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# The Potential Impact of CO<sub>2</sub> and Air Temperature Increases on Krummholz Transformation into Arborescent Form in the Southern Siberian Mountains

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## 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  $\geq 10$  m higher than Siberian pine treeline. Observed apical and radial growth increment increases were correlated with CO<sub>2</sub> 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.

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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, 2007; 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; Gamache and Payette, 2004; Devi et al., 2008; Kharuk et al., 2009).

Besides the warmer ambient air, tree growth is also facilitated by higher levels of CO<sub>2</sub> (Tans, 2010). Physiological growth modeling predicts increased tree growth from the combined effect of CO<sub>2</sub> and air temperature increases (Matala et al., 2005). Based on a series of elevated CO<sub>2</sub> level experiments, Ainsworth and Long (2005) concluded that the trees were responding to the higher CO<sub>2</sub> concentrations by growth and above-ground productivity increases. Norby et al. (2005) analyzed the available data on elevated CO<sub>2</sub> experiments and concluded that the response of forest net primary productivity (NPP) to elevated CO<sub>2</sub> is highly conserved across a broad range of productivity, with a stimulation level of  $23 \pm 2\%$ .

The most significant changes in temperature are observed in, and predicted for, Siberia (IPCC, 2007), but there are still few studies of climate-driven changes for Siberian forests (Shiyatov et al., 2007; Devi et al., 2008; Kharuk et al., 2006, 2008, 2009).

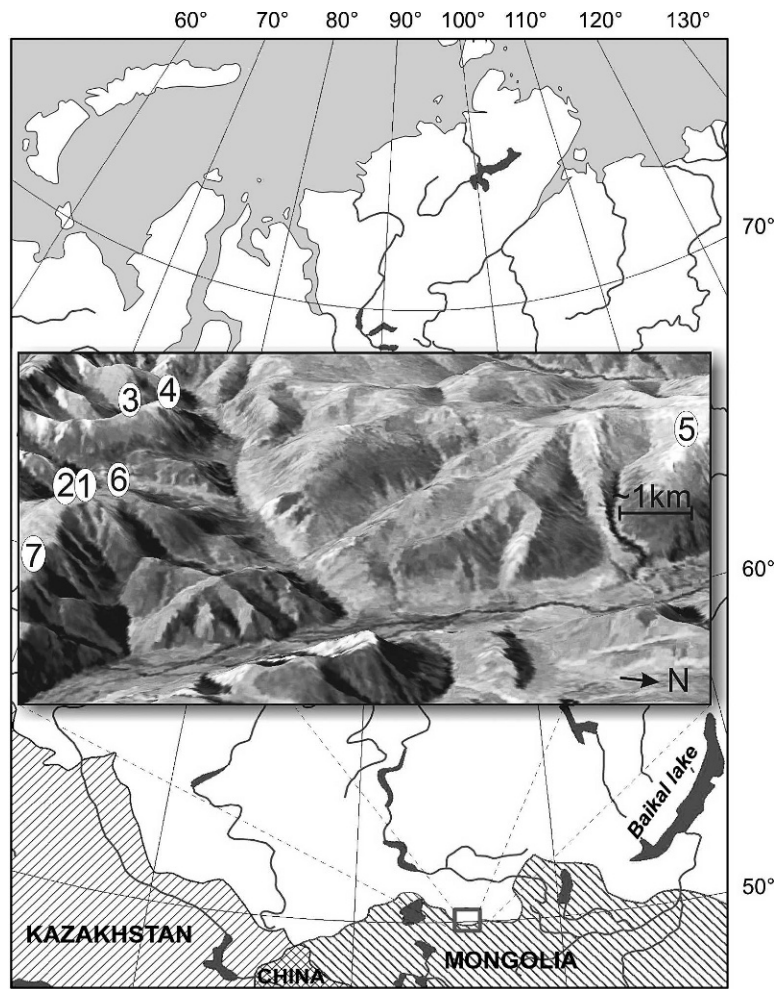
The main goal of this paper is to analyze the climate-induced changes to tree physiognomy in the alpine forest-tundra ecotone of the southern Siberian Mountains. We measured the radial and apical larch tree increments of the alpine forest-tundra ecotone.

