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Reaction of Coniferous Trees in the Kuznetsk Alatau Alpine Forest-Tundra Ecotone to Climate Change

I. A. Petrov[a], V. I. Kharuk[a, b], M. L. Dvinskaya[a], and S. T. Im[a, b]
[a]*Sukachev Institute of Forest, Siberian Branch, Russian Academy of Sciences,*
Akademgorodok 50, Krasnoyarsk, 660036 Russia
e-mail: petrovilsoran@gmail.com
[b]*Siberian Federal University, pr. Svobodnyi 79, Krasnoyarsk, 660041 Russia*

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Abstract—In recent decades there has been an increase in the radial growth of *Larix sibirica* Ledeb., *Pinus sibirica* Du Tour, and *Abies sibirica* in the Kuznetsk Alatau alpine forest-tundra ecotone. Larch growth correlates positively with summer temperatures; cedar and fir growth is determined by temperature, precipitation, and sunshine duration. It is shown that the current growth of maturing larch trees is about 55% higher than that of a similar age group observed 200 years ago. The rate of larch advancement along the height gradient is estimated at 1 m/10 years. A periodical limitation of the radial growth in fir by winter and summer temperatures is found; the strongest correlation is revealed with summer temperatures ($r = 0.9$). The growth rate of all conifers correlates highly with the concentration of CO_2 in the atmosphere ($r = 0.42–0.84$). Increased winter temperatures induce the transformation of the elfin forms in larch and cedar (the early 1970s) and later fir (the early 1980s) into vertical forms.

Keywords: alpine forest-tundra, *Larix sibirica*, *Pinus sibirica*, *Abies sibirica*, elfin forms, climate effect on growth rate

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INTRODUCTION

The alpine forest-tundra ecotone is a zone where the effect of climate on the growth of trees is most significant due to the growth limitation by temperature (Holtmeier, 2009). Actually, recent decades have seen the advancement of trees along the height gradient in the mountains of Eurasia and North America (Moiseev, 2002; Klasner and Fagre, 2002; Munroe, 2003; Baker and Moseley, 2007; Kullman, 2007; Kharuk et al., 2006, 2008, 2009; Lenoir et al., 2008). Along with that, the crown density increased (Shiyatov et al., 2007; Devi et al., 2008; Harsch et al., 2009). Another consequence of increased temperature is changes in the morphology of trees: the transformation of elfin forms into vertical ones (Holtmeier, 2009; Kharuk et al., 2009). Other than the influence of climate warming, a number of studies point out that increased CO_2 concentration in the atmosphere stimulates the growth of trees (Souza et al, 2010; Kharuk et al., 2011). The data from model experiments also prove that the productivity of trees increases as the content of CO_2 gets higher (Hoch and Körner, 2005; Canadell et al., 2007; Norby et al., 2010).

Climate change, as predicted, will influence the species diversity and productivity of boreal forests, causing the geographical redistribution of trees (Aitken et al., 2008; IPCC, 2007). Thus, the effect of climate change on the growth of major forest-forming taiga species is an urgent problem.

The purpose of this work is to compare reactions of cedar (*Pinus sibirica*), fir (*Abies sibirica*), and larch (*Larix sibirica*) to climate change in the Kuznetsk Alatau alpine forest-tundra ecotone. The following aspects of the problem were studied:

(1) What is the relative radial growth of *Pinus sibirica*, *Abies sibirica*, and *Larix sibirica* in reaction to climate change?

(2) What is the relation between climatic variables, CO_2 concentration in the atmosphere, and radial growth?

MATERIALS AND METHODS

The studies were performed in the Kuznetsk Alatau alpine forest-tundra ecotone (Fig. 1). The Kuznetsk Alatau includes several mountain ridges stretching from the north to the south with a length of up to 300 km and maximum altitudes of 2200 m. The ridges have relatively smooth slopes out of limestones and quartzites, as well as clayey and siliceous shales with numerous intrusions of granite, diorites, gabbro, and tuff.

