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Ecological Research

ISSN 0912-3814

Volume 30

Number 1

Ecol Res (2015) 30:67-74

DOI 10.1007/s11284-014-1210-x



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Received: 6 July 2014 / Accepted: 22 October 2014 / Published online: 6 November 2014
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Abstract Post-fire recovery of perennial plants depends on their capacity to regrow from surviving meristems. Plants are adapted to a particular fire regime, which can be altered by human activities and climatic change. Therefore, predicting the impact of changing fire regimes on post-fire vegetation recovery has become a major ecological concern. We studied the effects of fire temperature on survival and growth of the dominant tussock grasses *Festuca pallescens* and *Pappostipa speciosa* for two post-fire growing seasons in NW Patagonian grasslands. Using a portable propane burner, we applied two fire temperature treatments to individual plants: 200–500 °C (low temperature) and 500–900 °C (high temperature). Plant mortality was higher in *F. pallescens* than in *P. speciosa*, possibly due to morphological differences. Fire damaged active meristems in both species, which delayed emergence of new tillers. This in turn affected leaf length of tillers, which was lower in burned plants during the first growing season. Despite this, growth rate was higher in burned plants once they regrow only during the first growing season. In summer, post-fire hot and dry conditions affected *F. pallescens* survival. Although fire temperature affected negatively *F. pallescens* survival, both tussock grasses recovered quickly after the experimental burns. This response could favour their persistence and dominance in the community. Our study increases understanding of post-fire responses in grasslands and will provide important rangeland management information for grasslands in Patagonia.

Keywords Climate change · Fire intensity · Fire regime · Grassland · Tussock grasses

Introduction

Wildfires are one of the major drivers that structure the natural dynamics of grasslands (Whelan 1995; Bond and van Wilgen 1996). Fire regime is composed of several parameters, including intensity, severity, frequency and seasonality (Pausas and Keeley 2009; Keeley et al. 2011, 2012), and can be altered by human activities (e.g., land use) and climatic change (e.g., modifications in precipitation and temperature pattern). Vegetation is adapted to a particular fire regime (Pausas and Keeley 2009; Pausas Pausas 2010; Keeley et al. 2011). Therefore, predicting the impact of changing fire regimes on vegetation patterns has become a major ecological concern, particularly given that grasslands are one of the most susceptible ecosystems to changes in land use and are threatened by climate change (Sala et al. 2000; Ni 2003; Shinoda et al. 2010).

Fire intensity, one aspect of fire regime, is measured by energy released during combustion (Keeley 2009) and includes two components: peak temperature and residence time. Variation in these components among fires can determine the survival and post-fire resprouting potential of plant species (Whelan 1995; Fidelis et al. 2010). Temperatures in grassland fires range from 95 to 970 °C, although the intermediate values are the most common (Wright and Bailey 1982; Robberecht and Defossé 1995; Peláez et al. 2001; Gibson 2009). Because of their fine fuels, grassland fires also burn fast and, because soil provides good insulation, temperatures in the first two centimeters of soil depth are usually below 100 °C (Christensen 1985; Ramsay and Oxley 1996; Choczynska and Johnson 2009; Franzese and Ghermandi 2012). Experimental burns with temperature manipulations could help to improve the mechanistic understanding of the role of fire intensity on plant vegetation.

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Plant morphological traits are closely related with fire resistance or susceptibility. Post-fire regrowth generally occurs from below-ground buds located in rhizomes, gemmiferous roots, lignotubers and other underground meristematic structures (Canadell et al. 1991; Lloret and Vilá 1997; Montes et al. 2004). Plant meristems that are buried or protected by structures such as thick bark are more likely to survive high fire temperatures. In tussock grasses, meristems can be found at different depths below soil surface within or below litter, or may be protected by closely packed leaf sheaths (Miller and Findley 2001; Gibson 2009).