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 CO<sub>2</sub> 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  $390 \text{ mm yr}^{-1}$  (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



**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.

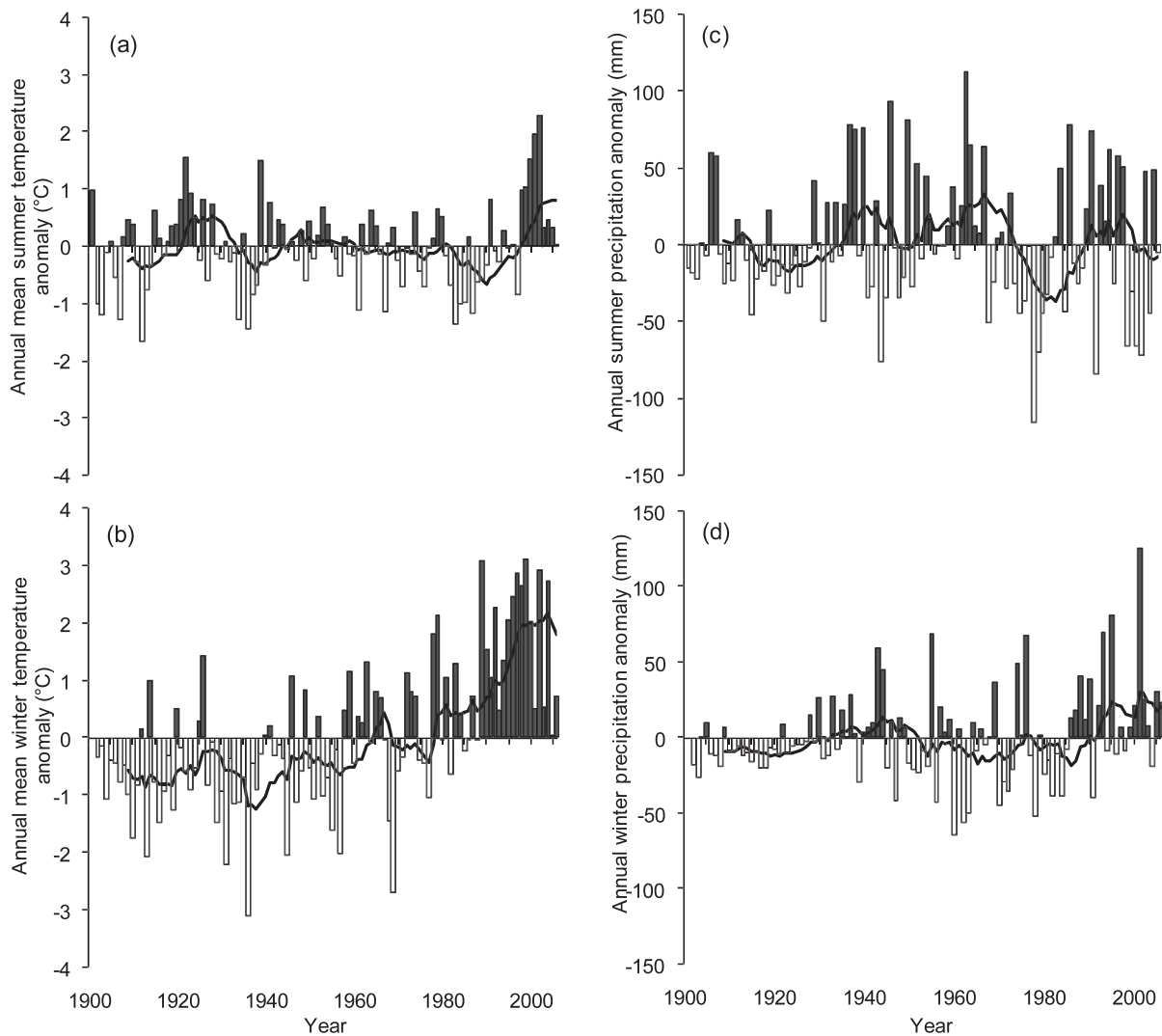
seed trees. Siberian pine is a zoochoric species, and its dissemination is primarily dependent on a “cedarbird” (nutcracker, *Nucifraga caryocatactes*). The cedarbird efficiently distributes the Siberian pine seeds upslope. This bird also stores seeds in places suitable for germination and facilitates 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 2.** A general view of the study area.



