Winter Damage is More Important than Summer Temperature for Maintaining the Krummholz Growth Form Above Alpine Treeline

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ABSTRACT

Cool summer air temperatures are currently thought to be the limiter of upright tree growth at alpine treelines globally. However, winter damage has long been recognized as a shaping force near alpine treelines. To distinguish between effects of growing season temperature, winter damage, and their interaction on preventing upright growth, we conducted an experiment on low-growing krummholz growth forms of *Pinus albicaulis* over summer and winter 2015-2016 at 10 sites in the Tobacco Root Mountains, Montana, USA. We experimentally manipulated four factors using a fully crossed design: shoot position (natural low position in the krummholz mat vs. propped up above the krummholz mat), summer warming (warmed vs. ambient), winter exposure (sheltered vs. exposed), and elevation position (local high vs. low krummholz limits). We also conducted an observational study of the climatic conditions associated with natural stem establishment. Winter-exposed propped shoots experienced higher mortality (10-50%) than sheltered propped shoots and shoots within the krummholz mat, whether caged or not (0-10%). Summer warming had little influence on shoot mortality. Surviving mat shoots had marginally higher growth rates than surviving propped shoots during the early growing season 2016. Natural stem establishment was associated with warmer summer temperatures, but also warmer winter temperatures, lower winter wind speeds, and lower snowpack. Our results indicate that winter damage plays a more important role than growing season temperature in maintaining krummholz. Warming may increase opportunities for shoot establishment but continuing upright growth in the krummholz zone may also require reductions in damaging winter wind and snow.

Keywords: growth limitation, krummholz flags, *Pinus albicaulis*, plant-climate interactions, snow transport, treeline ecotone, whitebark pine, wind

INTRODUCTION

Alpine treeline ecotones, where upright trees transition to low-growing alpine vegetation, are common in mountain ecosystems around the world. Similar growing season temperatures at alpine treelines globally suggest that temperature limitation of growth in upright stems could be the ultimate reason trees fail to grow at high-elevations (Körner 1998, Hoch and Körner 2003). At some treeline ecotones, however, tree species grow as shrub-like krummholz, which extends the species range above the treeline (the limit of upright stems; Körner and Paulsen 2004). Although low-growing krummholz may experience warmer growing seasons than upright stems, winter exposure to desiccation and damage from wind-transported snow is also known to harm stems that emerge from the snowpack (Hadley and Smith 1983).

Our objective was to identify the processes that maintain the krummholz growth form. We addressed this objective with two complimentary observational and experimental approaches. Specifically, we asked: 1) What climatic conditions were associated with the establishment of naturally occurring emergent stems from krummholz? 2) How do growing season temperature and winter damage affect survival of shoots within and above krummholz, and do effects vary with elevation?

METHODS

This study was conducted in the Tobacco Root Mountains located in southwestern Montana, USA. We used *Pinus albicaulis* Engelm. krummholz as a study system. P. albicaulis commonly forms krummholz above alpine treelines throughout its range. Genetic analysis indicates that growth form differences in the species represent phenotypic plasticity, not local differentiation (Rogers et al. 1999), likely resulting from dispersal across treeline ecotones by Clark's nutcracker