The differential susceptibility of perennial grasses to fire is linked to location of meristematic tissues, pre-fire plant condition (e.g. carbohydrate reserves and phenological stage) and plant characteristics (e.g., accumulated fine fuel) (Malanson and O'Leary 1985; Whelan 1995; Cruz and Moreno 2001). In the sagebrush region of southern Idaho, *Sitanion hystrix* was more tolerant to fire damage than *Stipa comata* (Wright 1970). In the grasslands of central semi-arid Argentina, *Stipa gynerioides* regrew more slowly after fire than *Piptochaestium napostaense* and *S. tenuis* (Peláez et al. 2003). In Idaho, *Festuca idahoensis* was less sensitive to fire than *Agropyron spicatum* (Robberecht and Defossé 1995).

Northwestern Patagonian semi-arid grasslands are the most productive of the region and are used for stockbreeding and forestry (Ares et al. 1990; Mermoz et al. 2009). Structure and composition of communities in these systems are strongly influenced by recurrent fires (Oddi 2013). Fires are generally caused by lightning and usually occur during the dry season (summer), although there are some fires in spring and autumn. It is likely that fire frequency will change due to the impact of human activities and increases in frequency and amplitude of El Niño Southern Oscillation (ENSO) as a consequence of climate change (Timmermann et al. 1999). In NW Patagonia, El Niño events are associated with high precipitation in winter and spring, and La Niña events with the opposite pattern (Daniels and Veblen 2000; Suárez et al. 2004). El Niño patterns increase biomass accumulation; subsequent La Niña events dry the vegetation, increasing flammability and thus the fire intensity. This ENSO sequence has occurred five times between 1933 and 1999 (Ghermandi et al. 2010). As a consequence of several changes, fire regime may be altered with potentially novel effects on post-fire regrowth of dominant grass species, which has important implications for rangeland management.

Northwestern Patagonian grasslands are dominated by two native tussock grasses: *Festuca pallescens* and *Pappostipa speciosa*. *Festuca pallescens* is an important forage species preferred by livestock and *P. speciosa* has low forage value (Sbriller et al. 1982; Defossé et al. 1997). Both species have shown high survival and rapid regrowth after fires (Ghermandi et al. 2004; Gittins et al. 2011), although *F. pallescens* had greater mortality (Gittins et al. 2011) which could be related to species morphology such as compact canopy and lower dry/wet

biomass ratio (Gonzalez et al. 2010). However, these observations were based on inferences from wildfires with unknown fire temperatures, which prevent the mechanistic understanding between the fire intensity (temperature and duration) and plant morphological traits, and their survival. Thus, the objective of this study was to determine the effect of different fire temperatures on the survival and regrowth of *P. speciosa* and *F. pallescens* for 2 years after experimental burns. We hypothesized that fire temperature differentially affects the post-fire survival and regrowth of *F. pallescens* and *P. speciosa*. Based on observations from previous studies, we expect that *P. speciosa* would have greater survival and regrowth at higher temperatures than *F. pallescens*. This research could increase understanding of post-fire responses in other grasslands and will provide important rangeland management information for grasslands in Patagonia.

Methods

Study site

The study area is located in northwestern Patagonia at the San Ramón Ranch (41°03'19"S and 71°01'50"W), 30 km east of Bariloche City, Argentina. The climate is temperate with a Mediterranean rainfall regime (60 % of precipitation concentrated in autumn and winter) (Soriano et al. 1983). Mean annual precipitation is 582 mm and mean annual temperature is 9 °C. After the experimental burns, the first growing season (2008 spring–2009 summer) was dry (spring: 135.7 mm; summer: 23.6 mm) and warm (spring: 10.7 °C; summer: 15.6 °C) compared with a mean historical value of accumulated precipitation (1959–2010: spring: 123.3 ± 48.2 mm; summer: 54.9 ± 28.3) and temperature (1970–2010: spring 9.4 ± 0.8 °C; summer: 13.60 ± 0.8 mm). The second growing season (2009 spring–2010 summer) was wet (spring: 314.9 mm; summer: 69.5 mm) and the spring was cold (7.8 °C) (San Ramón ranch Meteorological Station 1929–2013, unpublished data). Topography is undulating and includes rocky outcrops of volcanic origin (Anchorena et al. 1993). Dominant soils are Haploxeroles of sandy texture and moderate organic matter (Gaitán et al. 2004).