**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.

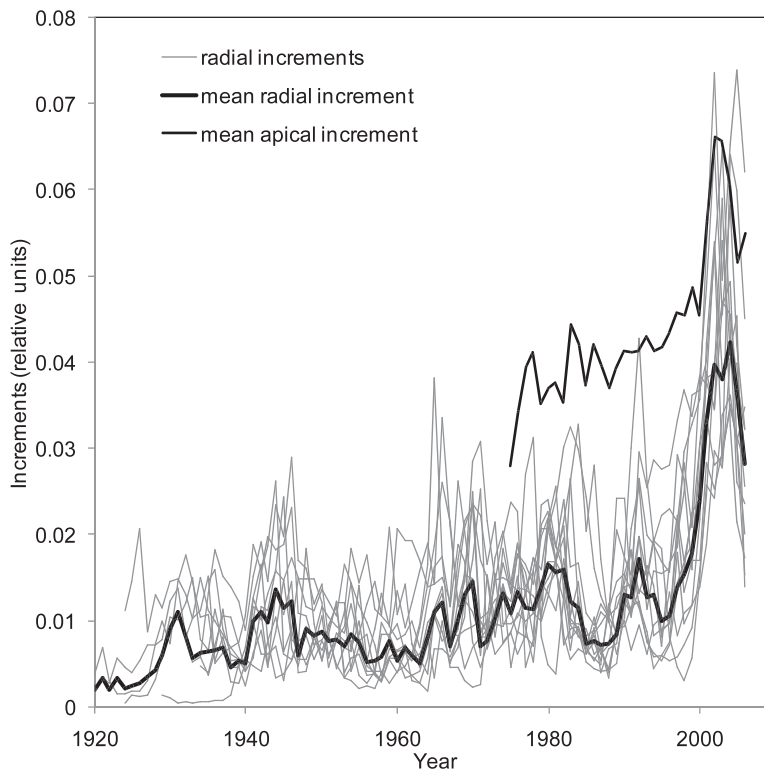
Discs were used for tree radial growth increment measurements. Tree ring width was measured using LINTAB-III equipment with a precision of 0.01 mm. A combination of cross-correlation analysis and graphical cross-dating was used to detect double counted and missing rings (Rinn, 1996; Holmes, 1983). For 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 CO<sub>2</sub> 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 4.** The radial ( $N = 13$ ,  $h \approx 2.6$  m,  $A \approx 74$  yr) and apical ( $N = 28$ ,  $h \approx 5.8$  m) dynamics of “post-krummholz” larch tree growth increment.

