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Causes for treeline stability under climate warming: Evidence from seed and seedling transplant experiments in southeast Tibet

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ABSTRACT

Few data have examined the warming-related controls on seedling recruitment above the treeline, which is critical to understand causes for treeline stability under climate warming. We tested the hypothesis that compared to controls on seed dispersal and germination, the warming-induced decrease of seedling survival above the treeline is more likely to cause treeline stability. Long-term microclimate observations and 4-year seed and seedling transplant experiments were conducted in two contrasting treeline ecotones on the opposite slopes of a U-shaped valley at the peak of the Sergyemla Mountains. Seeds and young seedlings of Smith-fir (*Abies georgei* var. *smithii*) were transplanted to the treeline (4320 m) and *Rhododendron* shrub (4390 m) on the north-facing slope and to the juniper treeline (4425 m) on the south-facing slope. Transplanted seeds were collected from the Smith-fir treeline and its distribution center (3800 m). We also investigated the distribution of naturally-established seedlings and its correlation with shrub cover along elevation transects above the treeline. Smith-fir seedlings growing under shrubs were observed up to 40 m in elevation higher above the treeline, and there was either no correlation or a low correlation between seedling density and shrub cover. Harsh environments above the treeline did not limit the germination of seeds from different seed sources. However, transplanted seedlings cannot survival well above the treeline or at the juniper treeline due to high frequency of early-season freezing events and strong light intensity, while the absence of early-season freezing events in the Smith-fir treeline forest was more beneficial to seedling survival. During 2006–2015, the frequency of early-season freezing events increased with increasing annual mean air temperature above the treeline and at the juniper treeline but not in the Smith-fir treeline forest. The warming-induced increase of early-season freezing events, combined with high light intensity, mainly limits the survival of young seedlings above the treeline, which is more likely to cause treeline stability. Early-season freezing events should be an important index for evaluating the vulnerability of treeline forests to global warming.

1. Introduction

As low temperature is generally considered to be the major limiting factor of tree growth at high elevations, alpine treeline is expected to respond sensitively to global warming (Körner, 1998; Körner and Paulsen 2004). Globally, it has been observed that one half of 166 alpine/boreal treelines have advanced in response to the warming of the past century while the other half remains stable (Harsch et al., 2009). Similar pattern is found in the world's highest treelines on the Tibetan Plateau (Liang et al., 2016) and in the central Himalaya (Sigdel, 2017). Treeline advance with climate warming has been commonly interpreted by the relief of low temperature limitation to tree growth and distribution (Danby and Hik, 2007), but little is known about the reason of treeline stability under global warming (Green, 2009; Harsch et al., 2012; Liang et al., 2016).

Upward shift of alpine treeline requires successful seedling recruitment above the treeline. Thus, failure in recruitment process impedes treeline advance (Camarero and Gutiérrez, 2004; Batllori et al., 2009; Smith et al., 2009). In general, treeline advance mainly depends on seed quality and production of treeline parent-trees and the capacity of seed dispersal upward, as well as subsequent seed germination and seedling survival above the treeline (Germino et al., 2002; Smith et al., 2003). The influence of warming on these processes is complicated and uncertain (Fig. 1). The seed quality and production of treeline trees are mainly limited by insufficient growing degree days (Payette and Gagnon, 1985; Juntunen and Neuvonen, 2007). It has been observed that seed quality and production generally increase with decreasing elevation (Sveinbjörnsson et al., 1996; Cuevas, 2000; Molau and

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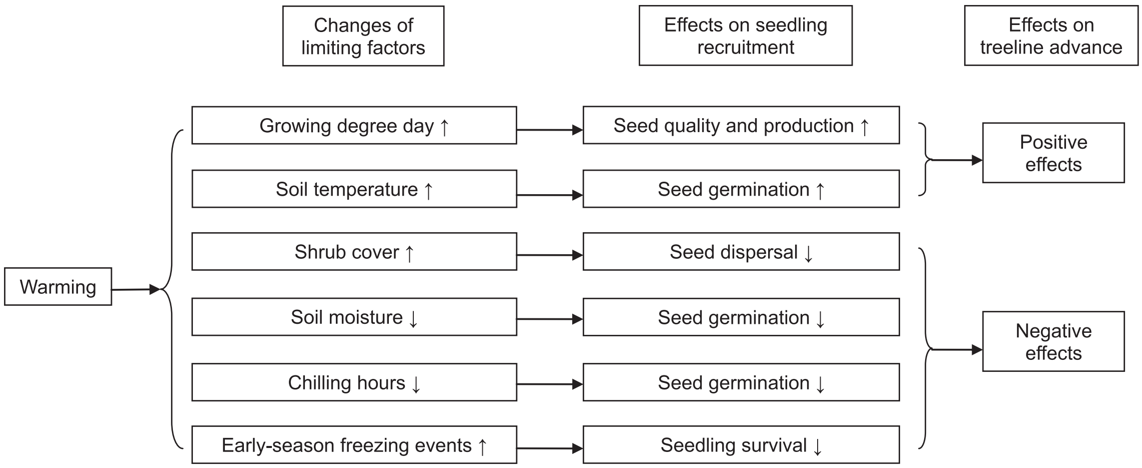

Fig. 1. A summary for effects of warming-induced environmental changes on seedling recruitment and treeline advance.

