C, for a duration of either 1, 2, 5, or 10-minutes (N = 160). The 23°C treatment provided a non-lethal temperature treatment and was applied to account for any effect submersion in water alone may have had on tillers. An additional control group of 10 tillers not subjected to a water bath was used to ensure no changes occurred in plants that would cause tillers to respond differently, even though plants were kept in a state of dormancy in the interim.

Followup Temperature and Exposure Time Experiment

Based on observations in the first experiment, another trial was conducted using fescue tillers (N = 120), this time using a narrower range of temperatures (50, 55, and 60°C) and shorter exposure times (4, 8, 16, and 32 s), closer to the critical conditions for rough fescue survival and growth. An untreated control of 10 tillers was again included for comparison.

Plant Response to Heat Stress and Defoliation

A third experiment was conducted to assess the biological impact of a combination of heat stress from a known temperature and subsequent defoliation on rough fescue plants. In March of 2000, 20 dormant fescue plants, each with uniform tiller distribution and 20–25 cm diameter, were removed with the sod intact from native Fescue Prairie at the AAFC research substation near Stavely. In the previous year (1999), only wild elk grazed the field during summer, with cattle cow/calf pairs grazing from 15 September to 15 October at moderate stocking rates. Prior to 1999, the pasture had not been grazed by cattle for 3 yr and was considered to be in excellent range condition.

Plants extracted in March were stored at –5°C to maintain dormancy until the third experiment was initiated. Treatments were applied over a 3-d period beginning 6 April 2000. In preparation, all plants were trimmed to a stubble height of 3 cm above the mulch layer and roots trimmed to 6 cm. Plants were randomly allocated to two groups of 10 plants each and assigned to heat treatments of either 5 min at 40°C (known low heat stress) or 5 min at 60°C (known high heat stress). Each plant was subsequently cut into quarters and randomly assigned to one of four defoliation treatments. The number of tillers on each quarter was counted and the plant material stored in the dark at 10°C until treatment 2 d later. During this time, approximately 1 cm of vegetative growth occurred.

Treatments consisted of submersing each individual quarter upside down to 1 cm below the crown using the same water bath procedure employed for the tiller studies. Heated water in the bath was stirred and monitored to ensure uniform heating. Following heat treatment, individual plant quarters were potted in soil and grown out in a greenhouse at 20 ± 3°C for 14 wk. Plant quarters were then randomly assigned one of four defoliation treatments to represent varying periods of deferment after heating prior to defoliation (2, 4, and 8 wk, and a control). All defoliation treatments were blocked by plant to control for genetic influences. The control remained undefoliated until the end of the 14-wk monitoring period. All defoliation treatments were applied 2 cm above the height of the original stubble (3 cm), leaving approximately 5 cm of culm above the soil surface.

Measurements

Following heat treatment, fescue tillers from the first two experiments were labeled by treatment and replicate to track individual tiller responses. Tillers were kept moist and in the dark on a vermiculite bed in a greenhouse at 20 ± 3°C for the duration of monitoring. Leaf elongation (mm) of fescue tillers was measured 72 h following treatment. Measurement was discontinued at this point as tiller growth had generally slowed and factors other than initial heat treatment could have begun to determine growth, such as inherent variability in tiller size and vigour (e.g., stored carbohydrates or the presence of disease). Tillers that exhibited no growth during this period were considered dead.

In the final experiment, measurements of tiller number, average plant height and phytomass removed were made at each defoliation period (e.g., 2, 4, and 8 wk) on each plant quarter. At the end of the 14-wk monitoring period, final tiller number, height, and phytomass was determined for all plants, including the control.

Analysis

Measurements of leaf elongation per tiller (first two experiments) and plant phytomass (third experiment) at the end of the monitoring period were normalized using a square root transformation to meet the conditions of normality and homoscedasticity based on the Shapiro-Wilk statistic. In the