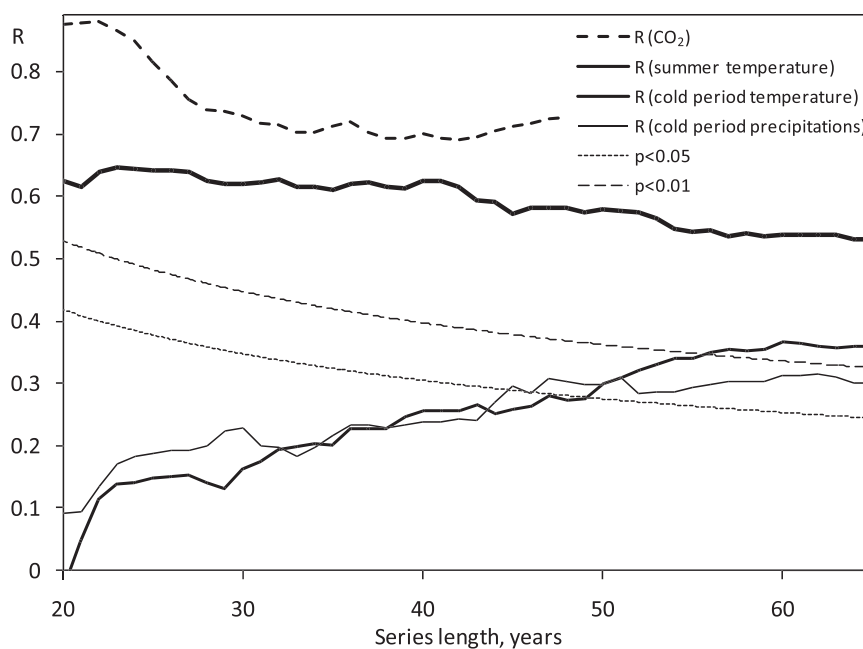
source provides the meteorological data averaged for half-degree grid cells (or  $35 \times 55$  km). Excel and StatSoft software (StatSoft, 2001) were used for statistical analysis.

## 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 ( $r = 0.83$ ;  $P \leq 0.05$ ).



**FIGURE 5.** The correlation between radial increments,  $CO_2$ , air temperature, and precipitation. The given data correspond to the analyzed series length.





**FIGURE 6. Multistem “post-krummholz” larch and prostrate Siberian pine. Apical shoot damage and needle discoloration above snow level caused by winter desiccation.**

Multiple correlation analyses showed that both factors, CO<sub>2</sub> and summer temperatures, were significant. The radial increments correlated to CO<sub>2</sub> concentration ( $r = 0.72$ ;  $P \leq 0.01$ ) and to the summer temperature ( $r = 0.58$ ;  $P \leq 0.01$ ). The radial increments correlation with both factors was at  $r = 0.78$  ( $P \leq 0.01$ ).

#### ARBORESCENT VS. KRUMMHOLZ

A widespread transformation of larch and Siberian pine krummholz into vertical or arborescent form was observed (Figs. 2, 6, and 7) with the exception of windward sites along the treeline. Notably, in the areas of highest elevation where larch can support vertical growth, Siberian pines attain a prostrate growth form, or were damaged by desiccation and snow abrasion (Figs. 6 and 7); regularly the Siberian pine treeline is below ( $\geq 10$  m) the larch treeline. “Post-krummholz” radial and apical growth increments strongly increased over the last two decades (Fig. 4). The beginning of radial growth increases was observed following the temperature minimum of the mid-1980s (Fig. 8).

In order to emphasize temporal trends the mean increment and summer temperature data were passed through an exponential filter with window width equal to 3 yrs. It is necessary to note that the filter shifted the extreme position by half of the window size, i.e., 1.5 years, Fig. 8). Figure 8 shows how the negative trend in incremental growth rate in the mid-1960s turned positive after the mid-1980s. The beginning of positive growth trend follows the positive temperature trend with 3 year lag (Fig. 8). The CO<sub>2</sub> concentration rate was approximately linear for the entire period of observations (Fig. 8).

