

Tree-Line Structure and Dynamics at the Northern Limit of the Larch Forest: Anabar Plateau, Siberia, Russia

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Abstract

The goal of the study was to provide an analysis of climate impact before, during, and after the Little Ice Age (LIA) on the larch (*Larix gmelinii*) tree line at the northern extreme of Siberian forests. Recent decadal climate change impacts on the tree line, regeneration abundance, and age structure were analyzed.

The location of the study area was within the forest-tundra ecotone (elevation range 170–450 m) in the Anabar Plateau, northern Siberia. Field studies were conducted along elevational transects. Tree natality/mortality and radial increment were determined based on dendrochronology analyses. Tree morphology, number of living and subfossil trees, regeneration abundance, and age structure were studied. Locations of pre-LIA, LIA, and post-LIA tree lines and refugia boundaries were established. Long-term climate variables and drought index were included in the analysis.

It was found that tree mortality from the 16th century through the beginning of the 19th century caused a downward tree line recession. Sparse larch stands experienced deforestation, transforming into tundra with isolated relict trees. The maximum tree mortality and radial growth decrease were observed to have occurred at the beginning of 18th century. Now larch, at its northern boundary in Siberia, is migrating into tundra areas. Upward tree migration was induced by warming in the middle of the 19th century. Refugia played an important role in repopulation of the forest-tundra ecotone by providing a seed source and shelter for recruitment of larch regeneration. Currently this ecotone is being repopulated mainly by tree cohorts that were established after the 1930s. The last two decades of warming did not result in an acceleration of regeneration recruitment because of increased drought conditions. The regeneration line reached (but did not exceed) the pre-LIA tree line location, although contemporary tree heights and stand densities are comparatively lower than in the pre-LIA period. The mean rate of tree line upward migration has been about 0.35 m yr^{-1} (with a range of $0.21\text{--}0.58$), which translates to a tree line response to temperature of about $55 \text{ m }^{\circ}\text{C}^{-1}$.

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Introduction

Tree response to observed climate change is expected to be significant at the climate-driven alpine and northern forest-tundra ecotones (i.e., the transitional area between the latitudinal or upper elevational limits of closed forests and tundra) (Harsch and Bader, 2011).

The northern forest-tundra ecotone in Asia is formed by larch (*Larix* spp.), the genus that comprises about 40% of forested areas of Russia and occupies about 70% of the permafrost areas in Siberia (Forest Fund of Russia, 2003). Within permafrost areas, larch competes effectively with other tree species because of its deciduous leaf habit and dense bark that protects stems from winter desiccation and snow abrasion (Shiyatov et al., 2007). In Eastern Siberia (i.e., eastward of the Yenisei River) the tree line is formed sequentially by *Larix sibirica*, *L. gmelinii*, and *L. cajanderi*, with the northern limit at about $72^{\circ}30'\text{N}$. Due to the mountainous topography of this area, the northern tree line is formed by both elevational and latitudinal temperature gradients.

The response of trees to climate change was predicted as expansion of the forest into the tundra and invasion of relatively warmer-adapted species into the established larch range (e.g.,

Richardson and Friedland, 2009). These predictions have been verified by observations worldwide. For example, the climate-driven invasion of *Pinus sibirica* and *Picea obovata* into forested regions dominated by larch has been reported (Kharuk et al., 2005). Upslope shift of the tree-line position was found in the Putorana Mountains in northern Siberia (Kirdyanov et al., 2011). For the most northward larch forest at Ary-Mas, Russia ($\sim 72^{\circ}\text{N}$), increased stand densification and regeneration advance into the tundra were documented by Kharuk et al. (2006). Similar observations were published for a number of sites within European and North American mountains (e.g., Klasner and Fagre, 2002; Kullman and Kjällgren, 2006). In the studies of Kullman and Öberg (2009), a 70- to 90-m upward shift of *Betula pubescens*, *Picea abies*, and *Pinus sylvestris* in the Swedish Scandes over the past century was reported.

The beginning of the observed upward migration of the tree line was at the end of the Little Ice Age (LIA). Thus, Munroe (2003) found a 60- to 180-m upward forest line shift since 1870 in the Uinta Mountains in western North America. LIA cooling caused transformation from a sparse forest structure within forest-tundra ecotone to near-tundra conditions (Kullman, 2007). Surviving trees were limited to refugia (i.e., locations able to support

living trees). Post-LIA warming caused re-colonization of the tundra area (e.g., Holtmeier, 2009; Körner, 2012). During this process refugia provided a seed source for seedling establishment. Also, tree population within the forest-tundra ecotones has dramatically increased worldwide since the LIA, but in some areas the current tree line has not yet reached its pre-LIA location (e.g., Shiyatov et al., 2007). During the last decades of warming, densification in tree line populations was more frequently occurring than actual elevational tree line advance (Kullman, 2007; Harsch et al., 2009).

The above-mentioned studies of climate impact in the past offer insights into the potential responses of forests to anticipated future warming (Kullman, 2005; Holtmeier, 2009). Meanwhile, there are only a few such studies for the subcontinent between the Ural Mountains and the Pacific Ocean (Esper and Schweingruber, 2004; Kharuk et al., 2006; Shiyatov et al., 2007; Devi et al., 2008). There are no studies at all for *Larix gmelinii* areas, which are within “hot spots” of observed and predicted climate change (IPCC, 2007).

The goal of this study was to analyze the *Larix gmelinii* tree line response to former (i.e., LIA) and current air temperature and precipitation changes within extreme northern Siberia forests (i.e., the Anabar Plateau; Fig. 1). We seek to answer the following questions: (1) Where were the tree line locations before, during, and after the LIA? (2) What was the impact of the post-LIA and recent climate changes on the forest re-population? (3) What is the rate of climate-induced upward tree migration?