The study area is a grassland dominated by the tussock grasses *Pappostipa speciosa* and *Festuca pallescens*, and scattered shrubs such as *Acaena splendens*, *Senecio bracteolatus*, and *Mulinum spinosum*. The gaps between tussock grasses and shrubs are occupied by annual grasses (e.g., *Vulpia australis*, *Apera interrupta*), annual herbs (e.g., *Draba verna*, Brassicaceae; *Holosteum umbellatum*, Caryophyllaceae; *Plagybohtrys verrucosus*, Boraginaceae; *Microsteris gracilis*, Polemoniaceae) and perennial herbs (e.g., *Rumex acetosella*, Polygonaceae; *Cerastium arvense*, Caryophyllaceae) (Ghermandi and Gonzalez 2009; Gonzalez et al. 2010).

Fire application on individual plants

We randomly selected 24 individuals of *F. pallescens* and *P. speciosa* within a 1-ha site fenced for livestock exclusion. The individuals were randomly assigned to three treatments: low fire temperature (200–500 °C), high fire temperature (500–900 °C) and no fire (unburned plants). These temperatures were chosen according to those temperatures registered in semi-arid grasslands (Wright and Bailey 1982) and reached during controlled burn in the same grasslands (Franzese unpublished data). Prior to application of fire treatments, aboveground biomass of each plant was cut down to a height of 10 cm to simulate a moderate grazing event. This defoliation was done because most of grasslands in the region are grazed at a moderate stocking rate of sheep and cattle.

On May 2008, we burned plants with a portable propane burner adapted from Wright and Klemmedson (1965) and Peláez et al. (2001) (Fig. 1). Three flame jets were oriented toward the individual, which was located in the centre of the portable propane burner. The gas was regulated by a valve in the carafe and fire temperature was monitored using one type K thermocouple connected to a datalogger, and located in the centre of the plant without touching the soil. We applied fire until the temperature within the range of each treatment was reached in the crown zone of the tussocks. Temperatures were recorded until they dropped below 60 °C. Finally, we placed wire closures around each burned and unburned plant to avoid herbivory by hares (*Lepus europaeus*) and native rodents.

Plant monitoring related to fire treatments

We recorded regrowth in each plant and calculated percent of mortality during two growing seasons (September–March 2008–2010). We considered the absence of regrowth as an indicator of plant mortality.

To measure growth, we counted the number of vegetative tillers in a fixed 10 cm² subplot of each plant and measured the basal diameter in two perpendicular (N–S and W–E) directions of each plant. Then, we estimated total number of tillers per plant by extrapolating from the subplot to entire basal area. These measurements were recorded in September, December and March (2008–2010). We also measured the longest leaf of six tillers (which were identified with different wire colours) on each plant from September 2008 to March 2010 (Peláez et al. 2003, 2009). These values were averaged and one value of mean maximum leaf length per plant was obtained.

We calculated the relative growth rate of leaves using the equation of Hilbert et al. (1981): $RGR = (\ln X_2 - \ln X_1) / (t_2 - t_1)$, where X is the length of the longest leaf between the time t_1 and t_2 .