### Discussion

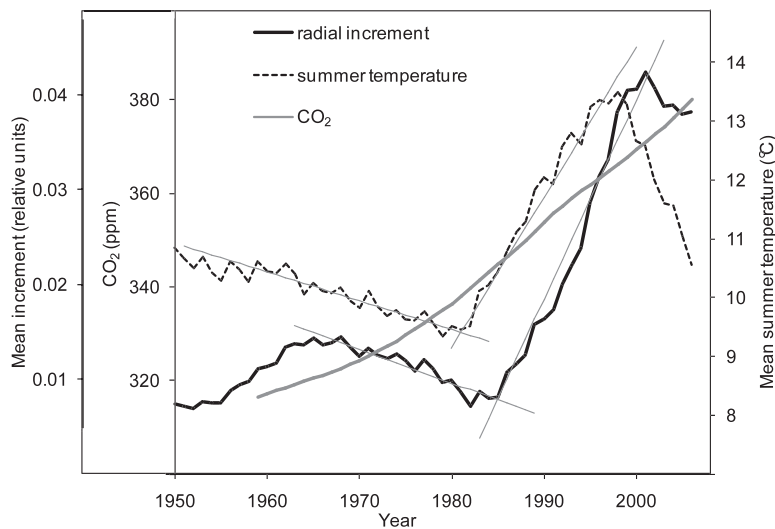
The high correlations between radial and apical increments and CO<sub>2</sub> concentration ( $r = 0.87$  and  $r = 0.83$ , respectively) does not necessarily mean a cause-and-effect dependence. It is known that CO<sub>2</sub> is a fertilizer, and in its present concentration is below the saturation level for photosynthesis (Canadell et al., 2007). In other words, CO<sub>2</sub> concentration is still one of the limiting factors of tree growth. Moreover, CO<sub>2</sub> concentration decreases with drops in barometric pressure, i.e. CO<sub>2</sub> limits tree growth stronger in the



**FIGURE 7. Within the alpine forest-tundra ecotone Siberian pine became established within sheltered microsites. Needles and stems above snow level were damaged by desiccation and snow abrasion, whereas larches were not damaged.**

highlands than in the lowlands. This implies that CO<sub>2</sub> 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<sub>2</sub> concentration partly controls tree growth. Woody species responded to CO<sub>2</sub> 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<sub>2</sub> concentrations are still below that limit, these data support the hypothesis that CO<sub>2</sub> partly controlled tree growth, and especially at treeline elevations where CO<sub>2</sub> 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



**FIGURE 8.** The dynamics of radial increment, summer temperature, and CO<sub>2</sub>. Trends in radial increment and summer temperature are shown by straight lines. Data were passed through an exponential filter with a three year window size. The filter shifted the extreme position for about two years.

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 ( $\sim 250 \text{ mm yr}^{-1}$ ; Kloeppe 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  $1000 \text{ mm yr}^{-1}$ , whereas larch can grow at a semi-desert level of precipitation ( $\sim 250 \text{ mm yr}^{-1}$ ).

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 ( $\geq 10 \text{ m}$ ). 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).



**FIGURE 9.** Larch is "diffusing" along the elevation gradient. Larch and Siberian pine regeneration survived at elevations up to 160 m higher in comparison with the maximum observed treeline recession during the Little Ice Age (Kharuk et al., 2010b).





**FIGURE 10.** Leafless larch stem is alive due to bark photosynthesis which is facilitating the trees' survival in harsh environment. Inset photo: bark chlorophyll under phellem.

In Swedish Scandia Kullman (2007), based on a 32 year monitoring period (1973–2005) of the *Pinus sylvestris* population's treeline, described two subperiods (1973–1987 and 1988–2005) viz. decline and increase, respectively. Surprisingly, these observations coincide with tree radial increment dynamics observed in Sengilen Ridge in south Eurasia (Fig. 8). Krummholz transformations into vertical forms were also reported for other parts of the southern Siberian Mountains (Kharuk et al., 2008, 2009).

The observed krummholz transformation into vertical forms is an indicator of milder wintertime wind regime; it is known that wind impact is significant for krummholz formation (e.g., Kullman and Kjällgren, 2006; Holtmeier and Broll, 2010). The second evidence of milder wind regime is tree migration to the relatively poorly sheltered areas which was observed during the last decades (Kharuk et al., 2010b).