Materials and Methods

STUDY AREA

The study area was located within the Anabar Plateau, part of the Siberian platform within the Kotuykan and the Kotuy Rivers watershed (Fig. 1) in Russia. The topography of the Anabar Plateau is gently sloping with maximal elevations of about 800–900 m. The plateau is composed of slates, gneisses, and granites (with maximal age about 3.5 billion years). The topography was shaped by ancient glaciation and rivers dissected into steep-sided valleys. The study area landscape, the forest type, and the climate are typical for the pre-tundra forests between the Yenisei and Lena Rivers (shaded on Fig. 1; Vinokurov et al., 2005). This region has minimal anthropogenic impact (population is <1 person per 100 km²). Forests are comprised of *Larix gmelinii* (Rupr.) with lichen and moss as a typical ground cover and underlain by clayey permafrost soils. Stands with a mean crown closure of about 0.3 (with mean up to 0.6 within protected and drained sites) were located within river valleys. The mean tree height was 6.6 ± 2.3 m, diameter at breast height (dbh) 12.5 ± 2.3 cm, and density 340 ± 160 trees ha⁻¹; age >250 years. Shrubs present included *Betula nana* L., *Juniperus* sp., *Rhododendron aureus*, and *Ledum palustre* L. Southern-facing terraces were partly covered by grass communities. The forest-tundra ecotone occupied the 200- to 500-m elevation belt (mean upper tree line limit is about 450 m a.s.l.). Stony tundra occupied areas above 320–500 m. There were no visible signs of fires within the forest-tundra ecotone.

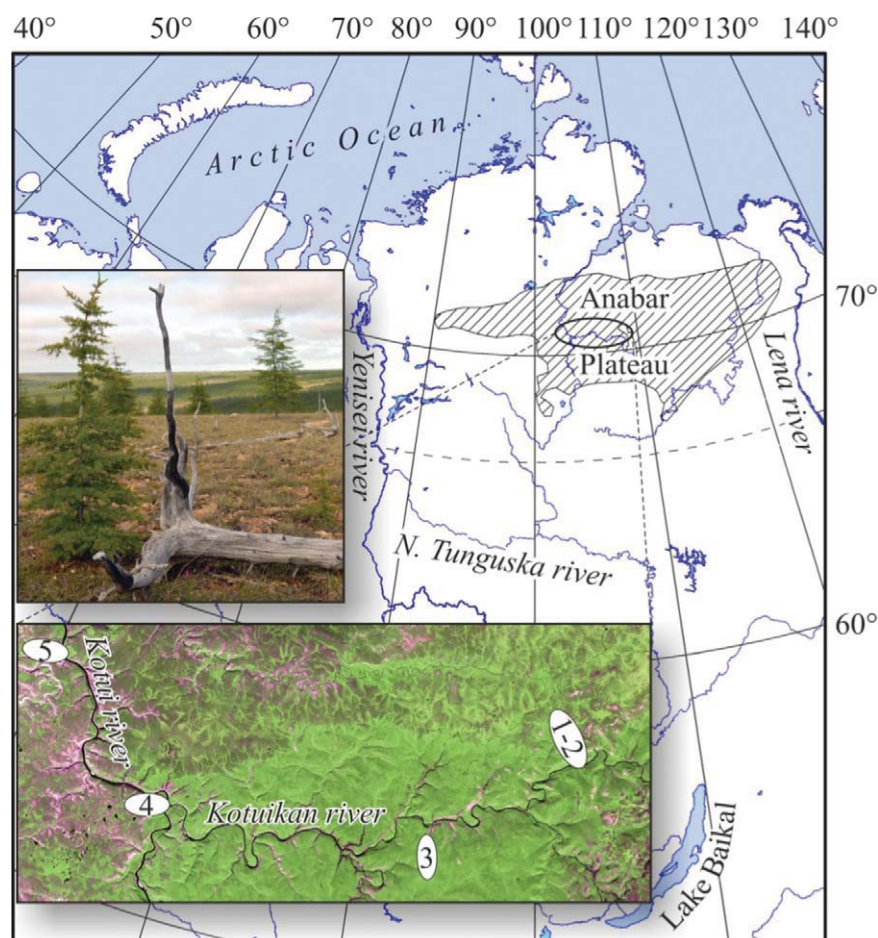


FIGURE 1. Sketch map of the study area with location of transects 1–5. Study areas were typical for shaded region on the map. Inset: a portion of the Landsat scene with locations of study transects (green: larch stands; pink: tundra and forest-tundra zones). Small inset: sub-fossil trees are sheltering regeneration.

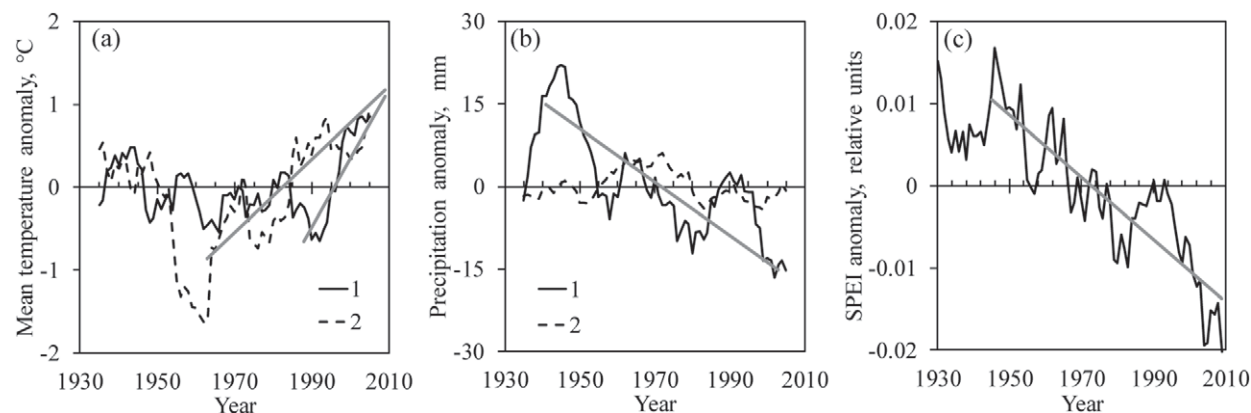


FIGURE 2. (a) Temperature, (b) precipitation, and (c) Standardized Precipitation-Evapotranspiration Index (SPEI) anomalies (filtered with 10-yr window). 1—summer; 2—cold period (Sept–May). Trends are significant ($P < 0.05$).

