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Seed-based treeline seedlings are vulnerable to freezing events in the early growing season under a warmer climate: Evidence from a reciprocal transplant experiment in the Sergyemla Mountains, southeast Tibet

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ABSTRACT

Seedling mortality is important to the formation and dynamics of alpine treeline. There is a need to understand the mechanisms governing seedling mortality at and above treelines under a warmer climate. We tested the hypothesis that under a warmer climate, seed-based treeline seedlings are especially vulnerable to freezing events in the early growing season. Using space-for-time substitution, we conducted a 5-yr reciprocal transplant experiment for >10 yr-old seedlings of seed-based fir and root-sprouting juniper between north-facing and south-facing slopes of a valley with elevations of 4200–4600 m in the Sergyemla Mountains, and additional experiments of seed germination and younger seedling transplants (with ages of 3–5 yr) at and above the fir treeline. Between both slopes, annual precipitation was similar but annual mean air-temperature above the treeline differed by 2.0 °C, being comparable to the temporal difference of 2.3 °C between the warmest and coldest years and the unchanged trend of precipitation during 1960–2008 at Nyingchi station nearby the study sites. The frequency, intensity and duration of growing-season freezing events were much higher under the warmer climate on the south-facing slope. Across years and non-forested sites above both treelines, annual mean air-temperature was well correlated with the early-season (April–June) freezing events. In pooled data across years and sites, annual mortality increased in fir seedlings but varied little in juniper seedlings with increasing freezing events in the early growing season. Similar patterns were also found in their annual growth rates. Partial correlation analysis indicated that the early-season freezing event was the major limiting factor determining annual mortality of fir seedlings, while that of juniper seedlings varied little with all the microclimate factors. Harsh environments above the treeline did not limit fir seed germination. The finding that the early-season freezing events under a warmer climate increased fir seedling mortality can explain the cause for the unique distribution pattern of fir and juniper treelines on opposite slopes of a valley in southeast Tibet, and suggests an explanation for the phenomenon that the world's highest fir-treeline position did not advance with climatic warming in past 200 years.

1. Introduction

It has been suggested that the likelihood of freezing events will tend to increase under future global warming (Inouye, 2000; IPCC, 2007; You et al., 2008). The number of freezing events generally increases with increasing elevation (Wieser and Tausz, 2007; Barry, 2008; Li et al., 2013). At high elevations, extreme low temperatures can occur during the growing season because of the severe radiation cooling at night under clear skies, light winds and dry conditions (Sakai and Larcher, 1987; Taschler and Neuner, 2004; Wieser and Tausz, 2007; Larcher et al., 2010). This can be fatal to the survival of alpine plants because they have the weakest ability to resist the unpredictable freezing events in the early growing season when alpine plants are fully active (Inouye, 2008; Mayr et al., 2012; Neuner and Hacker, 2012; Rixen et al., 2012). Alpine treeline seedlings are expected to be especially vulnerable to freezing events, resulting in the difficulty of seedling establishment at and above treelines (Smith et al., 2003; Kullman, 2007; Harsch and Bader, 2011). However, continuous and detailed

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measurements of microclimate at alpine treeline ecotones are rare (Barry, 2008; Körner, 2012), and characteristics of growing-season freezing events and their effects on the survival and growth of seedlings at and above treelines remain poorly understood (Kullman, 2007; Barbeito et al., 2012). Such knowledge is important to understand the formation and dynamics of alpine treeline since seedling mortality is one of the three general 'first level' mechanisms that determine treeline position and dynamics (Harsch and Bader, 2011).

Southeast Tibet, which is characterized by a cold and moist climate, has the highest elevation treeline in the world (Miehe et al., 2007; Opgenoorth et al., 2010). The 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). In the Sergyemla Mountains, the seed-regenerated fir treeline (*Abies georgei* var. *smithii*) generally dominates on the north-facing slope, while the sprout-regenerated juniper treeline (*Juniperus saltuaria*) dominates on the south-facing slope, forming a unique distribution pattern on opposite slopes of a valley where annual mean air-temperature above both treelines differs greatly and annual precipitation is similar (Zhang et al., 2010; Liu and Luo, 2011). There is evidence that little change has occurred in the seed-regenerated fir treeline position after 200 years of warming even though the fir population density has increased (Liang et al., 2011), which is consistent with the worldwide data that almost half of 130 alpine/boreal treelines did not advance in response to global warming (Harsch et al., 2009). This points to the importance of microsite availability in seedling establishment above treeline (Smith et al., 2003; Harsch and Bader, 2011; Wang et al., 2012). The unique distribution pattern of fir and juniper treelines on opposite slopes of a valley in the Sergyemla Mountains provides a natural laboratory to explore characteristics of growing-season freezing events and their effects on seedling mortality at and above both treelines, which might be useful for understanding why the world's highest fir-treeline position has not advanced with climatic warming. There is evidence that space-for-time substitution can be used for predicting climate-change effects on biodiversity (Blois et al., 2013).