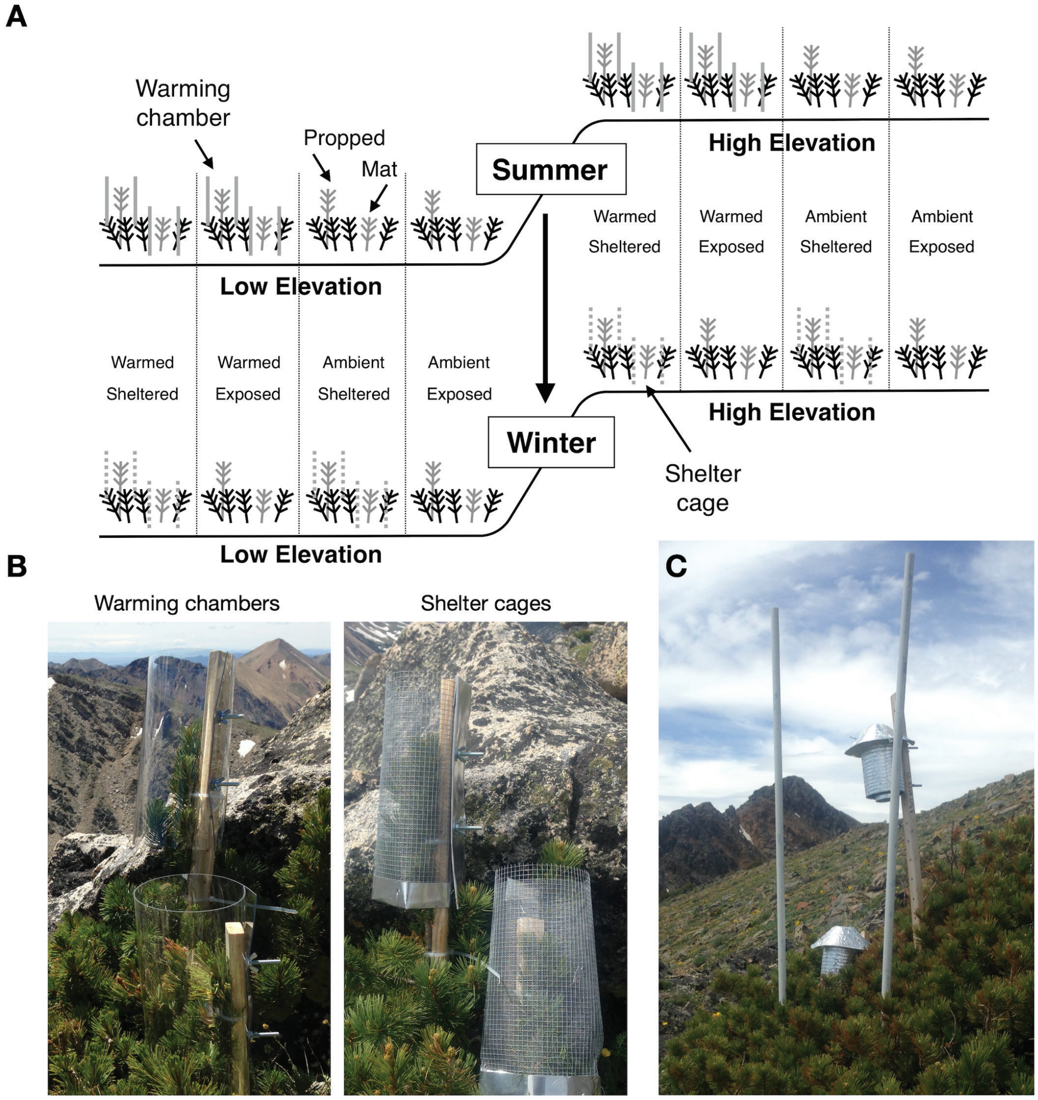

Figure 1. A) Design of krummholz shoot experiment showing four factors: shoot position (propped vs. mat), late summer warming (warmed vs. ambient), winter shelter (sheltered vs. exposed), and elevation position (local lowest krummholz vs. highest krummholz). Grey shoots represent experimentally manipulated shoots that were supported by wooden stakes. B) Warming chambers and shelter cages installed around propped and mat krummholz shoots. C) Radiation shields with temperature loggers to measure air temperature and wax cylinders to measure winter wind effects (Maher et al. 2020).

(*Nucifraga colombiana* Wilson; Bruederle et al. 1998). Thus, krummholz *P. albicaulis* represent potential trees, making this an appropriate species for investigating environmental influences along treeline ecotones. For our purposes, we defined krummholz as matted, shrub-like *P. albicaulis* that are wider (≥ 1 m across) than they are tall.