The highlands (1350–1500 m above sea level) are represented by tundra plant communities. The subalpine belt (1100–1350 m) comprises meadows and

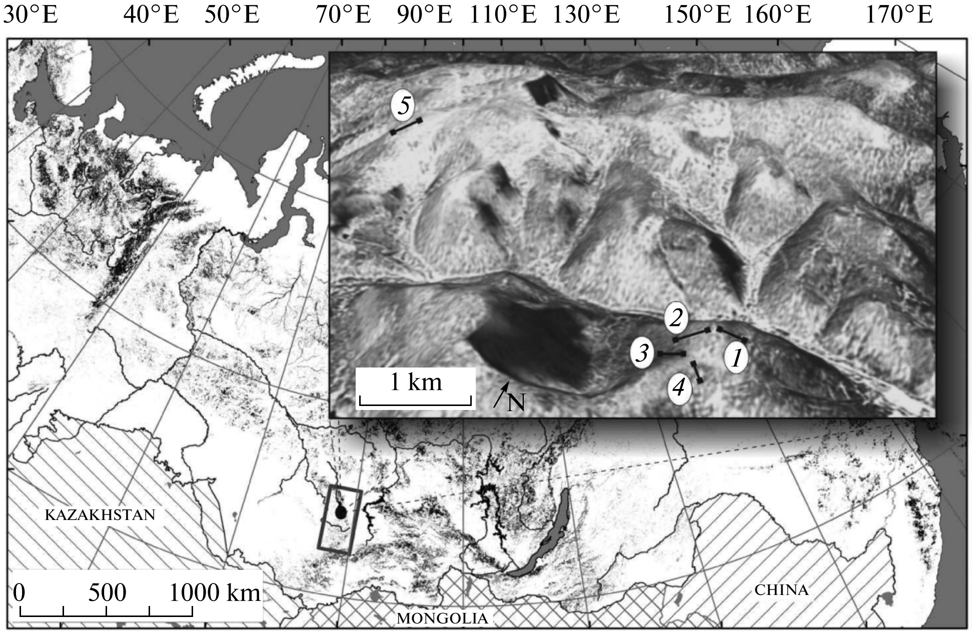

Fig. 1. Geographical location of the studied area. Sample plots are designated by lines. (*1*–*5*) Transects. Background: evergreen conifers.

sparse forests formed by *Larix sibirica*, *Pinus sibirica*, *Abies sibirica*, and *Betula tortuosa*. The upper and middle parts of the forest belt (600–1100 m) are cedar stands mixed with fir and spruce. The lowland forests are formed by larch and pine mixed with cedar and birch. The steppificated areas occur on the steep slopes at an altitude of 500–600 m.

The climate of the studied territory is continental, with cold and long winters, as well as warm or hot summers. On the west exposed slopes, the total amount of annual precipitation is 600–800 mm, while the central and windward parts receive up to 1500 mm of precipitation every year. The average temperatures in January and July are –15.3°C and +13.4°C, respectively (Table 1, Fig. 2). The calculations are based on data from the nearest (~10 km) meteorological station (Nenastnaya).

Field studies were performed in 2012–2013 in two areas of the alpine forest-tundra ecotone (54°38′ N 88°41′ E and 54°39′ N and 88°37′ E; Fig. 1). According to Shiyatov (2007), the "ecotone" is a transitional area between the upper limit of young growth and the border of dense tree stands (crown density ≥0.3). In Area 1 (at the altitude range from 1270 to 1330 m), all studied tree species were found; in Area 2 (at the altitude of 1370 m), only fir was present. Larch was represented by the cohorts of old ("refugial") trees (A ~ 230 years) and relatively young trees (A < 80 years). Cedar and fir were relatively young (A < 100) trees, including so-called "subelfins" (tree plants transformed from elfins into vertical forms). In the forest-tundra ecotone, 5 gradient transects (four in Area 1 and one in Area 2; Fig. 1) were laid within the altitude range of 1290–1390 m above sea level. In every transect, sample plots (SPs) were set up every 10 m along the height gradient for geobotanical and soil description, as well as counting of undergrowth and estimation of its living state (Table 2). The undergrowth was divided into two categories: viable and (nonviable + dead). SPs were set up in three replications; SP size varied from 3 × 3 m to 10 × 10 m, depending on the amount of undergrowth. The age of undergrowth was determined by counting annual rings at the height of root collar.

