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The Potential Impact of CO₂ and Air Temperature Increases on Krummholz Transformation into Arborescent Form in the Southern Siberian Mountains

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Introduction

The climate-driven impact on tree vegetation is expected to be most significant where climate variables limit tree growth, e.g., in the alpine forest-tundra ecotone (e.g., Holtmeier and Broll, 2007). It has been reported that during the last few decades, increased stand density and tree growth increments have been observed in the northern forest-tundra ecotone, which includes alpine and non-alpine ecotones (Kharuk et al., 2006; Shiyatov et al., 2007; Devi et al., 2008; Harsch et al., 2009). A number of advancing treeline cases have been reported for the alpine forest-tundra ecotones of the European, American, and Siberian mountains (Luckman and Kavanagh, 2000; Theurillat and Guisan, 2001; Klasner and Fagre, 2002; Munroe, 2003; Baker and Moseley, 2004; Kullman, 2007; Shiyatov et al., 2007; Kharuk et al., 2006, 2008, 2009; Devi et al., 2008; Lenoir et al., 2008). It has also been observed that species more common in the south have begun to appear in the northern forest communities (Payette et al., 2001; Grace et al., 2002; Smith et al., 2003; Esper and Schweingruber, 2004; Kharuk et al., 2005). Milder climates are also conducive to changes in tree morphology, i.e. transforming the mat and prostrate krummholz into their vertical form (Holtmeier, 2003; Klasner and Fagre, 2002; Munroe, 2003; Baker and Moseley, 2004; Kullman, 2007; Shiyatov et al., 2007; Kharuk et al., 2006, 2008, 2009; Devi et al., 2008; Lenoir et al., 2008). The main goal of this paper is to analyze the climate-induced changes to tree physiognomy in the alpine forest-tundra ecotone of the southern Siberian Mountains. We measured the radial and apical larch tree increments of the alpine forest-tundra ecotone. The specific questions are: (1) How widespread is the phenomenon of mat and krummholz transforming into its arborescent form? (2) When do trees start turning from krummholz into arborescent form? (3) Was this transformation connected with climate variables and CO₂ concentration in the ambient air?

Materials and Methods

The studies were conducted at the Sengilen Ridge, which is located in the Altai-Sayan mountain region in southern Siberia. This is a transition area between boreal forests and Mongolian steppes (Figs. 1 and 2). The Altai-Sayan mountain region is composed of a system of ridges with elevations up to 4500 m that is divided by a dense drainage network. The region has a severe continental climate. In January, the temperature ranges between −32 °C and −12 °C. The temperature ranges between +9 °C and +18 °C in July. Precipitation is about 390 mm yr⁻¹ (Fig. 3). Due to the prolonged severe conditions of the study area, we used “cold period” (September–May) temperatures instead of “winter period” (December–February) temperatures.

The dominant species is larch (Larix sibirica Ledeb) with an admixture of Siberian pine (Pinus sibirica Du Tour). The life span of the study area’s larches and Siberian pines is 600–700 yrs and 400–500 yrs, respectively. Larch is an anemophilous species and drops its seeds during fall and wintertime. Strong mountain winds facilitate regeneration establishment up to 200–300 m away from

Abstract

Trees in the southern Siberian Mountains forest-tundra ecotone have considerably increased their radial and apical growth increments during the last few decades. This leads to the widespread vertical transformation of mat and prostrate krummholz forms of larch (Larix sibirica Ledeb) and Siberian pine (Pinus sibirica Du Tour). An analysis of the radial growth increments showed that these transformations began in the mid-1980s. Larch showed a greater resistance to the harsh alpine environment and attained a vertical growth form in areas where Siberian pine is still krummholz. Upper larch treeline is $\pm 10$ m higher than Siberian pine treeline. Observed apical and radial growth increment increases were correlated with CO₂ concentration ($r = 0.83–0.87$), summer temperatures ($r = 0.55–0.64$), and “cold period” (i.e. September–May) air temperatures ($r = 0.36–0.37$). Positive correlation between growth increments and winter precipitation was attributed to snow cover protection for trees during wintertime.
seed trees. Siberian pine is a zoochoric species, and its dissemination is primarily dependent on a “cedarbird” (nutcracker, *Nucifraga caryocatactes*). The cedarbird efficiently distributes the Siberian pine seeds upslope. This bird also stores seeds in places suitable for germination and facilitates regeneration.

The region of study included the belt of forests at higher elevations, and the forest-alpine tundra ecotone. This is a relatively undisturbed area with no signs of grazing or wildfires. The “forest-alpine tundra ecotone” is defined as the transitional area between the regeneration line and the upper limit of closed forests. “Post-krummholz” trees (i.e., trees which attained vertical growth form from prostrate forms) were sampled on seven sites, whose elevations ranged between 2400 and 2600 m (Fig. 1). These ground studies were conducted in 2007. The tree stems were cut at their base, and then discs were sampled at the base level for analysis (sample size: 13 trees). The mean tree height was 2.6 m; the mean age was 74 yrs; the trees grew at a mean elevation of about 2500 m.