To determine rates of establishment of natural upright stems from krummholz in the Tobacco Root Mountains, we sampled 45 upright stems at 9 sites. At each site, 5 stems were selected by standing at the highest accessible point above the local krummholz limit and randomly choosing a downslope compass direction. We sampled the first upright stem we encountered in that direction and its 4 nearest neighbors. We assumed that the current krummholz mat represents the average snow depth over the lifespan of each sampled stem. We measured each stem's vertical height above the krummholz mat and took a cross-section where it intersected the krummholz mat. In the laboratory, we counted rings to the pith on each stem cross-section and verified our counts by visually crossdating (Stokes and Smiley 1968) using a pattern of frost-damaged rings.

To test hypotheses about environmental influences limiting the krummholz growth form, we used a replicated ($n = 10$) factorial experiment with shoot position (upright vs. mat), late summer warming (warmed vs. ambient), shelter from winter damage (sheltered vs. exposed), and elevation position (lowest local krummholz vs. highest local krummholz) as factors and shoot mortality as the response (Fig. 2). We simulated upright shoot growth by securing naturally prostrate krummholz shoots to wooden stakes to place them ~0.5 m above the top of the krummholz mats (Fig 1.). We paired these "propped" shoots with shoots within the mat that we also secured to short wooden stakes (stakes located entirely within the mat). We used clear polycarbonate warming chambers and sturdy fine mesh cages for summer warming and winter shelter, respectively (figure 1). At each site, we installed treatments near both local high- and low-elevation limits of krummholz. Each factor was crossed such that propped/mat shoot pairs were either warmed in the summer and protected in the winter, only warmed in the summer, only protected in the winter, or neither warmed nor protected (figure 1). The experiment was replicated at 10 treeline sites (sites are blocks; $n = 10$). Low-elevation replicates were downslope from the higher ones. Treatments were randomly assigned to four krummholz at each low- and high-elevation location. Warming chambers were installed between 17 July to 10 August 2015. These were exchanged for shelter cages between 9 October and 15 October 2015. The experiment was recovered between 23 June and 4 July 2016.