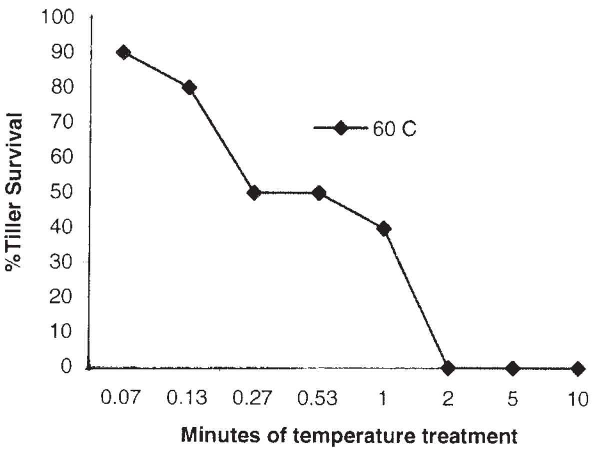

Fig. 1. Percent survival of rough fescue tillers following various exposure times at 60°C.

tiller heating experiments, ANOVA in Proc GLM (Steel et al. 1997) was used to analyze the leaf elongation and fescue tiller survival data for temperature and time of exposure, as well as their interactions. Where significant effects were found, polynomial contrasts (Proc GLM; Steel et al. 1997) were used to determine the nature and significance of any linear, quadratic or cubic trends.

In the plant heating and defoliation experiment, plant height and phytomass for the potted rough fescue plant quarters at the end of the monitoring period were analyzed using ANOVA (Proc GLM; Steel et al. 1997). ANCOVA (Proc GLM; Steel et al. 1997) was used to analyze tiller counts among plant quarters at the end of the monitoring period using pre-treatment tiller numbers as a covariate. For significant effects, mean comparisons were performed on the LS-means using Tukey's procedure, with differences considered significant at $P < 0.05$.

RESULTS AND DISCUSSION

Tiller Mortality in Response to Temperature and Exposure Time

In the first two experiments, tiller death at temperatures of 55°C and lower in both trials was limited, with 0, 3, 9, and 10% of all tillers undergoing mortality at temperatures of 23, 40, 50, and 55°C, respectively. Furthermore, the limited mortality evident had no pattern with respect to exposure time (data not shown). At 60°C, however, mortality increased markedly, particularly with longer exposure, reaching 100% at 2 min (Fig. 1). These findings suggest rough fescue is less tolerant to heat stress than other perennial cool season (e.g., speargrass) and warm season (e.g., sideoats grama, blue grama, galleta, and squirreltail) grasses (Jameson 1961; Wright 1970). Wright (1970) found that a duration of 55 min was required to kill speargrass tillers at 60°C, although the required exposure time to cause mortality dropped to 3.4 min when the temperature was raised an additional 10°C. Decreased heat stress tolerance in rough fescue may be due to its historical adaptation to relatively cool, mesic conditions compared to the warmer, more arid shortgrass prairie and semi-desert communities within which the other species are found.

Tiller Leaf Growth in Response to Temperature and Exposure Time

Most studies determine the threshold at which temperature-time relationships cause mortality in plant tissue. In this study, tiller responses to temperature-time combinations were unique because tiller growth was examined as well. Analysis indicated tiller growth varied linearly and quadratically with temperature in each experiment (Tables 1 and 2). Additionally, the main effect of exposure time was not significant in either trial, but did interact significantly with temperature to affect tiller growth (Tables 1 and 2). These results are depicted in Figs. 2 and 3 for the first and second experiments, respectively. An initial point at time-zero was added to Fig. 2 for comparison, but not included in the statistical trend analysis. This treatment was comprised of tillers not subject to water bath treatment.

Overall, increasing temperatures tended to reduce tiller growth, although growth initially increased with extended exposure times at a moderate heat stress of 40°C (tiller experiment 1) and for relatively short times at 55°C (tiller experiment 2), before declining at greater temperatures (data not shown). Within the 50 and 60°C temperature treatments in the first experiment, significant linear trends within exposure time were found (Table 1), with tiller growth responding negatively to increasing exposure time. As exposure time increased at temperatures of 23 and 40°C, there was a positive, but somewhat weak ($0.05 < r < 0.10$) correlation with tiller growth (Fig. 2). One additional quadratic effect was observed at 50°C, as there was an initial stimulatory effect of temperature on tiller growth at an exposure time of 1 min before growth declined with longer exposure (Table 1; Fig. 2). The negative trend on tiller growth at 60°C in the first experiment (Table 1) may be inconsequential, as it coincides with severe tiller mortality at exposure times greater than 1 min (Fig. 1).