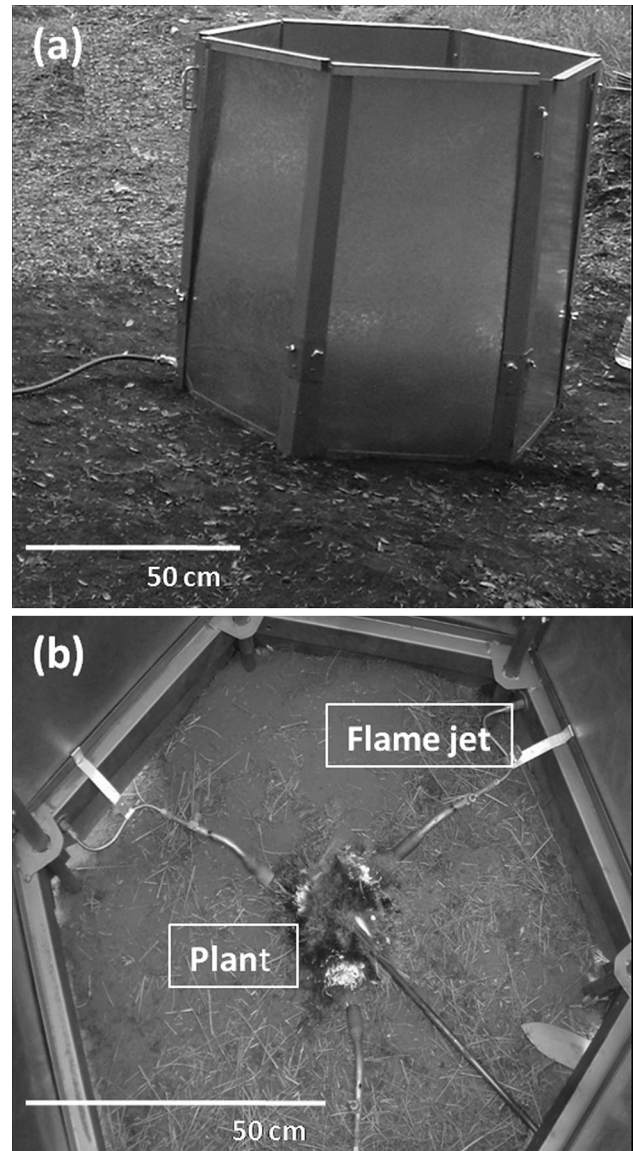


Fig. 1 Portable propane burner for plant burns (a). Inside view of the portable propane burner with three flame jets oriented toward the plant located in the centre (b)

Statistical analyses

The mean number of tillers, maximum leaf length, and relative growth rates of leaves per plant were analyzed among treatments (low fire temperature, high fire temperature and unburned) in each date sample using a one-way ANOVA following a complete randomized design. When statistical differences were found, we used a Tukey post hoc test to compare means of treatments. Non-parametric Kruskal–Wallis test (H) was used when data did not meet the normality and homocedasticity assumptions.

Results

Fire treatments characteristics

Mean maximum temperatures registered in crown zone of *Festuca pallescens* plants during the burns were 369 ± 92 °C in low fire temperature treatment (LT), and 669 ± 89 °C in high fire temperature (HT) (Fig. 2a). In *Pappostipa speciosa*, mean maximum temperatures registered in LT was 381 ± 64 °C and in HT treatment was 615 ± 95 °C (Fig. 2b). In both species and treatments, maximum temperatures were quickly reached (between 10 and 40 s) although *P. speciosa* plants reached maximum temperature more slowly than *F. pallescens* plants (Fig. 2a, b). Exposure time of plants of *F. pallescens* to high fire temperatures was twice than plants of *P. speciosa* (Fig. 2a, b).

Plant survival

Burn treatments delayed the regrowth in both tussock grasses. In September 2008 (4 months after burns), all unburned plants (UNB) had resprouted (Fig. 3a). In *F. pallescens*, we detected mortality due to fire in high temperature treatment (Fig. 3a). Some *F. pallescens* plants resprouted and then died during the first and second growing season in all treatments (Fig. 3a, b). In *P. speciosa*, all burned and unburned plants survived. In the HT treatment, 16.6 % of the *P. speciosa* plants were damaged by fossorial rodents.