CLIMATE

The climate of the area is strongly continental with long severe winters and short summers. Frequent and extreme weather changes are typical. Mean annual, winter, and summer temperatures are -14 , -35 , and $+9^{\circ}\text{C}$, respectively. Average summer, winter, and annual precipitation is 120, 33, and 267 mm, respectively (reference period: 1930–2009; i.e. since the beginning of instrumental observations). Since about 1980, the year when annual temperature values crossed the perennial mean (Fig. 2, part a), mean summer temperature has been $+9.1^{\circ}\text{C}$, and annual precipitation about 259 mm (115 mm and 32 mm in summer and winter periods, respectively). Since the period with freezing temperatures was about 250 days, the “cold period” (i.e., September–May) was considered (instead of the traditional winter season). A positive warming trend has been observed since the 1970s for the “cold period” and since the 1990s for summer. A negative trend in summer precipitation has been observed since 1950 (Fig. 2, parts a and b). Climate variables were obtained from the CRU TS3.1 data set (CRU TS3.1, KNMI Climate Explorer; <http://climexp.knmi.nl>) and were extrapolated by a 0.5° latitude and longitude grid (Mitchell and Jones, 2005). Temperatures were determined as mean values for the reference season (e.g., May–August), and then averaged for the base period 1930–2009. Precipitation was determined as the sum of values for the reference season and then averaged for the base period 1930–2009.

SPEI (THE STANDARDIZED PRECIPITATION-EVAPOTRANSPIRATION INDEX)

For estimation of the water balance, the Standardized Precipitation-Evapotranspiration Index (SPEI; Vicente-Serrano et al., 2010) was used. Like the PDSI (Palmer Drought Severity Index; Palmer, 1965), and the SPI (Standardized Precipitation Index; Hayes et al., 1999), the SPEI can measure drought severity according to its intensity and duration, and can identify the onset and end of drought episodes. The SPEI uses the monthly difference (D_i) between precipitation (P) and PET (potential evapotranspiration):

$$D_i = P_i - PET_i \quad (1)$$

PET (mm) is obtained by:

$$PET = 16 \cdot K \cdot (10 \cdot T \cdot I^{-1})^m, \quad (2)$$

where T is the monthly mean temperature in $^{\circ}\text{C}$; I is a heat index, which is calculated as the sum of 12 monthly index values [$I = (T/5)^{1.514}$], m is a coefficient depending on I , and K is a correction coefficient computed as a function of the latitude and month, which takes into account number of sun hours in a day. Within the study area, SPEI showed a strong decrease since 1950 (Fig. 2, part c). A map generated from calculated SPEI for northeast Siberia (Fig. 3) indicates that the study area is in a region of negative SPEI values.

FIELD STUDIES

In the year 2008 five transects were established within the forest-tundra ecotone and oriented along the elevation gradient (Fig. 1; Table 1). Initially transect selection was based on topographic maps and Landsat scenes. Sites with distinctive forest-tundra ecotone were selected. Field studies revealed that transects 1–3 had a very short forest-tundra zone (Appendix Figs. A1–A3). Actually only transects 4 and 5 had clearly defined forest-tundra ecotones (Appendix Fig. A4). The other constraint was the presence of sufficient intact (i.e., not rotten) subfossil wood for tracking tree-line evolution. Field studies showed that only within transect 5 was subfossil wood present in an amount and quality sufficient for dendrochronology analysis, i.e., the main source of data for this climate-induced tree line evolution study. All transects originated within closed stands, and ended within alpine tundra (with no signs of regeneration, living, or fossil trees). Transect width was 20 m.

TABLE 1
Elevation transects data

#	Transect start (m a.s.l.)	Transect end (m a.s.l.)	Δ elevation (m)	Total length (m)
1	150	440	290	2050
2	370	440	70	630
3	400	430	30	2020
4	150	290	140	1310
5	170	350	180	1760

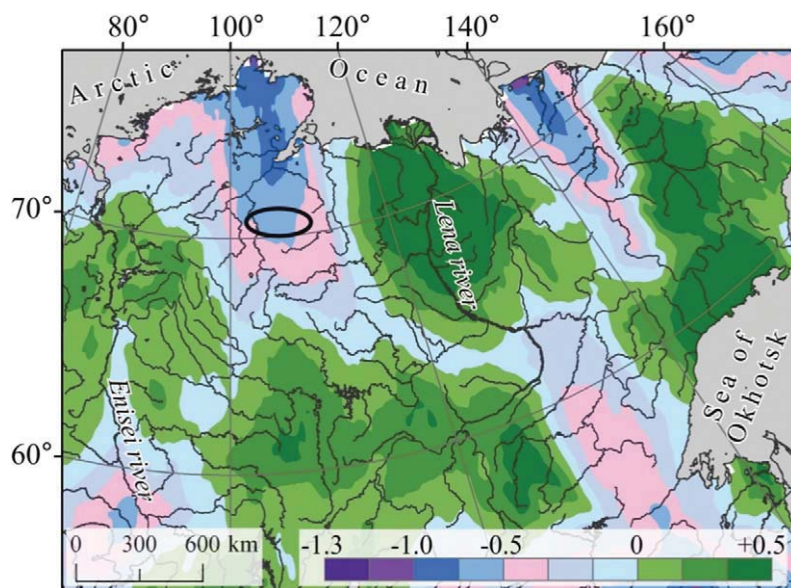


FIGURE 3. A map of SPEI values for Northeast Siberia. Data averaged for period 2000–2009. Study area location indicated by oval. Inset scale (right): SPEI anomaly.

Living and subfossil trees and regeneration were sampled within plots established along the transects, or within the entire transect area, depending on abundance of trees. In the first case, test plots (10×10 m with triple replication) were established within a 10 m elevation range. In the case of very sparse material (<100 trees ha^{-1}), all regeneration, living, or subfossil trees within a sequential 10-m elevation range were sampled. Plots were referenced to the midpoint of a given range. Sample plots were also established whenever a non-even distribution of trees was encountered, such as strips of trees/regeneration along relief features. The measured parameters were: tree heights and diameters, density of living and subfossil trees, regeneration abundance, and age structure.

Living trees were sampled at the root collar by cutting disks for dendrochronology analysis. Disks from subfossil wood were sampled at the position nearest the root collar. Subfossil wood resting on stony ground was well preserved. On the contrary, in isolated old-growth stands (i.e., refugia), subfossil wood was typically rotted and not suitable for dendrochronology analysis because of excessively moist moss and lichen ground cover.

The following tree-line limits were georeferenced: regeneration line; current, pre-LIA, and refugee tree lines; and upper limits of refugia. The regeneration line was defined as the highest observed position of regeneration. Regeneration is defined as tree vegetation with age ≤ 30 years. Definitions that are based on the tree height (e.g., 2.5 m; Holtmeier, 2009) were not applicable at least for the upper ecotone, since for 2.5-m-tall trees age may vary within 30–80 years. The current tree line was defined as an upper limit of trees with age > 30 years. The pre-LIA line was determined as the highest elevation where subfossil tree remains were found. The refugee tree line was identified from trees that survived the LIA (age > 300 years). The refugia line was defined as the upper boundary of stands that survived the LIA.