FIGURE 1. The area of investigation; the Sengilen ridge is located in Siberia’s southern Altai-Sayan Mountains. Numbers 1 to 7 indicate study plots locations.

FIGURE 2. A general view of the study area.
Discs were used for tree radial growth increment measurements. Tree ring width was measured using LINTAB-III equipment with a precision of 0.01 mm. A combination of cross-correlation analysis and graphical cross-dating was used to detect double counted and missing rings (Rinn, 1996; Holmes, 1983). For this purpose master chronology (the statistics of all tree rings for a given period and given area; Fritts, 1991) was used as a reference. The master chronology was generated on the basis of eight living larch trees and covered the years 1900–2006, and had satisfactory mean correlation and sensitivity values of 0.66 and 0.33, respectively.

Along with radial growth increment, an annual apical increment was measured based on the distance between whorls. These measurements were complicated because a tree does not always produce one visible whorl every year in a harsh treeline environment. Another source of error is shoot formation between whorls which may lead to falsely counting an “extra” whorl. Actually, measurable increment values covered the period <25 years, i.e., which corresponds to observed response of growth increments to warming and to the beginning of the krummholz transformation into a vertical form (Fig. 4). In other words, the apical increment was not measurable for the “pre-transforming” period since annual whorls were not differentiated. The resulting error in apical increment measurement was about 1–2 years; this value was estimated based on the measurements of two independent lab assistants. In this study apical increment was used as a complementary (and secondary) indicator of tree response to climate variables. Apical growth increment dynamics allows linking radial growth increment increase with transformation of the krummholz to vertical form by matching apical and radial annual increments on a year-by-year basis. For the apical growth increment 28 trees were sampled (both post-krummholz and “normal” trees) with a mean height of 5.8 m. The mean elevation of sampled trees was 2420 m.

Since growth increments of individual trees varied depending on local site conditions, the measurements were normalized for comparison purposes. The increment values (i.e. tree ring widths and distances between the whorls) of a given sample were normalized through a summation of their annual totals. This sum was made equal to 1.0. The increment value of a given year was taken to be equal to its proportion of the total sum. The increment data were processed using the method of exponential approximation to detect temporal trends. According to this method, data weights were exponentially increased within a sliding window along the window (StatSoft, 2001).

The CO₂ dynamics of ambient air data was acquired with Tans’s (2010) data. The temperature and precipitation data originated from Mitchell and Jones (2005). This information

**FIGURE 3.** (a, c) Summer and (b, d) winter temperature and precipitation anomalies for the Sengilen ridge. The solid line shows a 10-yr filter.
source provides the meteorological data averaged for half-degree grid cells (or $35 \times 55$ km). Excel and StatSoft software (StatSoft, 2001) were used for statistical analysis.

Results

CORRELATIONS

The radial increment had a positive correlation to the summer and “cold period” (September–May) temperatures (Fig. 5). The correlation value depended on the period of observation. For summer temperatures, this correlation peaked at a value of 0.64 for a period of about 20 years; for “cold period” temperatures, this correlation becomes significant for periods $>50$ yrs; $r = 0.36$ (Fig. 5). No significant correlations were observed for precipitation with the exception of “cold period” precipitation (Fig. 5). A high correlation was observed for CO$_2$ concentrations ($r = 0.87$). Apical growth increment correlated with summer ($r = 0.55$) and “cold period” ($r = 0.37$) temperatures, and CO$_2$ concentration ($r = 0.83; P \leq 0.05$).
concentration. The radial increments correlation with both factors was at $r = 0.78 (P \leq 0.01)$. 

The high correlations between radial and apical increments and CO$_2$ concentration ($r = 0.87$ and $r = 0.83$, respectively) does not necessarily mean a cause-and-effect dependence. It is known that CO$_2$ is a fertilizer, and in its present concentration is below the saturation level for photosynthesis (Canadell et al., 2007). In other words, CO$_2$ concentration is still one of the limiting factors of tree growth. Moreover, CO$_2$ concentration decreases with drops in barometric pressure, i.e. CO$_2$ limits tree growth stronger in the highlands than in the lowlands. This implies that CO$_2$ fertilization effect will be more pronounced within the alpine forest-tundra ecotone. However, Hoch and Körner (2003, 2005) suggested there is limitation of carbon investment rather than carbon acquisition at treeline. Meanwhile there is evidence that present CO$_2$ concentration partly controls tree growth. Woody species responded to CO$_2$ increase with a consistent linear increase in plant biomass from pre-industrial to ambient concentrations, and often a saturating growth response in the range 450–550 ppm (Canadell et al., 2007; Norby et al., 2010; Souza et al., 2010). A progressive nutrient (especially nitrogen) limitation is likely to be the principal factor driving the saturation (Reich et al., 2006). Since the current ambient CO$_2$ concentrations are still below that limit, these data support the hypothesis that CO$_2$ partly controlled tree growth, and especially at treeline elevations where CO$_2$ concentration drops about 25% in comparison with the lowlands.