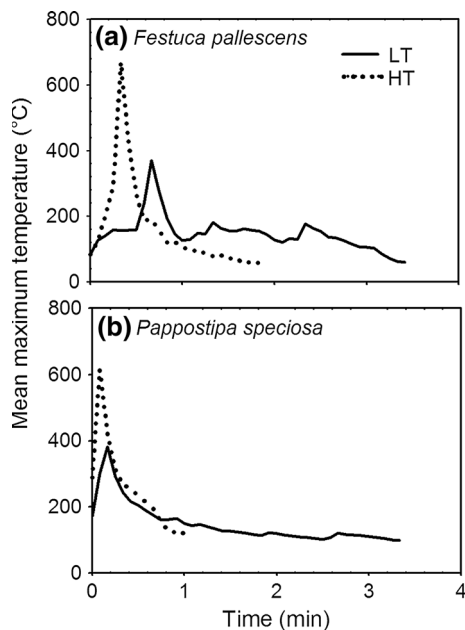


Fig. 2 Time-mean maximum temperature curves in the crowns of *Festuca pallescens* (a) and *Pappostipa speciosa* (b) plants during low and high fire temperature treatments in May 2008. LT low temperature, HT high temperature

Post-burn growth

In September 2008, the number of tillers per plant in both grasses was significantly higher in unburned than in burned plants (*F. pallescens*: $F_{2,22} = 45.06$, $P < 0.001$; *P. speciosa*: $H = 16.99$, $P < 0.001$) (Fig. 4a, b). In early autumn (March 2009 and 2010) plants of *F. pallescens* in LT treatment produced more tillers than plants in HT treatment (March 2009: $F_{2,18} = 4.43$, $P = 0.027$; March 2010: $F_{2,16} = 6.11$, $P = 0.01$) (Fig. 4a). The number of tillers per plant in *P. speciosa* was not significantly different among treatments within sampling dates (March 2009: $F_{2,19} = 0.51$, $P = 0.60$; March 2010: $F_{2,18} = 1.54$, $P = 0.241$) (Fig. 4b).

Fire treatments reduced ($P < 0.001$) growth of tillers (measured as maximum leaf length) of *F. pallescens* plants in the first post-burn growing season. In September and October 2008, maximum leaf length of tillers of plants exposed to either fire temperature treatment was lower than in unburned plants. Tiller leaf length increased until December, but remained lower than in unburned plants (Fig. 5a). Except in October and December 2008 (first growing post-fire season), the mean maximum leaf length in burned plants of *P. speciosa* was

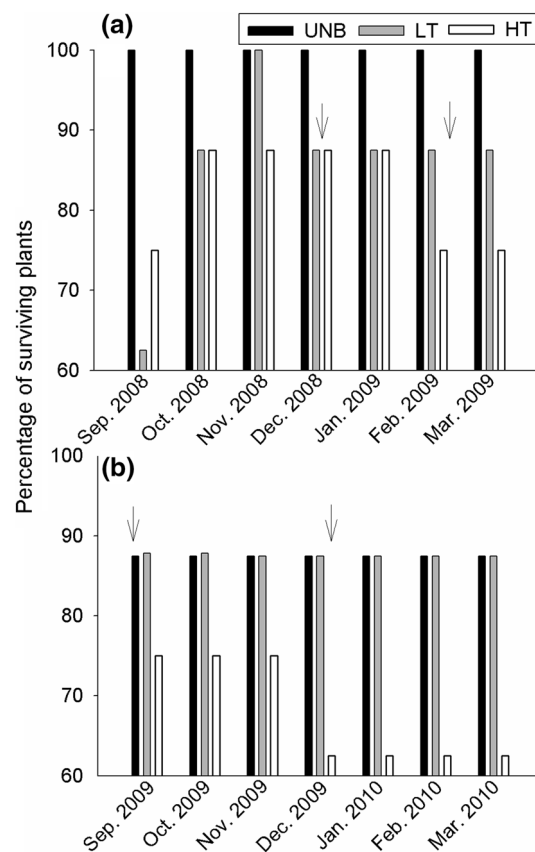


Fig. 3 Percentage of surviving plants of *Festuca pallescens* during September 2008–March 2009 (a), September 2009–March 2010 (b). UNB unburned, LT low temperature, HT high temperature. Arrows show mortality