The consistent increase in tiller growth with increased exposure time at low temperatures or short exposure at high temperatures, may be due to several factors. Increased exposure to the waterbath itself may further hydrate the tiller, accelerating the potential for subsequent growth. However, this is unlikely, particularly given that all tillers were kept moist during the monitoring period. A more likely explanation is that the increase in temperature within the tiller meristematic region increased the rate of necessary biochemical reactions for facilitating vegetative growth. For example, the temperature increase may have enhanced carbohydrate mobilization or metabolism within the meristem, leading to increased growth. Although no studies specifically reporting these kinds of carbohydrate changes have been done for native grasses, including rough fescue, there are indications that Kentucky bluegrass (*Poa pratensis* L.), growing under controlled conditions and exposed to constant moderate temperature increases (i.e., 26°C), may enhance carbohydrate use and subsequent shoot growth

Table 1. Analysis of linear, quadratic and cubic trends within the tiller growth^z data for a series of contrasts in the first water bath experiment using rough fescue tillers

Contrast	df	Mean square	*F* value
Lin time	1	0.068	0.08
Quad time	1	3.071	3.73
Cubic time	1	0.04	0.05
Lin temp	1	80.013	97.18**
Quad temp	1	104.517	126.95**
Cubic temp	1	0.777	0.94
Lin time × Temp	3	4.89	5.94**
Quad time × Temp	3	2.81	3.41*
Lin in 23°C	1	3.182	3.87
Lin in 40°C	1	3.141	3.81
Lin in 50°C	1	5.155	6.26*
Lin in 60°C	1	3.26	3.96*
Quad in 23°C	1	0.015	0.02
Quad in 40°C	1	0.704	0.85
Quad in 50°C	1	8.246	10.02**
Quad in 60°C	1	2.537	3.08

[z] Analysis performed on square root transformed data.

*, ** Indicates observed *F*-ratio is significant at $P < 0.05$ and $P < 0.01$, respectively.

Table 2. Analysis of linear, quadratic and cubic trends within the tiller growth^z data for a series of contrasts in the second water bath experiment using rough fescue tillers

Contrast	df	Mean square	*F* value
Lin time	1	13.0883	5.18*
Quad time	1	0.0628	0.02
Cubic time	1	8.4570	3.35
Lin temp	1	19.3612	7.67**
Quad temp	1	12.0477	4.77*
Lin time × Temp	2	10.593	4.19*
Lin in 50°C	1	4.2248	1.67
Lin in 55°C	1	1.3206	0.52
Lin in 60°C	1	28.7288	11.38**

[z] Analysis performed on square root transformed data.

*, ** Indicates observed F-ratio is significant at $P < 0.05$ and $P < 0.01$, respectively.

(Aldous and Kaufmann 1979). Notably, the temperature found to be stimulatory in the aforementioned study is considerably lower than the temperature documented here, although there are differences in both the nature of the heat treatments and their duration. In any case, the potential for enhanced growth under short-term moderate temperatures is of importance and merits further investigation, as it indicates a low intensity burn could stimulate tiller growth.

Although the second experiment was conducted using a narrower range of exposure times and temperatures, growth again varied linearly with exposure time (Table 2). This response, however, was largely driven by the strength of the negative linear trend associated with an increasing duration of heat exposure at 60°C (Fig. 3), as there was no significant trend for temperature within the 50 and 55°C treatments (Table 2). These results indicate the specific exposure threshold for injury to tillers that results in decreased growth appeared to occur between 16 and 32 s of exposure at 60°C (Fig. 3). Alternatively, rough fescue tillers appear capable of withstanding 60°C for short time periods (e.g., 16 s or less) without experiencing reduced growth (Fig. 3). This implies that during fire events, weather and existing fuel conditions resulting in greater and more sustained temperatures near or above 60°C within the plant crown, increase the risk of harming foothills rough fescue plants. As weather conditions can only be predicted for prescribed burns and are variable during wildfire events, the only option for preventing these temperatures during fire is likely the manipulation of fuel.

Plant Tiller Responses to Temperature Stress and Deferred Defoliation

In the third experiment, plant mortality was minimal following the heat and defoliation treatments. All plants survived exposure to 40°C and subsequent defoliation. At 60°C, all quarters from one plant died within 4 wk, suggesting this plant may have been in a weakened state prior to experimentation or genetically more susceptible to heat stress. One other plant quarter died following defoliation 8 wk after the 60°C treatment.