DENDROCHRONOLOGY ANALYSIS

The surface of each sampled disk was sanded, planed with a scalpel, and treated with a contrast-enhancing powder. The tree-ring width was measured with 0.01-mm precision using a linear



FIGURE 4. Single Little Ice Age (LIA) “survivors” (middle of photos; age > 400 yr) were found at more than 100 m upward in elevation of refugium border. These trees facilitate regeneration reproduction as the climate warms.

table instrument (Lintab-III). The COFFECHA (Holmes, 1983) and TSAP (Rinn, 1996) programs were used to detect missing rings. Due to the harsh growth conditions, even some very old trees (400–700 years old) had diameters of only 13–15 cm (Fig. 4). A master chronology method (Fritts, 1991) was used for determining dates of subfossil tree natality/mortality, as well as living tree natality. The master chronology for the study region was generated by Naurzbaev and Vaganov (2000). We included in the analysis 34 subfossil and 5 living trees (all which were collected along transect #5). Mean tree-ring width chronology was constructed using a combination of all individual series. Individual ring width series were “detrended” by exponential approximation (Cook and Kairiukstis, 1990). Correlation between individual series (i.e., data of sampled subfossil and living trees) and the master chronology were very high (0.5–0.89). Dendrochronological parameters were strongly correlated with all individual series with average mean sensitivity of 0.57, series intercorrelation of 0.61, standard deviation of 0.18, and autocorrelation of 0.56. The average percentage of missing rings was 1.78. In most cases, the sapwood of subfossil trees was well-preserved, and the estimated error of mortality dates did not exceed 5–10 years. About 15% of samples lacked the outer woody portion (i.e. sapwood); in this case the estimated error was about 20–40 years. Statistical analysis was based on Excel and Statsoft software (StatSoft, 2001). Student’s *t*-test was used to estimate significance of the result.

Results

AGE STRUCTURE OF TREES AND REGENERATION

The age distribution showed that both regeneration and mature trees were mainly established during the last 80 years (Fig. 5). Data for Figures 5–9 are presented for transect #5, the only transect with sufficient sampled subfossil trees suitable for analysis. Within the forest-tundra ecotone (175–350 m elevation range) tree age was not significantly dependent on elevation, whereas tree height decreased

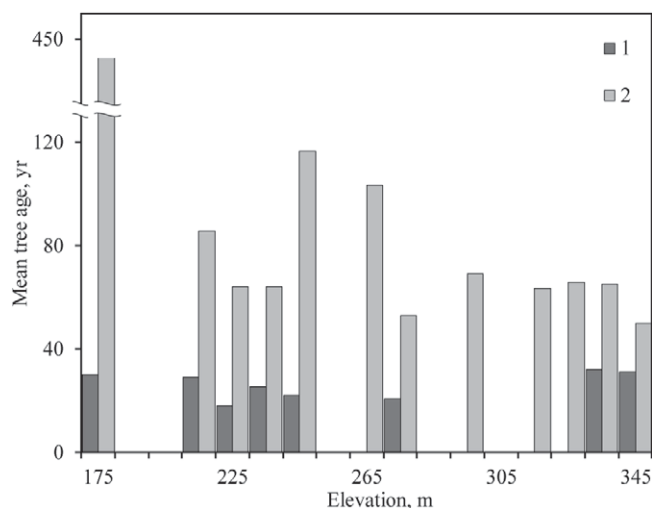


FIGURE 6. Mean tree age distribution along the elevation gradient. 1—regeneration, 2—trees.

with increasing elevation (Figs. 6 and 7). A tree cohort with ages of 60–70 years was found even within the areas without regeneration (i.e., elevation range of 295–325 m; Fig. 6). The upper regeneration limit occurred where krummholz were prevalent. Tree density also exceeded regeneration density (about 15 trees ha^{-1} vs. 5 trees ha^{-1}) within the upper part of the transect (300–345 m; Fig. 7). The maximum regeneration density, up to 2000 stems ha^{-1} , was observed within the lower portion of the transect (i.e., in the vicinity of a refugium; Fig. 7). Tree distribution along the slope was very uneven (Fig. 7). Relief features, as well as subfossil trees, facilitated regeneration recruitment by sheltering (Fig. 1, inset).

TREE RADIAL INCREMENT

LIA cooling decreased radial increment (Fig. 8, part a). The response of LIA survivors to post-LIA warming was relatively weak in comparison with the cohort established after the LIA (Fig.

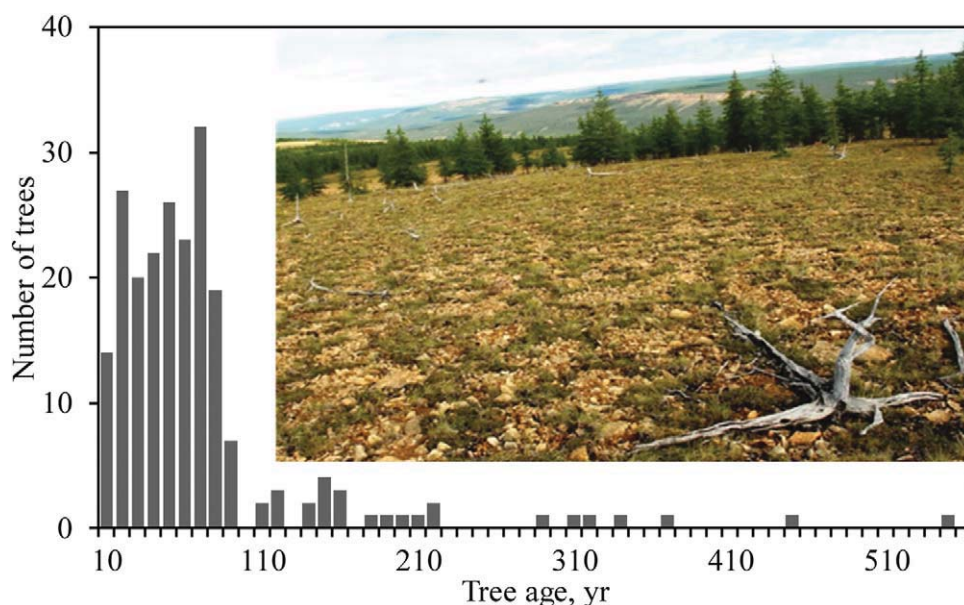


FIGURE 5. Regeneration and tree age distribution. Data presented on Figures 4–6 were from transect #5. Inset: tree clusters are located mainly within linear terrain features; areas between clusters are low populated, and tree heights were still lower than for trees from the pre-LIA period.