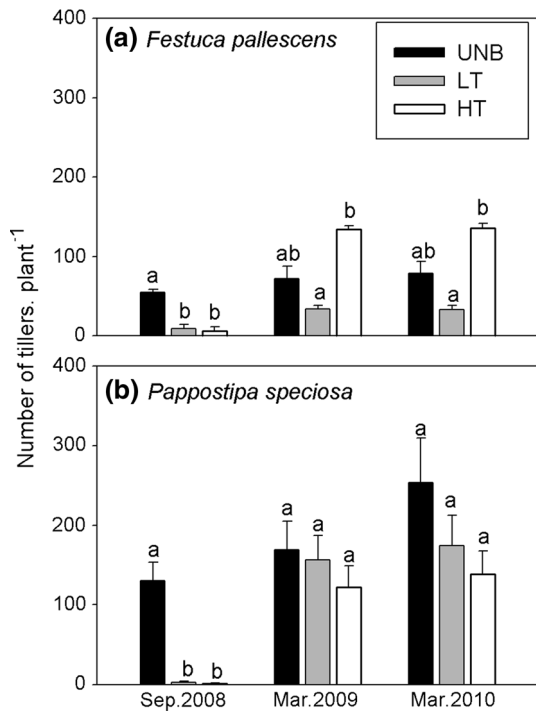


Fig. 4 Mean number and standard error (SE) of tiller plant⁻¹ of *Festuca pallescens* (a) and *Pappostipa speciosa* (b) estimated for three monitoring dates (September 2008, March 2009 and 2010) in the unburned treatment (UNB), and fire treatments with low temperature (LT) and high temperature (HT). Within each monitoring date, values with the same letter are not significantly different ($P > 0.05$)

lower ($P < 0.01$) than in unburned plants (Fig. 5b). During the second growing post-fire season, the mean maximum leaf length in both species was not significantly different ($P > 0.05$) among burned and unburned plants.

In both post-fire growing seasons, the relative growth rates of leaf length did not differ significantly ($P > 0.05$) in burned and unburned plants of *F. pallescens* (Fig. 6a only for first post-fire growing season). In *P. speciosa*, the relative growth rates of leaf length were greater in burned plants than in unburned plants during September–October 2008 ($F_{2,20} = 16$; $P < 0.001$), but in November–December 2008 relative growth rates of unburned plants were higher than in burned plants ($F_{2,20} = 8$; $P = 0.003$) (Fig. 6b).

Discussion

Fire temperature affected the survival of *Festuca pallescens* and *Pappostipa speciosa* plants. Plant survival after fire is related to the position of meristematic tissues and their time of exposure to elevated temperatures (Wright and Bailey 1982; Whelan 1995; Gibson 2009). Plants with meristematic tissues on soil surface are more susceptible to fire damage (Whelan 1995; Gibson 2009). In our study, *F. pallescens* and *P. speciosa* have axillary

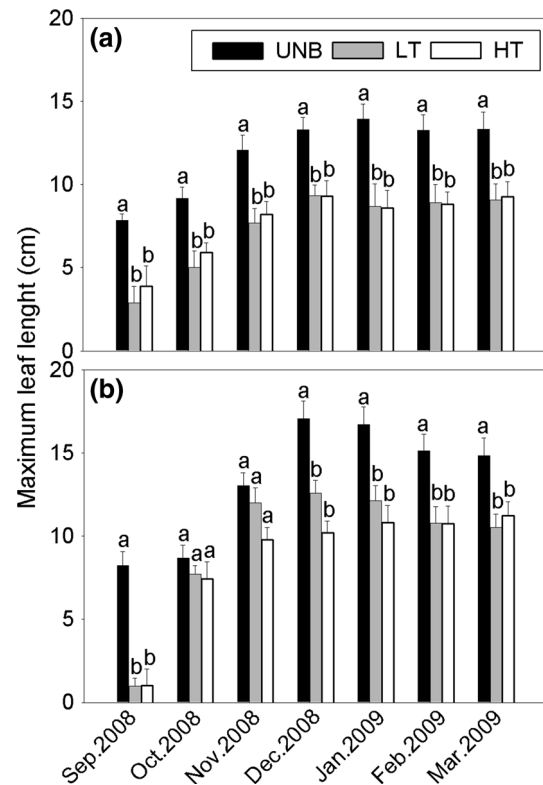


Fig. 5 Maximum mean leaf length and standard error (SE) of *Festuca pallescens* (a) and *Pappostipa speciosa* (b) in unburned (UNB), low temperature (LT) and high temperature (HT) treatments measured in the first post-burn growing season (2008–2009). Within each monitoring date, values with the same letter are not significantly different ($P > 0.05$). We do not show data from the second growing season because no significant differences were found

and basal buds that are protected from heat by soil accumulated by strong Patagonian winds (Gonzalez 2011). Thus survival differences can be accounted for differences in exposure time of meristematic tissues.