Temperature significantly affected the final plant tiller number and average height of tillers per plant (Table 3). Increasing the temperature of heated water from 40 to 60°C reduced the number of tillers and plant height (Table 3), corroborating the earlier response observed in individual tillers. Relative to pretreatment tiller counts, overall tiller numbers increased at 40°C (+44%) but declined at 60°C (–65%) over the duration of monitoring (Table 4). The favorable tiller development at the lower temperature may partly be a physiological response to the factors discussed earlier affecting individual tillers, such as increased carbohydrate mobilization. However, the lack of a true control (e.g., plants not subject to any temperature treatment) precludes confirmation of this.

Tillers tended to remain loosely grouped within the plant following heat treatment and did not form tightly packed bunches, as has been observed within rough fescue plants burned in the field (Bogen 2001). The laboratory procedures used here ensured uniform heating, resulting in more consistent heat treatment among tillers. In a parallel field study (Bogen 2001), tillers near the center and on the windward side of burned plants received some protection from heat as smoldering preferentially occurred around the perimeter of the leeward side of the tussock after passage of the fire front.

Timing of defoliation also affected tiller numbers per plant, but not plant height (Table 3). As the recovery time lengthened following heat treatment prior to defoliation, final tiller numbers per plant were reduced (Table 3). Only plants undefoliated during the entire 14-wk monitoring period experienced an overall increase in tiller numbers relative to the pre-treatment tiller data (Table 4).

Contrary to expectations, no temperature by time of defoliation treatment interactions were evident on any morphological parameters, suggesting that defoliation imposed no additive stress on the 60°C heat treatment. That is, tiller numbers stayed relatively constant during the monitoring period after an initial increase in tillers for plants subject to

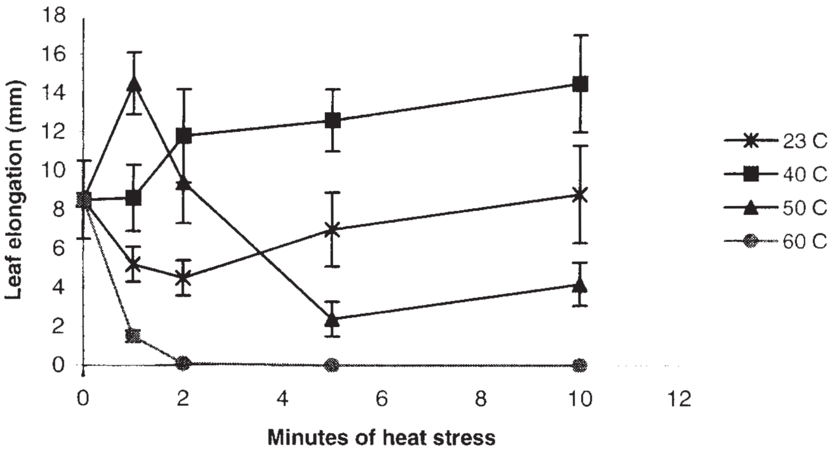

Fig. 2. Mean growth (untransformed data) of rough fescue tillers (± SE) following exposure to various temperature treatments in the first water bath experiment.

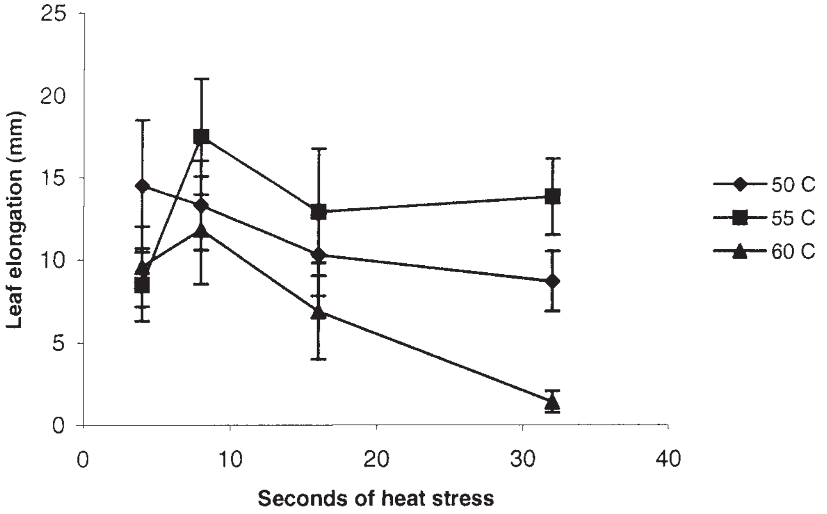

Fig. 3. Mean growth (untransformed data) of rough fescue tillers (± SE) following exposure to various temperature treatments in the second water bath experiment.