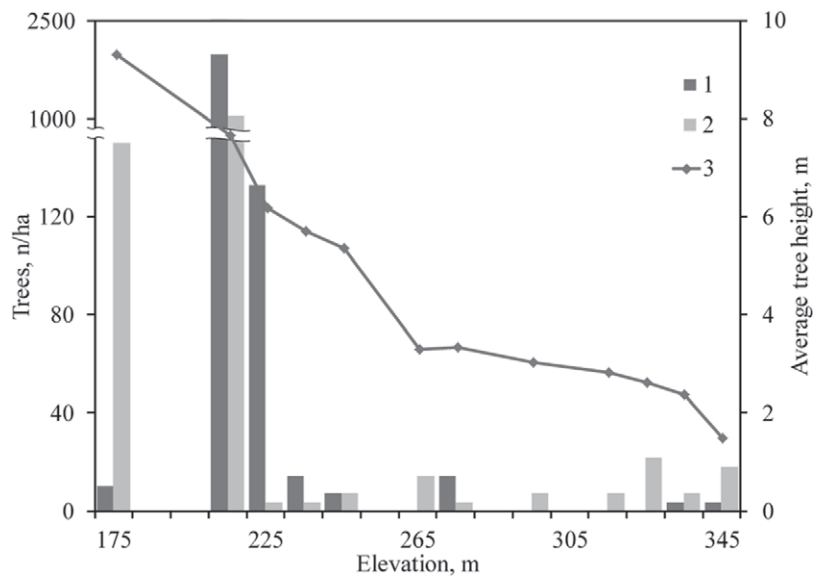


FIGURE 7. Regeneration and tree mean density along elevation gradient. 1—regeneration (trees ha^{-1}), 2—number of mature trees (trees ha^{-1}), 3—tree heights.

8, part a and part a inset). In the second part of 20th century a decrease in growth was observed, coinciding with a negative SPEI trend (Figs. 8, part a, and 2, part c).

TREE LINE EVOLUTION

Tree mortality within the forest-tundra ecotone occurred from the 16th century to the beginning of the 19th century, corresponding to the period of LIA cooling in Siberia (Fig. 9). The mean distance of forest retreat caused by cooling (i.e., distance between the pre-cooling tree line and the refugium) varied between transects within the range of 30–110 m (Table 2). The wave of tree establishment started in the middle of the 19th century (Fig. 9). Tree establishment also occurred within periods of warming during the LIA (Figs. 8,

part b, and 9). Some of those trees survived the LIA and were still living at the time of the measurements (Fig. 8, part b). Even though these trees exhibited signs of damage by the harsh environment, they were still cone-producing (Fig. 4).

Discussion

The waves of downslope and upslope tree migration that occurred during the LIA cooling and the post-LIA warming are apparent in Figure 9.

REFUGEE TREE LINE AND REFUGIUM ZONE

The refugee tree line was located 70–110 m in elevation above the refugium and was formed by over-mature trees (with ages up

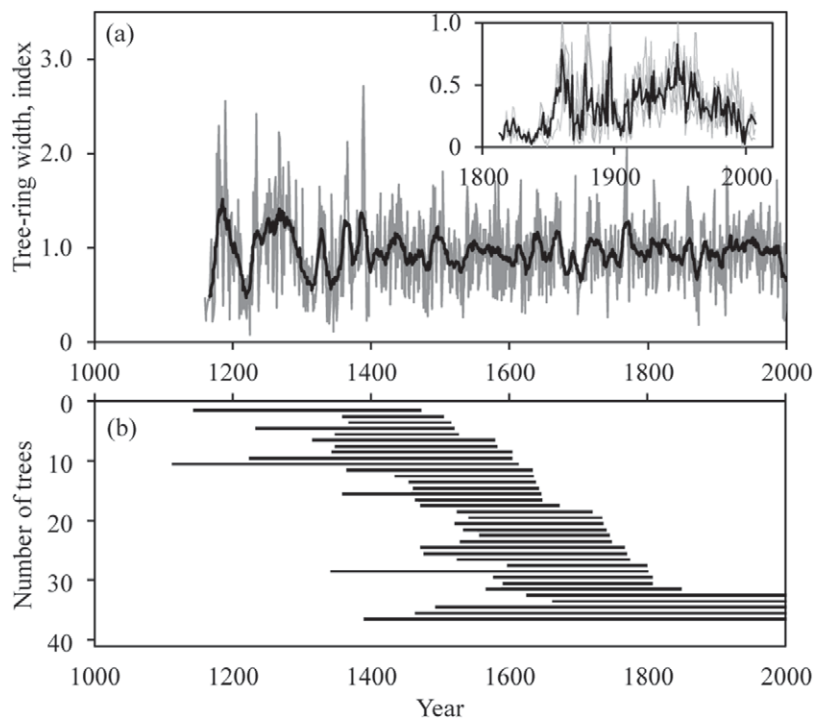


FIGURE 8. (a) Tree-ring width index chronology of subfossil and living trees; (b) trees natal/mortality dates. Inset: tree-ring width (mm) chronology of trees established after LIA. Gray and solid lines are individual and mean data, respectively.

TABLE 2
Tree lines and boundaries location and migration rate.

Transect No.	Tree lines location (m a.s.l.)					†Tree line upward shift (m °C ⁻¹)	Tree line migration rates (m yr ⁻¹)
	Pre-LIA	Regeneration	Current	Refugee	Refugium		
1	440	440	420	350	240	75	0.47
2	440	440	440	370	–	58	0.37
3	430	430	430	400	–	25	0.16
4	290	290	290	250	150	33	0.21
5	350	350	350	240	170	92	0.58
Mean				~320	~190	~55	~0.35

LIA = Little Ice Age.