Larsson, 2000) and the population density of treeline species has increased with recent warming (Klasner and Fagre, 2002; Camarero and Gutiérrez, 2004), being consistent with the suggestion that seed quality and production can be improved by warming (Kullman, 2007; Dufour-Tremblay and Boudreau, 2011). Thus, seed quality and production may not explain the treeline stability under climate warming. On the other hand, the seed dispersal to higher elevations above the treeline is generally impeded by low wind speed (Holtmeier and Broll, 2010) and dense shrubs (Bader et al., 2007; Wang et al. 2012; Liang et al., 2016). As alpine shrubs tend to be denser under climate warming (Myers-Smith et al., 2011; Tremblay et al., 2012), dispersal limitation may be one of the causes for treeline stability. Furthermore, seed germination above the treeline is mainly affected by soil conditions. Warmer soil can enhance seed germination, but soil desiccation and insufficient chilling hours induced by warming may reduce germination (Jones et al., 1991; Rawat et al., 2008; Wesche et al., 2008). Also, the low-temperature photoinhibition resulted from the combination of freezing temperature at night and high sunlight during the day may significantly reduce seedling survival above the treeline (Ball, 1994; Ball et al., 1997). The growing-season freezing events may vary little or even increase with warming (Sierra-Almeida and Cavieres, 2010; Rixen et al., 2012; Shen et al., 2014). Therefore, warming-induced decreases of seed germination and seedling survival may also cause treeline stability. However, few data have examined the whole early life stages of tree regeneration above the treeline (Cuevas, 2000; Moen et al., 2008; Dufour-Tremblay et al., 2012), and the warming-related causes of treeline stability remain poorly understood.

Southeast Tibet is characterized by a cold and moist climate, and has the highest elevation timberline in the world (Miehe et al., 2007; Opgenoorth et al., 2010). Instrumental climatic data indicate a significant warming trend since the 1960s, which has been recorded in ring-width chronologies of treeline trees (Liang et al., 2009) and alpine shrubs (Liang and Eckstein, 2009; Kong et al., 2012). However, Smith-fir (*Abies georgei* var. *smithii*) treeline position in this region varied little while the population density has increased in the past 200 years of warming (Liang et al., 2011). There are few experimental data investigating the warming-related controls on recruitment processes at and above the treeline (Shen et al., 2014; Wang et al., 2016). On the other hand, it is still difficult to understand why seed-regenerated Smith-fir species is excluded from the south-facing juniper treeline and nearby non-forested sites where there is a warmer climate compared to Smith-fir treeline forest (Liu and Luo, 2011; Shen et al., 2014). In this study, we hypothesize that compared to controls on seed dispersal and germination, the warming-induced decrease of seedling survival above the treeline is more likely to cause treeline stability. We tested the hypothesis based on seed and seedling transplant experiments and microclimate observations at alpine treelines in the Sergyemla Mountains, southeast Tibet. First, we tested whether Smith-fir seeds can disperse to higher elevations above the treeline by investigating the distribution pattern of naturally-established young seedlings along elevation transects from the treeline forest to the alpine shrubland. We also examined whether there is a negative relationship between seedling density and canopy cover of *Rhododendron* shrubs, given that climate warming may increase shrub cover and then impede seed dispersal (Bader et al., 2007; Wang et al., 2012; Liang et al., 2016). Second, we tested whether chilling hours and/or harsh environments above the Smith-fir treeline and at the juniper treeline (both had a warmer climate than the Smith-fir treeline forest) may not limit the germination of seeds from different seed sources by conducting a seed transplant experiment using seeds collected from the Smith-fir treeline (4320m) and its distribution center (3800 m, ca 2–3 °C warmer than the treeline). Third, we further conducted a seedling transplant experiment to test whether and how harsh environments above the Smith-fir treeline and at the juniper treeline may generally limit the survival of Smith-fir seedlings, assuming that the warming-induced increase of early-season freezing events may increase seedling mortality via low-temperature photoinhibition (Ball, 1994; Ball et al., 1997; Shen et al., 2014). Also, we tested whether the frequency of early-season freezing events during 2006–2015 may increase with increasing annual mean air temperature above the Smith-fir treeline and at the juniper treeline, while there are few freezing events in the Smith-fir treeline forest.

2. Materials and methods

2.1. Study sites

The study sites are situated on the opposite slopes of a U-shaped valley at the peak of the Sergyemal Mountains (29°36′N, 94°36′E, 4200–4600 m a.s.l). *A. georgei* var. *smithii* and *Juniperus saltuaria* are the dominant species of treeline forests on the north-facing and south-facing slopes, respectively. Above both treelines, the vegetation changes to an open mosaic of *Rhododenron* shrubland and alpine grassland. In August 2005, three automatic weather stations were installed at the sites for treeline forests of Smith-fir (4320 m) and juniper (4425 m) and alpine low-shrub of *Rhododendron* above Smith-fir treeline (4390 m). Air temperatures, relative humidity, soil temperature and volumetric moisture, radiation, wind speed, rainfall and snow depth were recorded hourly by HL20 dataloggers (Jauntering Inc., Taiwan). Detailed information on the sensor types and site conditions is found in Liu and Luo (2011).

According to the meteorological observations during 2006–2015, annual mean air temperature was 0.59 °C, 0.81 °C and 1.01 °C at and