40°C and a decline in tillers for plants subject to 60°C. Detailed examination of the data, however, indicated some differences in tiller development patterns were visible among the temperature × defoliation treatments (Table 4), particularly in the time period immediately following defoliation within each treatment. For example, the decline in tillers within plants defoliated 8 wk after heat treatment clearly coincided with the post-defoliation interval, and was evident in both temperature treatments (Table 4).

The mechanism for the increased susceptibility of plants to defoliation at 8 wk deferment rather than 2 or 4 wk is unknown, but may be linked to the amount of regrowth prior to defoliation. Defoliation at 2, 4, and 8 wk removed an average of 0.19, 0.34, and 1.26 g of phytomass per plant. Thus, later defoliation times (e.g., 8 wk) removed more phytomass, potentially resulting in greater physiological stress and subsequent mortality to rough fescue tillers. Carbohydrate reserves may also become greatly reduced as grasses near the completion of vegetative growth prior to seed formation (Smith 1972). Although it is possible that the reduced tiller counts on plants defoliated at 8 wk was due to their shorter recovery period prior to final monitoring, this was unlikely given that 6 wk elapsed between defoliation and monitoring to facilitate recovery, as well as the favorable growing conditions present in the greenhouse. Additionally, there was no visual indication that these plants were beginning to initiate new tillers at the end of the monitoring period. Notably, the negative impacts of defoliation on plants in the greenhouse at 8 wk deferment corresponded to the findings of an associated field study (Bogen 2001), where plants defoliated 12 rather than 4 wk following wildfire experienced a greater 2-yr reduction in tillers. Plant growth is generally accelerated in a greenhouse environment due to ideal growing conditions and as a result, the 8 wk plant quarters may have been in a similar phenological stage as those in the field.

Plant Phytomass Responses to Temperature Stress and Deferred Defoliation

Temperature and timing of defoliation following heat treatment both significantly affected the phytomass harvested from rough fescue plants at the end of the monitoring peri-

Table 3. Observed significance levels for rough fescue mean plant tiller numbers, height, and final and accumulated phytomass, along with mean tiller phytomass, in response to different temperatures and defoliation deferment intervals, as measured at the end of the 14-wk monitoring period

Treatment		Tillers (number per plant)	Height (cm)	Final plant phytomass (g)^{z}	Accumulated plant phytomass (g)	Accumulated tiller phytomass (mg)
Temperature	*F* value	43.4**	11.4**	22.7**	31.3**	0.49
	40°C	49	25	1.85	2.47	42.9
	60°C	17	18	0.80	1.08	47.2
	SE	4	1	0.16	0.18	4.4
Length of deferment	*F* value^{y}	4.29**	1.91	9.51**	0.69	2.50
	2 weeks	33*ab*	24	1.44*ab*	1.63	55.0
	4 weeks	31*ab*	22	1.20*bc*	1.54	40.9
	8 weeks	22*b*	18	0.51*c*	1.77	33.3
	14 weeks	47*a*	24	2.15*a*	2.15	50.9
	SE	6	2	0.22	0.25	6.2
Temp. × length of deferment	*F* value	0.79	0.05	1.40	0.31	0.11

^{z}Analysis performed on square root transformed data with original data presented for clarity.
*,** Indicates observed *F*-ratio is significant at $P < 0.05$ and $P < 0.01$, respectively.
a–c Within a treatment and variable, means followed by different letters differ significantly ($P < 0.05$).