The effects of burning duration and the amount of heat transmitted to meristematic tissues during the experimental burns are related to morphological traits such as retention of senescent biomass (fine fuel load) and canopy architecture and plant compactness (Pickett and White 1986; Whelan 1995; Bond and van Wilgen 1996; Schwilk 2003). Wright (1970) found that *Sitanion hystrix* was more tolerant to fire than *Stipa comata* because the first species had less dry biomass accumulated at the base of the plants. In our study, compact and dense plant structure of *F. pallescens* (Boó et al. 1996; Gonzalez et al. 2010) affects fire behavior and maximum temperature is reached latter in both treatments than in *P. speciosa* plants which have opened canopy (Fig. 2). Consequently, *F. pallescens* burnt slowly and for a longer period than *P. speciosa* plants (Fig. 2), increasing the residence time of fire that affected negatively the bud meristems. This mechanism probably explains, at least in part, the increased mortality observed in *F. pallescens* at high temperatures, even if other factors such as the

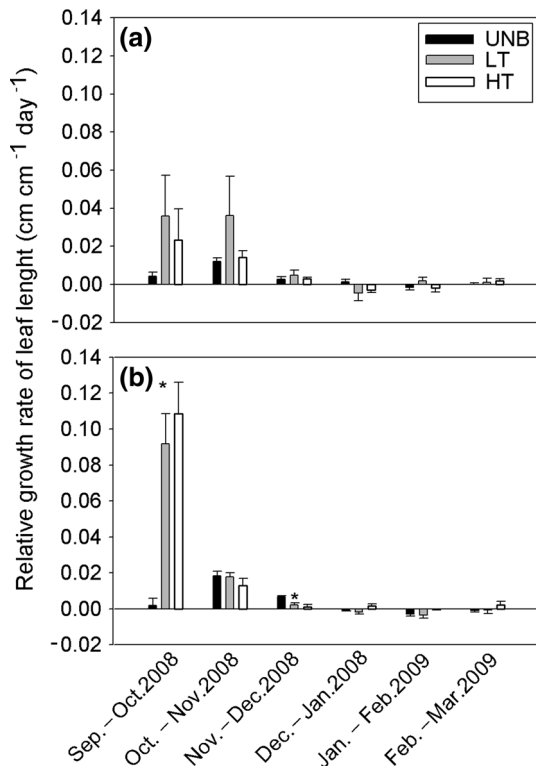


Fig. 6 Relative growth rate for length of tiller leaves of *Festuca pallescens* (a) and *Pappostipa speciosa* plants (b) in unburned (UNB), low fire temperature (LT), and high fire temperature (HT) treatments during the first post-burn growing season (2008–2009). In each sample date, asterisks indicate significant differences between the unburned plants and fire treatments ($P < 0.05$). We do not show data from the second growing season because no significant differences were found

difference of nutrient acquisition could have influenced plant survival. Further studies must be performed to demonstrate the higher susceptibility of *F. pallescens* than *P. speciosa* to fire.

Several *F. pallescens* plants initially regrew after fire treatments, but died during the first two post-fire growth seasons. Other factors such as weather conditions or grazing could affect the post-fire tussock grass survival (Robberecht and Defossé 1995; Whelan 1995; Peláez et al. 2009). Effect of water deficit might be more significant than effect of fire in water-limited environments, increasing the mortality of plant species which do not tolerate water stress (Daubenmire 1968). There is experimental evidence that *F. pallescens* has less tolerance to water stress and less competitive ability for water than *P. speciosa* (Fernández et al. 2006a, b; Franzese 2012). Also, Gittins et al. (2011) reported that higher mortality of *F. pallescens* after a fire was due to this species being less adapted to warmer and drier conditions. Thus, hot and dry post-burn weather conditions, which occurred in spring 2008 and summer 2009, could have increased the mortality of burned *F. pallescens* plants.