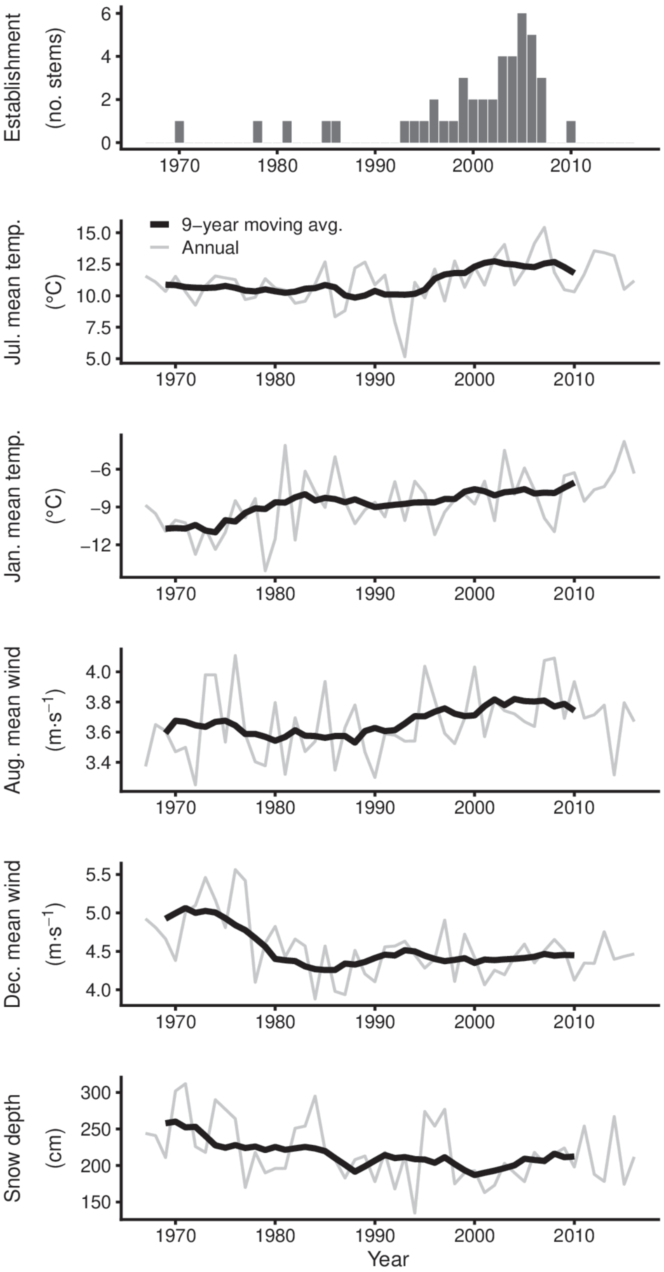

Figure 2. Number of naturally occurring emergent stems establishing each year in the treeline ecotone and associated climatic conditions during the period 1967-2016 ($n = 45$). Establishment represents when stem heights reached the top of the current krummholz mat. Climate variables are displayed as 9-year moving-window averages (-2 years to +6 years for each year of establishment; thick black lines) and as annual values (thin grey lines). Significant ($P \leq 0.001$ in these cases) Spearman rank correlations of stem establishment with 9-year climate averages are as follows: July temp = 0.59, January temp = 0.58, August wind speed = 0.63, December wind speed = -0.23, Snow depth = -0.56 (Maher et al. 2020).

We recorded shoots as dead (in 2016) if the shoot tip was broken off or if all needles were stripped off and the apical bud was brown and desiccated.

We characterized environmental conditions during our natural emergent stem study using available long-term monthly climate data (1970-2016). We obtained interpolated monthly gridded temperature from the TopoWx model (1/120° or ~800 m resolution; Oyler et al. 2014) and surface wind time series data from the TerraClimate dataset (1/24° or ~4 km resolution; Abatzoglou et al. 2018). Long-term snow depth records were obtained from US National Resource Conservation Service snow course data at Branham Lakes (marker 11D14 at 2700 m asl).

To characterize daily climatic conditions during our experiment (Aug. 2015 - June 2016), we installed temperature loggers in radiation shields at a random subset of 5 sites. Loggers were placed on wooden stakes within krummholz mats and at ~0.5 m above the mat to capture ambient air temperature differences between mat interiors and propped shoots (figure 1).

Complete description of methods and analyses can be found in Maher et al. (2020).

RESULTS

Natural upright stems mostly established between 2000-2008 (figure 2). Only four stems had establishment dates before 1990. The oldest stem established in 1978, and the youngest in 2010. Stem heights in our sample of stems were less than or equal to 1 m above krummholz mats, except for one 1.2 m stem that established in 1998 (range = 0.2 to 1.2 m, median = 0.5 m). The observed period of establishment was significantly associated with relatively warmer summer and winter temperatures and relatively lower winter winds and snowpack. Summer winds were higher during this period (figure 2).

Exposed, propped shoots—whether they were warmed or not and across both elevations—clearly experienced higher mortality (10-50%) than did sheltered propped shoots and mat shoots (figure 3). We observed no mortality in sheltered shoots (propped or mat locations) at high-elevation and only one (10%) mat shoot (which was in a shelter cage) died at low elevation. Summer warming had no noticeable effect on this relationship at high-elevation sites. These effects (main effects and interactions) were not statistically detectable at the $P < 0.05$ level. However, the shelter by shoot position interaction was significant at the $P < 0.1$ level. Air temperature differences between above mat and withing mat environments were more pronounced during summer/fall and spring than during winter.

Complete results can be found in Maher et al. (2020).