Finally, there is a factor that facilitates tree survival and post-krummholz formation in harsh environments: this is “bark photosynthesis”. Even some leafless shoots were found to have been alive due to the bark chlorophyll that was observed under the phellem (Fig. 10). In some species the bark was responsible for 10–15% of the tree's entire carbon balance (Kharouk et al., 1995). According to Cernusak and Marshall (2000), bark photosynthetic refixation in branches of *Pinus monticola* Dougl reaches ~75% of dark respiration. Live larch stems with a few needles at the upper tree limit may indicate that in environmental extremes bark photosynthesis can support almost total dark respiration (which can be called the “cactus-effect”). We made similar observations for some willow species.

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<sub>2</sub> concentration in ambient air was found, as well as with air temperature increase.

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## References Cited

- Ainsworth, E. A., and Long, S. P., 2005: What have we learned from 15 years of free-air CO<sub>2</sub> enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO<sub>2</sub>. *New Phytologist*, 165(2): 351–371.
- Baker, B. B., and Moseley, R. K., 2007: Advancing treeline and retreating glaciers: implications for conservation in Yunnan, P. R. China. *Arctic, Antarctic, and Alpine Research*, 39(2): 200–209.
- Bekker, M., 2005: Positive feedback between tree establishment and patterns of subalpine forest advancement, Glacier National Park, Montana, U.S.A. *Arctic, Antarctic, and Alpine Research*, 37(1): 97–107.
- Bowman, W. D., 1992: Inputs and storage of nitrogen in winter snowpack in an alpine ecosystem. *Arctic and Alpine Research*, 24: 211–215.
- Canadell, J. G., Pataki, D. E., Gifford, R., Houghton, R. A., Luo, Y., Raupach, M. R., Smith, P., and Steffen, W., 2007: Saturation of the terrestrial carbon sink. In Canadell, J. G., Pataki, D., and Pitelka, L. (eds.), *Terrestrial Ecosystems in a Changing World*. The IGBP Series. Berlin Heidelberg: Springer-Verlag, 59–78.
- Cernusak, L. A., and Marshall, J. D., 2000: Photosynthetic refixation in branches of Western white pine. *Functional Ecology*, 14: 300–311.
- Devi, N., Hagedorn, F., Moiseev, P., Bugmann, H., Shiyatov, S., Mazepa, V., and Rigling, A., 2008: Expanding forests and changing growth forms of Siberian larch at the Polar Urals treeline during the 20th century. *Global Change Biology*, 14(7): 1581–1591.
- Esper, J., and Schweingruber, F. H., 2004: Large-scale treeline changes recorded in Siberia. *Geophysical Research Letters*, 31: L06202, doi:10.1029/2003GL019178.
- Fritts, H. C., 1991: *Reconstruction Large-Scale Climatic Patterns from Tree-Ring Data: a Diagnostic Analysis*. Tucson-London: University of Arizona Press, 286 pp.
- Gamache, I., and Payette, S., 2004: Height growth response of treeline black spruce to recent climate warming across the forest-tundra of eastern Canada. *Journal of Ecology*, 92: 835–845.
- Grace, J., Berninger, F., and Nagy, L., 2002: Impacts of climate change on the treeline. *Annals of Botany*, 90: 537–544.
- Hadley, J. L., and Smith, W. K., 1983: Influence of wind exposure on needle desiccation and mortality for timberline conifers in Wyoming, USA. *Arctic and Alpine Research*, 15: 127–135.
- Harsch, M., Hulme, P., McGlone, M., and Duncan, R., 2009: Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecology Letters*, 12(1): 1040–1049.