Although we did not analyze the effect of fire on the viability of the axillary buds of studied grasses, the low number of tillers found in both species after burn indicated that many buds had been killed. Peláez et al. (1997) found that tillers of burned plants of *Stipa tenuis*, *S. gyneroides* and *Piptochaetium napostaense* had more dead axillary buds and fewer metabolically active buds than tillers of unburned plants. Mortality of more superficial buds could also explain the delay in the production of new tillers in the first post-fire growing season. The activation and differentiation of new axillary buds is a slow process because meristems that survive fire are deeply buried in the crown, and new resprouts require time to reach the surface, which would delay the appearance of new tillers (Moreno and Oechel 1991; Van Loo 1992; Vesik and Westoby 2004).

Axillary bud mortality and the consequent delay in the activation of the meristematic tissues could explain, at least in part, the shorter length of leaf tillers recorded in the burned plants in the first post-fire growing season (Fig. 5). High relative growth rates would indicate that tillers of burned plants of both grasses grew between September and December 2008 as well as the tillers of unburned plants. These plants would have invested most of their available post-fire resources to restore a critical mass of photosynthetic tissues as quickly as possible. In the second post-burn growing season, the tiller length in burned plants of both grass species was always shorter than the tiller length in unburned plants. However, the differences were not significant. This indicates that tillers of burned plants of *P. speciosa* and *F. pallescens* might need at least two growth cycles to reach the length of the tillers of unburned plants. Also, Daubenmire (1968) reported that tillers of *Chionochloa rigida* took approximately 3 years to reach the length that they had before burns.

At the end of the first post-fire growth season, both perennial grass species had a high number of new tillers. These results confirmed the great recovery capacity of these species already observed in other studies (Ghermandi et al. 2004; Gittins et al. 2011). Fire removed dead and/or senescent material accumulated in the base of individual plants which could have favored the activation of axillary buds due to changes in quantity and quality of the incident light. Tillering is regulated by the quantity and quality of light that reaches the bases of the tillers which is determined by the presence of other plants and tillers (Deregibus et al. 1985). In the second post-burn growing season, tiller production decreased in both species. This reduction is likely due to changes in light quality because of accumulation of senescent tillers (Davies 1988; Leoni et al. 2006) and the increased carbon demand of maintain existing tillers (Whelan 1995).

Post-fire plant survival is the result of a complex interaction of fire and plants characteristics, meteorological conditions and other disturbances as grazing (Robberecht and Defossé 1995; Peláez et al. 2009). Our

results suggested that *F. pallescens* is more susceptible to high fire temperature. However, both tussock grasses recovered quickly after fire. At least in part, this behaviour might favour the persistence and dominance of these species in the grasslands of the Patagonia. Both perennial species had evolved in a fire-prone system adapting to a particular fire regime. Possible alterations in the present fire regime due to the global climatic change could affect the abundance and/or persistence of these species in the region. According to Ghermandi et al. (2004), *F. pallescens* and *P. speciosa* are mainly responsible for the high resilience of grasslands in NW Patagonia. Although our data provide valuable information on the response of two of the major grass species in the grasslands of the Patagonia to fire, further research is needed in order to prescribe management guidelines.

Acknowledgments We are grateful to D. Andrusova, N. Beletzky, A. Celedón, J. Franzese, and C. Brockerof (PNMF) for their assistance during the experimental burns. M.L. Suárez, G. Pirk and J. Franzese for their assistance in the field work, and A. Spoturno and C. Reemst for their help in English revision. We also thank San Ramón ranch managers Ing. D. Marty and Ing. A. Hodgson. This work was funded by UNCo, ANPCYT, CONICET and Idea Wild donated the datalogger and thermocouples.

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