DISCUSSION

Our findings clearly indicate the importance of winter damage in preventing upright shoot survival and growth in krummholz, although our inferences about the effects of warming are more limited. While warming chambers did increase the air temperatures shoots were exposed to, chambers

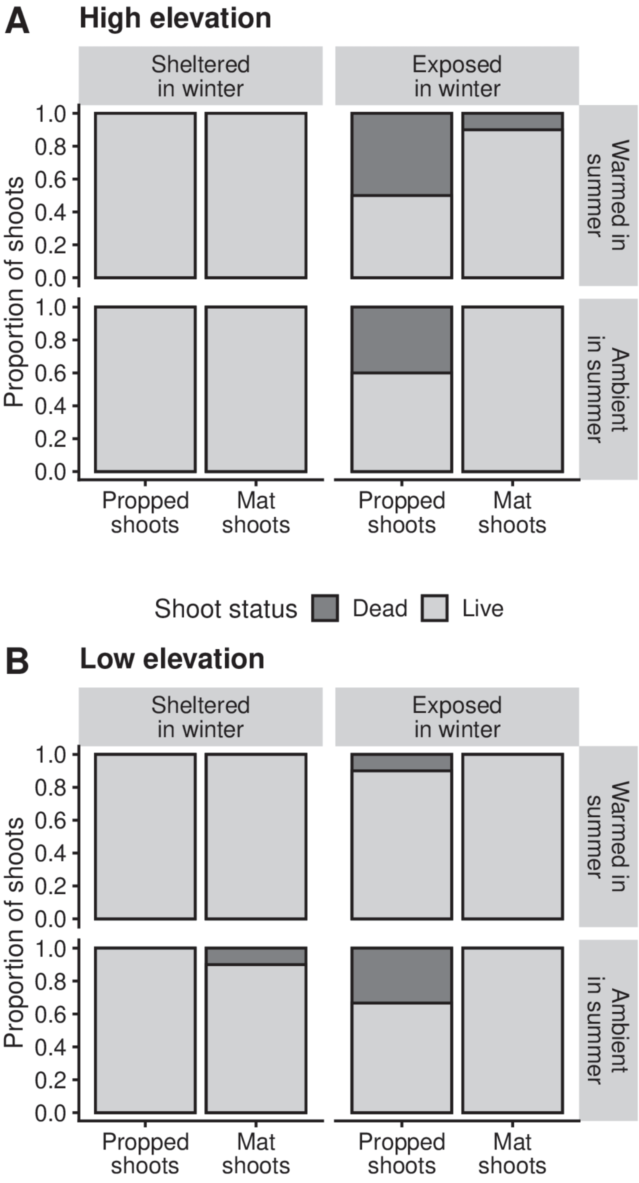

Figure 3. Post-winter survival (proportion living of all shoots; light grey) and mortality (proportion dead of all shoots; dark grey) of experimentally manipulated krummholz shoots in June/July 2016 (*n* = 10 sites). A) shows treatments at high-elevation, B) shows treatments at low-elevation (Maher et al. 2020).

were installed relatively late in the growing season and may not have strongly affected growth or development. Still, at low elevations there seems to have been a reduction in mortality in the exposed propped shoots that were also warmed. This could reflect greater cuticle development from warmer temperatures and thus greater resistance to winter damage (Tranquillini 1979). On the other hand, many shoots died as a result of mechanical breakage of stem tips (the top 5-10 cm was torn off). Intense physical force like this probably won't be overcome by cuticle development or a year's height increment. Dead shoots that were not broken appeared desiccated—a well-documented cause of death in conifer needles due to cuticle loss from winter wind exposure (Hadley & Smith 1986, 1989). We reason that winter damage is a first-level mechanism limiting upright growth in krummholz, with the effects of temperature on growth rates important, but subordinate.

Alpine treeline ecotones are complex ecological boundaries that are unlikely to be explained by a single factor alone (Sullivan et al. 2015; Cansler et al. 2018). Our findings of the importance of a factor other than summer temperature, winter damage in this case, calls into question the usefulness of alpine treelines as bellwethers of the effects of warming. At treelines where abrasion by wind-driven snow is possible, a warming climate may not directly result in treeline advance, unless warming also causes changes that reduce the risk of damage in winter.

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