- Hoch, G., and Körner, C., 2003: The carbon charging of pines at the climatic treeline: a global comparison. *Oecologia*, 135: 10–21.
- Hoch, G., and Körner, C., 2005: Growth, demography and carbon relations of *Polylepis* trees at the world's highest treeline. *Functional Ecology*, 19(6): 941–951.
- Holmes, R. L., 1983: Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bulletin*, 43: 69–78.
- Holtmeier, F.-K., 2003: *Mountain Timberlines: Ecology, Patchiness, and Dynamics*. Dordrecht, Netherlands: Kluwer Academic Publishers, 438 pp.
- Holtmeier, F.-K., and Broll, G., 2007: Treeline advance—Driving processes and adverse factors. *Landscape Online*, 1: 1–33.
- Holtmeier, F.-K., and Broll, G., 2010: Wind as an ecological agent at treelines in North America, the Alps, and the European Subarctic. *Physical Geography*, 31(3): 203–233.
- IPCC, 2007, *Climate Change 2007: Synthesis Report*. Valencia, Spain, <[http://www.ipcc.ch/pdf/assessment-report/ar4/syr/ar4\\_syr\\_spm.pdf](http://www.ipcc.ch/pdf/assessment-report/ar4/syr/ar4_syr_spm.pdf)>. Last accessed on 14 December 2009.
- Kharouk, V. I., Middleton, E. M., Spencer, S. L., Rock, B. N., and Williams, D. L., 1995: Aspen bark photosynthesis and its significance to remote sensing and carbon budget estimates in the boreal ecosystem. *Journal of Water, Air and Soil Pollution*, 82: 483–497.
- Kharuk, V. I., Dvinskaya, M. L., Ranson, K. J., and Im, S. T., 2005: Expansion of evergreen conifers to the larch-dominated zone and climatic trends. *Russian Journal of Ecology*, 36(3): 164–170.
- Kharuk, V. I., Ranson, K. J., Im, S. T., and Dvinskaya, M. L., 2006: Forest-tundra larch forests and climatic trends. *Russian Journal of Ecology*, 37(5): 291–298.
- Kharuk, V. I., Dvinskaya, M. L., Im, S. T., and Ranson, K. J., 2008: Tree vegetation of the forest-tundra ecotone in the Western Sayan Mountains and climatic trends. *Russian Journal of Ecology*, 39(1): 8–13.
- Kharuk, V. I., Ranson, K. J., Im, S. T., and Dvinskaya, M. L., 2009: *Pinus sibirica* and *Larix sibirica* response to climate change in southern Siberian alpine forest-tundra ecotone. *Scandinavian Journal of Forest Research*, 24(2): 130–139.
- Kharuk, V. I., Ranson, K. J., Im, S. T., and Vdovin, A. S., 2010a: Spatial distribution and temporal dynamics of high elevation forest stands in southern Siberia. *Global Ecology and Biogeography Journal*, 19: 822–830.
- Kharuk, V. I., Im, S. T., Dvinskaya, M. L., and Ranson, K. J., 2010b: Climate-induced mountain treeline evolution in southern Siberia. *Scandinavian Journal of Forest Research*, 25(5): 446–454.
- Klasner, F. L., and Fagre, D. B., 2002: A half century of change in alpine treeline patterns at Glacier National Park, Montana, U.S.A. *Arctic, Antarctic, and Alpine Research*, 34: 49–56.
- Kloeppel, B. D., Gower, S. T., Trechel, I. W., and Kharouk, V. I., 1998: Foliar carbon isotope discrimination in *Larix* species and sympatric evergreen conifers: a global comparison. *Oecologia*, 114: 153–159.
- Kullman, L., 2007: Treeline population monitoring of *Pinus sylvestris* in the Swedish Scandes, 1973–2005: implications for treeline theory and climate change ecology. *Journal of Ecology*, 95: 41–52.
- Kullman, L., and Kjällgren, L., 2006: Holocene pine tree-line evolution in the Swedish Scandes: recent tree-line rise and climate change in a long-term perspective. *Boreas*, 35: 159–168.