†Upward shift was calculated based on refugee line.

to 700 years; Fig. 4). In this paper refugia are defined as areas where LIA environmental circumstances have enabled a larch to survive after larch extinction in higher elevation areas, and from which re-colonization and recruitment into uphill tundra occurred (e.g., cf. Sedell et al., 1990). “Refugee trees” are the single survivors above refugia. Some of those trees were established during the LIA (Fig. 8, part b). “Refugee trees” (as well as refugium trees) typically had signs of harsh environmental impact (e.g., dead or substituted tops, leaning and curved boles; Figs. 4 and 9, inset). On the contrary, post-LIA trees had mainly straight boles, non-suppressed tops, and well-developed crowns (Fig. 4). It is known that the shape of larch crowns is age-dependent (i.e., conical for pre-mature trees vs. irregular for old trees), but crown shapes of LIA survivors and old larches from non-harsh habitat were different. Due to phellem damage (caused by desiccation and snow abrasion), LIA survivor trees often had only a strip of living bark twisted around the bole (Fig. 10). The refugium itself was formed with old-growth trees ($A > 300$ years; Fig. 9, inset). LIA cooling caused the tree line to recede to the “refugee line” and closed stands to recede to the refugium border. The downward shifts varied within a range of 30–110 m in elevation with respect to the refugee line and 140–200 m for the refugium border (Table 2). Tree mortality lagged behind the lower temperatures (Fig. 9), because mature trees are resistant to harsh environments due to greater bark thickness. On the other hand, LIA survivors’ radial growth response to post-LIA warming was lower in comparison with the cohort established after LIA (Fig. 8, part a and part a inset). In the second part of 20th century radial growth decreased; this event coincided with a negative SPEI trend (Figs. 8, part a, and 2, part c).

CURRENT TREE LINE

Observed increase of larch population within the forest-tundra ecotone is unique since the 16th century (Fig. 9). Re-population of the forest-tundra ecotone was facilitated by refugia, which provided of seeds for regeneration establishment and sheltering saplings (Fig. 4). Typically, post-LIA established mature and pre-mature trees exceed the “mother larches” in height and had well-developed crowns and straight boles indicating a reduction of winter desiccation and snow abrasion (Fig. 4). Meanwhile, within the upper portion of the forest-tundra ecotone, tree heights and stand

density were still lower than in the pre-LIA period (50–150 ha⁻¹ of sub-fossil trees vs. 10–20 ha⁻¹ living trees; Fig. 5 inset). The current tree line was found to be restored to its pre-LIA location on four out of five transects (Table 2). For other areas in Siberia, data are controversial. In the Polar Ural Mountains the current tree line has not yet reached its pre-LIA location; this has been attributed to prevailing winds limiting upslope seed dispersal (Shiyatov et al., 2007). In the southern Altai Mountains the current tree line exceeds the pre-LIA position in the majority of studied cases, although tree-line positions were lower in some sites (Kharuk et al., 2010a). In addition to single trees, the forest-tundra ecotone is populated by isolated tree clusters (with density ≤ 1 cluster ha⁻¹). Some clusters originated from individual trees by layering. Along with this, there were single trees with multiple stems. In both cases trees originated from mat and krummholz forms. Similar phenomena were described for the Polar Ural and Altay Mountains, where the number of clusters and multistem forms were 5–10 times higher than in our study area (Shiyatov et al., 2007; Kharuk et al., 2011). This can be attributed to differences in level of winter damage (desiccation, wind damage, and snow abrasion; Holtmeier, 2009; Körner, 2012), and availability of shelters, including snow cover. Thus, observed upward tree-line shift in the Polar Urals was attributed to a doubling of snow precipitation during the last decades (Devi et al., 2008).

REGENERATION LINE

Analysis of age structure (Fig. 5) showed that regeneration appeared in the forest-tundra ecotone mainly during the last 70–80 years. A uni-modal distribution with a maximum shift to older ages indicates that the re-population increase started in the 1930s, but was not accelerated during the last decades even with the observed warming. In addition, tree density within the upper portion of the ecotone exceeds that of regeneration, and trees were found in areas where regeneration was still absent (Fig. 6). Thus, tree establishment during the warming of the 1930s–1940s was at least as effective as the warming of the last two decades. Relative regeneration decrease (in comparison with the 1930s–1940s) during the last decades was accompanied by a decrease in the SPEI index (Figs. 2, part c, and 3). The SPIE index has negative values during the last three decades, with minimal values during the last decade (Fig.

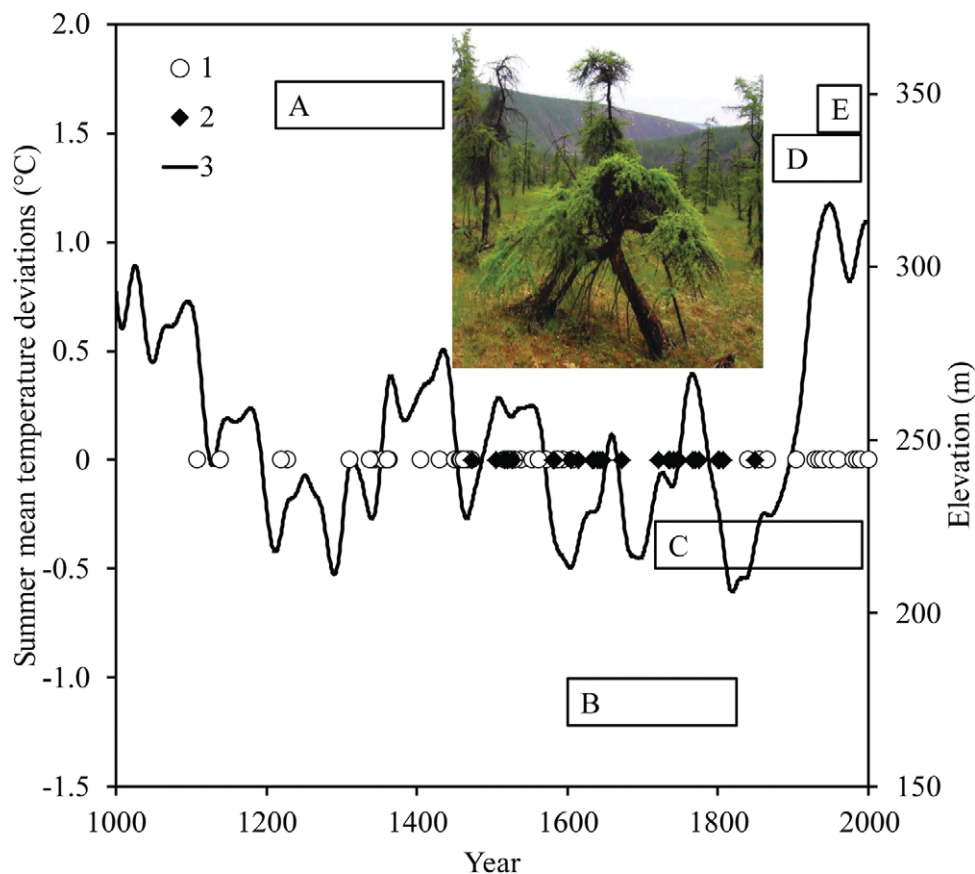


FIGURE 9. Elevation limits of tree lines before, during, and after LIA; tree natality/mortality dates and summer air temperature deviations for northern boreal zone. 1, 2—the dates of tree natality and mortality, respectively. 3—reconstructed summer air temperature deviations for northern boreal zone (<http://www.cru.uea.ac.uk/cru/people/briffa/qsr1999/>). Bars show elevation limits of tree lines and refugia: A—pre-LIA tree line, B—refugium border, C—refugee line, D—current tree line, and E—regeneration lines. Inset: refugium larches (A > 300 yr).