Table 4. Pre-treatment and final tiller numbers of rough fescue plants ($N = 80$) subject to 40 or 60°C temperature treatments and defoliated at 2, 4, 8, or 14 (final count) wk, along with changes in tiller numbers between consecutive measurement periods. Bolded values coincide with periods immediately following defoliation within a temperature × deferment combination

			Change in tiller numbers per plant during each time interval				
Temperature	Deferment length	Pre-treatment tiller count	Pre-treat to 2 wk	2 to 4 wk	4 to 8 wk	8 to 14 wk	Final tiller count/plant
40°C	2 wk	32.8	+7.2	**–3.3**	+3.2	+12.4	52.3
	4 wk	33.3	+9.6	–1.0	**+0.3**	–1.6	40.6
	8 wk	38.1	+10.2	–1.4	+4.8	**–18.0**	33.7
	14 wk	33.3	+9.6	–1.9	+4.9	+23.4	69.3
60°C	2 wk	46.7	–29.1	**–6.6**	+0.8	+0.9	12.7
	4 wk	53.8	–29.0	–5.2	**–3.2**	+5.5	21.9
	8 wk	51.9	–31.2	–3.7	+0.1	**–7.3**	9.8
	14 wk	44.3	–21.5	–2.8	+1.9	+2.3	24.2

od (Table 3). In contrast, total accumulated phytomass of fescue plants was significantly affected by temperature, but not the timing of defoliation following heat treatment (Table 3). Increased heat treatment from 40 to 60°C decreased final standing crop and accumulated phytomass by more than 50% (Table 3). As plant height was not significantly affected by defoliation after varying rest periods, changes in tiller number likely accounted for the differences in plant phytomass. A visible, but non-significant ($P > 0.05$), decline in accumulated tiller phytomass was detected in association with longer rest periods up to 8 wk between heat stress and defoliation (Table 3).

Although accumulated phytomass was not affected by the defoliation regimes examined in this study, morphological changes in plant tiller number may be indicative of changes in plant vigour and phytomass production in future years. Furthermore, it should be noted that this study examined a single defoliation treatment only. Repeated defoliation is more likely to negatively impact long-term yields. In a study of repeated defoliation on rough fescue, Willms (1991) found a moderate cutting frequency of two or four defoliations during the growing season was detrimental to plant phytomass, but differences were first observed in subsequent years, suggesting that longer times may be needed to produce these changes. Our findings also indicate that defoliation had the greatest impact on tiller number when plants were given an opportunity to regrow photosynthetic material prior to defoliation, which may translate into future declines in growth.

SUMMARY

The response of rough fescue to temperature has been studied within the context of the normal range of climatic conditions experienced by the plant in the absence of fire (Willms 1988; King et al. 1995). In contrast, the response of fescue following exposure to intense heat stress is relatively unknown. The results of this research indicate that a temperature of 60°C within growing points appears to be the threshold for causing reductions in growth, and possibly mortality, of rough fescue. Tillers of this species appear capable of withstanding temperatures of 60°C for a very short time (e.g., 16 s or less), but undergo a reduction in growth at exposure times of 32 s or more and mortality at 2 min or greater. The duration of elevated temperature is also an important determinant of injury to fescue, as a temperature of 50°C maintained for 5 min or greater produced a similar response to higher temperatures for shorter times. Rough fescue may also experience some benefit from elevated temperatures. Stimulation of growth was observed at higher temperatures (50°C) for short exposure times (e.g., 1 min), and at more moderate temperatures (40°C) for longer exposure times.

Results of the study also indicate that rough fescue tiller survival and growth may be reduced by defoliation. In particular, defoliation 8 wk after plants have initiated regrowth appears to have the most detrimental effect. Decreased plant vigour, as evidenced by lower tiller numbers, reinforces the notion that rough fescue is sensitive to defoliation, particularly during a period of active regrowth.

Understanding the role of temperature-exposure time relationships on the injury or mortality of dormant tillers and plants is important, as this information can be used to interpret fire effects on fescue plants. Future research should be conducted to determine at what point fuel loads and their distribution in rough fescue grassland become capable of causing sustained temperatures in excess of the thresholds identified here. If the goal of land managers is to maintain or enhance this species within native rangelands, then actions may be taken to avoid conditions that will cause the duration of elevated temperatures to be above that of the upper threshold documented here. These actions may include the manipulation of fuel loads and fuel properties through prescribed grazing, or the periodic use of prescribed fire to limit fuel accumulation.

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