- Lenoir, J., Gegout, J. C., Marquet, P. A., de Ruffray, P., and Brisse, H., 2008: A significant upward shift in plant species optimum elevation during the 20th century. *Science*, 320(5884): 1768–1771.
- Luckman, B. H., and Kavanagh, T., 2000: Impact of climate fluctuations on mountain environments in the Canadian Rockies. *Ambio*, 29: 371–380.
- Matala, J., Ojansuu, R., Peltola, H., Sievänen, R., and Kellomäki, S., 2005: Introducing effects of temperature and CO<sub>2</sub> elevation on tree growth into a statistical growth and yield model. *Ecological Modelling*, 181(2–3): 173–190.
- Mitchell, T. D., and Jones, P. D., 2005: An improved method of constructing a database of monthly climate observations and associated high resolution grids. *International Journal of Climatology*, 25(6): 693–712.
- Munroe, J. S., 2003: Estimates of Little Ace Age climate inferred through historical rephotography, northern Uinta Mountains, USA. *Arctic, Antarctic, and Alpine Research*, 35(4): 489–498.
- Norby, R., Warren, J., Iversen, C., Medlyn, B., and McMurtrie, R., 2010: CO<sub>2</sub> enhancement of forest productivity constrained by limited nitrogen availability. *Proceedings of the National Academy of Sciences*, 107: 19368–19373.
- Norby, R. J., DeLucia, E. H., Gielen, B., Calfapietra, C., Giardina, C. P., King, J. S., Ledford, J., McCarthy, H. R., Moore, D. J. P., Ceulemans, R., De Angelis, P., Finzi, A. C., Karnosky, D. F., Kubiske, M. E., Lukac, M., Pregitzer, K. S., Scarascia-Mugnozza, G. E., Schlesinger, W. H., and Oren, R., 2005: Forest response to elevated CO<sub>2</sub> is conserved across a broad range of productivity. *Proceedings of the National Academy of Sciences*, 102: 18052–18056.
- Payette, S., Fortin, M., and Gamache, I., 2001: The subarctic forest-tundra: the structure of a biome in a changing climate. *BioScience*, 51(9): 709–718.
- Reich, P. B., Hobbie, S. E., Lee, T., Ellsworth, D. S., West, J. B., Tilman, D., Knops, J. M. H., Naeem, S., and Trost, J., 2006: Nitrogen limitation constrains sustainability of ecosystem response to CO<sub>2</sub>. *Nature*, 440: 922–925.
- Rinn, F., 1996: *TSAP V 3.6 reference manual: computer program for tree-ring analysis and presentation*. Heidelberg: Rinntech, 263 pp.
- Shiyatov, S. G., Terent'ev, M. M., Fomin, V. V., and Zimmermann, N. E., 2007: Altitudinal and horizontal shifts of the upper boundaries of open and closed forests in the Polar Urals in the 20th century. *Russian Journal of Ecology*, 4(38): 223–227.
- Smith, W. K., Germino, M. J., Hancock, T. E., and Johnson, D. M., 2003: Another perspective on altitudinal limits of alpine timberlines. *Tree Physiology*, 23: 1101–1112.
- Souza, L., Belote, R. T., Kardol, P., Weltzin, J. F., and Norby, R. J., 2010: CO<sub>2</sub> enrichment increased forest understory biomass and accelerates successional development of an understory community. *Journal of Plant Ecology*, 3: 33–39.
- StatSoft Inc., 2001, *Electronic Book of Statistics*. Moscow: StatSoft, <<http://www.statsoft.ru/home/textbook/default.htm>>. Last accessed on 14 December 2009 (in Russian).
- Tans, P., 2010: *NOAA/ESRL*. <<http://www.esrl.noaa.gov/gmd/ccgg/trends/>>. Last accessed on 2 August 2010.
- Theurillat, J. P., and Guisan, A., 2001: Potential impact of climate change on vegetation in the European Alps: a review. *Climatic Change*, 50: 77–109.

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