FIGURE 10. Larch tree damaged by winter desiccation and snow abrasion. A strip of living tissue is twisted around the bole clockwise (looking from tree base). NB: all sampled trees showed “twisted” pattern of bole tissues. This may increase larch resistance to wind damage and frost cracking. Inset: cross section of a tree that survived the LIA showing bark tissue damage.



3). This data indicate that negative SPEI trends (i.e., increase of drought) may be the cause of relatively lower regeneration establishment during the last decade (Fig. 5). It is known that seedlings are disproportionately affected by drought due to their small root systems (e.g., Harsch and Bader, 2011). Notably, SPEI trends are heterogeneous through northeast Siberia (Fig. 3); thus, in the other regions, different tree establishment patterns can be expected. Elsewhere in the Lake Baikal region, increased drought caused decline and mortality in birch stands (Kharuk et al., 2012b).

Within the forest-tundra ecotone regeneration density was very low (<20 stems ha^{-1} for the majority of the forest-tundra ecotone), whereas in areas adjacent to seed sources (refugium border or refugee trees), regeneration reached 100–2000 stems ha^{-1} . This indicates the limitation of seed availability for regeneration establishment. “Mother larch” sheltering may play a role in seedling establishment; also, observations on post-fire regeneration contradict the hypothesis that this is a primary factor, because larch regeneration density may reach 700 thousands ha^{-1} (Kharuk et al., 2008) after fires. Secondly, self shading of the tree root zone, as well as moss and lichen cover growth, decreased soil temperatures and leads to a limitation of tree growth by decreasing the root habitat zone (Körner, 1998; Kharuk et al., 2012a), which leads to root nutrient competition and low tree density (with mean of 340 ± 160 trees ha^{-1} within the study area). Meanwhile, photoinhibition, one of the reported factors of seeding mortality (e.g., Körner, 2012), was unlikely within the study area because of the low elevation of the forest-tundra ecotone (about 400 m a.s.l.), i.e., solar irradiation was much less than within similar ecotones in the southern mountains. In addition, larch itself is a highly light-demanding species.

Seed production and dispersal are known as two of the main limiting factors for successful recruitment of seedlings in some regions (e.g., Harsch and Bader, 2011). Seed limitation was reported for *Larix sibirica* regeneration in the Polar Urals (Shiyatov et al., 2007) and in the southern Altai-Sayan Mountains (Kharuk et al., 2009), as well as European mountains (Holtmeier and Broll, 2007). Larch migration is dependent on winds since it is an anemophilous species and also requires wind to disperse seeds. Within the study area, established trees reach cone-producing age at about 30 years, which increases the seed potential. Along with seeds, small broken branches with attached cones can also be dispersed by wind over snow-covered ground. In the mountains, seed dispersion is also complicated by the elevation gradient, as well as spring runoff, which moves seeds downhill. Contrary to larch, advances of zoochoric Siberian pine into mountain tundra were promoted by the Siberian nutcracker (*Nucifraga caryocatactes macrorhynchos*), which may spread pine nuts up to 1–2 km away from seed trees (Kharuk et al., 2010a). Along with seed limitation, regeneration recruitment may be also limited by poor seed germination capacity. Even in favorable conditions, recruitment levels of 30–50% decrease to 5–15% because of inbreeding, which is typical for sparse stands. Although larch produces cones annually, good seed yield occurs only every 6–7 years (e.g., Gorbunova, 2006).

Within the refugium, regeneration was very sparse or absent since seedlings establishment was limited by the moss and lichen “pillow” ground cover that had developed. Soil surface mineralization, caused by fires and a critical condition for successful larch

regeneration, was very rare because of the very long fire return interval (>300 years) (Kharuk et al., 2012a).

RELIEF FEATURES

Along with limited seed availability, topoclimatic conditions caused by relief features (slope aspect, azimuth, and elevation) play an important role for seedling recruitment (Holtmeier, 2009; Körner, 2012). In the forest-tundra ecotone, trees presently are found mostly along linear relief features (terraces; Fig. 5, inset). Refugee trees were also located on relatively sheltered areas. This is a potential cause of uneven distribution of trees and regeneration at a given elevation (Fig. 7). Typically, trees formed linear-shaped clusters adjacent to the upper terrace boundary, i.e. areas with maximum slope steepness (which was about $10\text{--}12^\circ$), whereas areas between terraces (with slope steepness about $5\text{--}8^\circ$) were populated by single pioneer trees (Fig. 5, inset). Along with wind protection, terrace boundaries were also areas where accumulated snow sheltered seedlings and reduced the impacts of droughts. Tree establishment also provided a positive feedback mechanism (Kullman, 2007). Reported negative impacts of excessive snow on survival of regeneration (due to a shorter growing period) should not be the case, since “cold period” precipitation within the study area was only about ~ 170 mm. Along with relief features, shelters for larch regeneration (especially at its upper limit) were provided by *Betula nana* canopies and subfossil trees (Fig. 1, inset). Since larch is a highly shade non-tolerant species, it can grow only within *Betula* canopy “gaps.”