In this study, we hypothesize that under a warmer climate, seed-based treeline seedlings are especially vulnerable to freezing events in the early growing season. Using space-for-time substitution, we conducted a 5-yr reciprocal transplant experiment for >10 yr-old seedlings of fir and juniper between opposite slopes of a valley with elevations of 4200–4600 m in the Sergyemla Mountains, and additional experiments of seed germination and younger seedling transplants at and above the fir treeline. Our aims are to: (1) examine if growing-season freezing events are significantly higher under the warmer climate on the south-facing slope; (2) determine whether the annual mortality and growth rates of transplanted fir and juniper old-seedlings are generally associated with the growing-season freezing events across sites and years; (3) investigate to what extent harsh environments above the treeline limit fit seed germination and its young-seedling growth and survival.

2. Materials and methods

2.1. Study sites

This study was conducted at the treeline observation sites of the Southeast Tibet Observation and Research Station for Alpine Environments, Chinese Academy of Sciences. The study sites are located on the opposite slopes (north-facing vs. south-facing) 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 *J. 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 shrublands and grasslands. In August 2005, four automatic weather stations were installed at the sites for treeline forests of fir (4320 m, N2) and juniper (4425 m, S2) and their nearby low-shrubland (4390 m, N3) and grassland (4441 m, S3). Air (1 m and 3 m aboveground) and soil (−5 cm and −20 cm) temperatures, radiation (global radiation, net radiation, photosynthetically active radiation, long wave radiation, red light radiation), wind speed, relative humidity, rainfall, snow depth and soil volumetric moisture were recorded hourly by HL20 data loggers (Jauntering Inc., Taiwan). According to the treeline meteorological observations during 2006–2012, the difference of annual mean air-temperature between the warmest and coldest years was 0.7–1.2 °C for south-facing sites (S2 and S3) and 0.8–1.0 °C for north-facing sites (N2 and N3). Both forested sites (S2 and N2) had similar annual precipitation (850–940 mm) and growing-season mean air-temperature (6.5–6.6 °C). Annual mean air-temperature differed by 0.5 °C between S2 and N2, and by 2.0 °C between S3 and N3 with a warmer climate on the south-facing slope. This is comparable to the temporal difference of 2.3 °C between the warmest and coldest years and the unchanged trend of precipitation during 1960–2008 at Nyingchi station (3000 m, ca. 10 km away from our study sites; Liang et al., 2009; Kong et al., 2012). The maximum snow depth was 80–100 cm on the north-facing slope and 20–30 cm on the south-facing slope. The spring soil warming dates (with −20 cm soil temperature >0 °C) were 20–30 days earlier on the south-facing slope than on the north-facing slope. The −5 cm soil temperature amplitude in the growing season was much lower at N2 (<1 °C) than at the sites of N3, S2 and S3 (2–5 °C). The daily mean soil moisture during the growing season was typically >20% across slopes and sites. Detailed information on the sensor types and site conditions is found in Liu and Luo (2011).

2.2. Reciprocal transplant experiment of fir and juniper old-seedlings

Our previous survey indicated that the seed-based fir seedlings were limited to a stable soil temperature environment (the −5 cm temperature amplitude <1 °C) in the north-facing forests, compared to the relatively widespread root-sprouting juniper seedlings (Liu and Luo, 2011). This suggests an explanation for the unique distribution pattern of both species treelines on opposite slopes of a valley in the Sergyemla Mountains. Knowledge of how the survival and growth of fir and juniper seedlings differ between north-facing and south-facing treeline ecotones is helpful for understanding the mortality of fir seedlings under a warmer climate. We performed a reciprocal transplant experiment of both species old-seedlings between the two slopes. In early June of 2008, fir and juniper old-seedlings (20–50 cm in height) growing well at forest edges in the two lower slopes (4180–4200 m) were selected, and then carefully dug out with soil to a depth of 20 cm. In total, 60 old-seedlings per species were sampled and randomly divided into four groups. The grouped seedlings of each species were transplanted to the four study sites (N2, N3, S2, S3) at and above both treelines. The four study sites represented two typical habitats across both slopes (forested: N2 and S2; non-forested: N3 and S2). At each site, the seedlings were planted around the weather station, at least 1 m apart. Before transplanting, the height and/or age of each seedling were measured. The ages of transplanted fir old-seedlings ranged from 10 to 15 years, which was determined by counting the internodes along the main stem. However, it was difficulty to determine the ages of juniper seedlings because the internodes were not obvious. During 2008–2012, the mortality of transplanted seedlings was recorded and their new top-shoot growth rates (cm yr^{-1}) were