Radial and apical growth increments also had reasonable correlation with summer temperatures ($r = 0.64$ and $r = 0.55$, respectively). In addition, lower but significant correlations were found with “cold period” temperatures ($r = 0.36$ for radial and $r = 0.37$ for apical increments). This could be explained by shoot damage during extreme winter since the correlations with observed temperature increase are not straightforward (Fig. 3, b). The synergy of low temperatures and winds, desiccation, and snow abrasion caused apical shoot decrease or mortality (Figs. 6 and 7). Resultant vertical growth of lateral branches caused formation of multiple stems. Larch could also form multiple stems by layering; this was observed, for example, on the Polar Ural Mountains (Shiyatov, personal communication). Also within the Sengilen Ridge we did not observe this phenomenon, which may be attributed to a drier climate. Siberian pine multiple stem formation, along with leader substitution by lateral branches, could also be caused by intergrowth of several seedlings stems at their base, because the before-mentioned cedarbird “planted” several seeds in one place. The mature multiple stem larches and

Discussion

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Siberian pine trees were also observed in areas below their present treelines. We consider this as evidence of position of the former treeline.

Surprisingly, the radial growth increment’s correlation to summer precipitation was not significant, whereas “cold period” precipitation had a positive impact (Fig. 5). One potential explanation involves the highly stochastic pattern of summer rain activity (Fig. 3, c). The other possible reason is that summer precipitation does not limit larch growth; larch has been known to survive in semi-arid levels of precipitation (Kloepfl et al., 1998). The third factor is rain-induced temperature decreases: snow or hail can cover the mountains even in midsummer. Radial increment positive correlation with winter precipitation could be explained by tree growth facilitation through increased soil water content. Finally, positive correlations with “cold period” precipitation could be caused by snow cover protecting the trees from winter desiccation and snow abrasion (Hadley and Smith, 1983; Bowman, 1992; Kharuk et al., 2005; Devi et al., 2008). Wind-blown snow also facilitates seedling recruitment. These seedlings in turn modify their environment, thus allowing forest advancement. This feedback was strong during 1980s, but appears to have had little effect on establishment patterns since that time (Bekker, 2005). Similar effect was observed at Sengilen Ridge: presently regeneration is “diffusing” into relatively unprotected areas (Kharuk et al., 2010a) (Fig. 9). Also within a treeline, microtopography still strongly controls seedling recruitment, which is especially significant for evergreen Siberian pine. Low mean snow deposition (about 40 cm only) and harsh environment caused chlorosis in needles and shoot mortality (Figs. 6 and 7). At the upper treeline Siberian pine grows exceptionally leeward of rock outcrops, in the protected and snow-accumulated areas. Snow accumulation facilitates Siberian seedling survival since *Pinus sibirica* is more sensitive to drought in comparison with larch; its optimal growth is about 1000 mm yr$^{-1}$, whereas larch can grow at a semi-desert level of precipitation (∼250 mm yr$^{-1}$).

A widespread transformation of krummholz into vertical forms was observed within the forest-tundra ecotone of Sengilen Ridge. Within this study area krummholz have been observed only at their upper tree limits. Currently, at the Sengilen Ridge, larch is much less likely to be found in its krummholz form than the Siberian pine. Siberian pine is a relatively “warm-adapted” species, whereas dense bark and a deciduous pattern make larch a leader in cold-tolerance among Siberian conifers. Larch attained a vertical growth form in areas where Siberian pine exists in krummholz form or suffers damage by the harsh environment. Moreover, Siberian pine establishment under the protection of larch trees was observed (Fig. 6). Regularly Siberian pine treeline is below that of larch treeline (≥10 m). We cannot compare how larch and Siberian pine respond to climate change in the study area—the canopy’s proportion of Siberian pine is too low. But in the areas where both species were present, we found indications that positive trends in temperature and precipitation had a more favorable effect on the Siberian pines (with respect to growth and regeneration amounts; Kharuk et al., 2009). The beginning of krummholz transformation into upright forms occurred during the 1986–1987 time period (Fig. 8). This date followed the upturns in the summer temperatures trend with about a 3 year lag (Fig. 8).
Thus, on the elevational tree limit in the southern Siberian Mountains larch and Siberian pine responded to warming by increasing radial and apical growth increments. This increase leads to the widespread transformation of krummholz into vertical forms. Based on the analysis of growth increments, the beginning of this transformation was started in the mid-1980s. Larch showed a greater resistance to the alpine harsh environment and attained a vertical growth form in areas where Siberian pine still grew in krummholz form. A correlation between growth increments and CO\textsubscript{2} concentration in ambient air was found, as well as with air temperature increase.

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