TREE-LINE EVOLUTION AND AIR TEMPERATURE CHANGES

Larch stands within the forest-tundra ecotone experienced gradual deforestation during the 16th century through the beginning of the 19th century, transforming into tundra with single “refugee” trees (Fig. 9). The magnitude of tree-line shift was heterogeneous across the study area as the tree line receded within a wide range (40–110 m with respect to refugee line), with the mean about 70 m (Table 2). Similar shifts were described for the alpine forest-tundra ecotone of the southern Sayan Mountains in Siberia (Kharuk et al., 2010b). The estimated summer air temperature change since the LIA cooling (ca. A.D. 1450–1850) was about $+1.2^\circ\text{C}$ (Naurzbaev et al., 2003). Based on this, an upward tree-line shift was estimated (Table 2). The mean value of tree-line response to $+1^\circ\text{C}$ was about 55 m (with a range of $25\text{--}92\text{ m }^\circ\text{C}^{-1}$). Similar values ($100\text{ m }^\circ\text{C}^{-1}$) were published by Grace (1989). We estimated rates of upward migration based on the assumption that upward migration of trees started in the middle of the 19th century, i.e. in 1850. This point was marked by the beginning of tree establishment and air temperature deviations crossing the mean millennium value (Fig. 9). The time period between the beginning of upward tree migration and the date of sampling within the study area was 158 years. Based on this, the mean rate of the upward migration was estimated as 0.35 m yr^{-1} (with a range of $0.21\text{--}0.58$; Table 2). These values are lower than estimates for the southern Siberia Mountains (0.9 m yr^{-1} ; Kharuk et al., 2010b) and are similar to the data of Bekker (2005) for tree-line migration in Glacier National Park in Montana, U.S.A. ($0.28\text{--}0.62\text{ m yr}^{-1}$) and Shiyatov et al. (2007) for the Polar Ural Mountains, Russia (0.4 m yr^{-1}).

Conclusions

The waves of downslope and upslope tree migration following LIA cooling and post-LIA warming were observed within northern Siberia. The magnitude and pattern of the tree-line migration were dependent on local topoclimatic conditions. Tree-line response to summer air temperature increase was about $55 \text{ m } ^\circ\text{C}^{-1}$, with mean tree-line rate of upward migration of about 0.35 m yr^{-1} . The current forest-tundra ecotone was populated by tree cohorts that appeared mainly after a warming period in the 1930s. Larch regeneration reached (but did not exceed) the pre-LIA tree line, and tree heights and density were still lower than in the pre-LIA period. Refugia were essential for forest-tundra ecotone repopulation as a source of seeds and for sheltering regeneration. The warming in recent decades did not accelerate regeneration recruitment, which was limited by drought conditions as well as seed limitation. The observed migration of larch into the tundra in Siberia supports the hypothesis of climate-driven advance of forests to the Arctic coast-line.

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APPENDIX

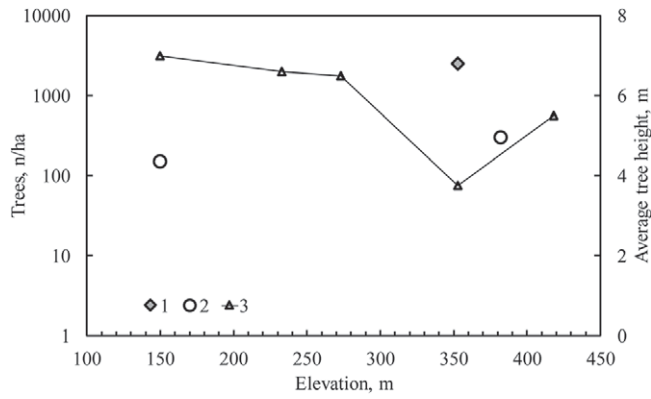


FIGURE A1. Transect #1. Regeneration and tree mean density and height along elevation gradient. 1—regeneration (n/ha); 2—trees (n/ha); 3—average tree height (m).

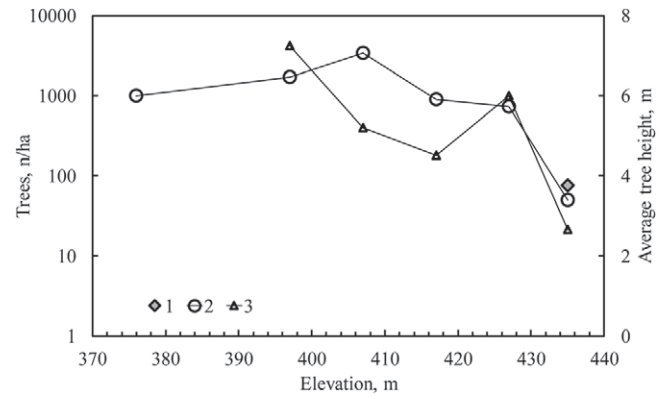


FIGURE A2. Transect #2. Regeneration and tree mean density and height along elevation gradient. 1—regeneration (n/ha); 2—trees (n/ha); 3—average tree height (m).

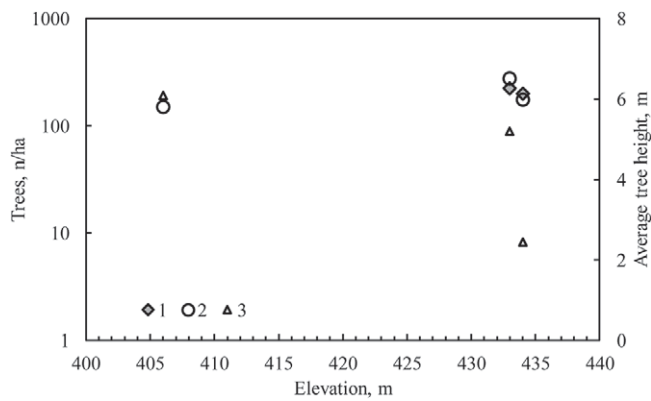


FIGURE A3. Transect #3. Regeneration and tree mean density and height along elevation gradient. 1—regeneration (n/ha); 2—trees (n/ha); 3—average tree height (m).

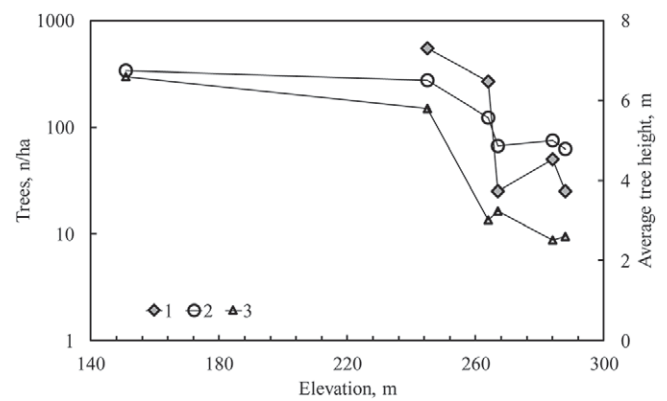


FIGURE A4. Transect #4. Regeneration and tree mean density and height along elevation gradient. 1—regeneration (n/ha); 2—trees (n/ha); 3—average tree height (m).