Dendrochronological Analysis

To construct chronologies, 57 larch samples, 20 cedar samples, and 32 fir samples (16 samples per area) were collected. The surface of each sample was polished, cut, and treated with chalk powder to

Table 1. Climatic data for sample plots

Parameter	Annual	June–August	December–February
Average temperature, °C (1940–2010)	–2.1	11.6	–14.7
Average precipitation amount, mm (1966–2010)	1603	381	341

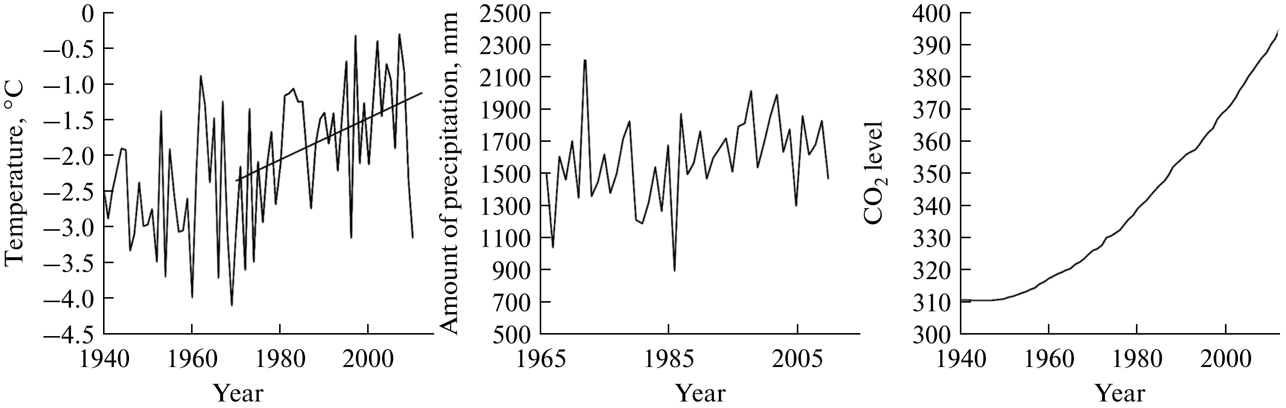

Fig. 2. Long-term dynamics of average annual temperatures (a) and annual amount of precipitation (b) at the studied territory; (c) abnormal concentrations of CO_2.

increase contrast. The width of annual rings was measured using an LINTAB III device (precision of 0.01 mm). Cross dating was performed by the standard methods (Shiyatov, 2000). For a statistical verification of cross dating and the construction of generalized tree-ring chronologies, the following programs were used: COFECHA, ARSTAN, and TSAP (Holmes, 1983; Rinn, 1996). After cross dating, three chronologies were obtained for each species: averaged, standard, and residual. Averaged chronologies were constructed by the simple averaging of individual chronologies. Standard chronologies were constructed using the ARSTAN program and the method of double detrending to eliminate low-frequency oscillations. As a result, nondimensional indices of the radial growth were obtained. Residual chronologies were constructed based on the standard ones by removing autocorrelation, thereby increasing the climatic signal (Cook and Holmes, 1986). The analysis was carried out with areas from 1940 to 2012; the lower border of the interval corresponds to the onset of reliable changes in meteorological parameters. For the amplification of the climatic signals, averaged chronologies smoothed with a 5-year filter were used. The filter length was selected in a way to remove the high-frequency component by maximizing low-frequency climatic signals. Climatic data were also smoothed with a 5-year filter. Statistical processing was performed in Excel and Statsoft (StatSoft, 2001). To analyze climatic signals, correlation coefficicents (r_{ach}) between averaged chronologies and meteorological data were used, as well as correlation coefficients between meteorological data and standard (r_{sch}) and residual (r_{rch}) chronologies. Using the STATISTICA program, correlation coefficients between the growth indices and average monthly climatic data were calculated.

RESULTS

The abundance of cedar undergrowth (Area 1) is 2.0–2.5 thousand/ha; in larch, this parameter is considerably (ten times) lower (Fig. 3). Dead or damaged specimens were not found among young larch trees. Fir undergrowth was represented by isolated specimens.

The population of larch divided into two cohorts: "refugial," which developed during the Little Ice Age (LIA; A ~ 230 years), and relatively young (A ~ 80 years), which grew after the LIA (~1850). Trees in the first cohort formed a crooked forest with damaged or dried tops, while those in the second cohort were straight-stemmed. The age of larch decreases with altitude above the sea level, thereby reflecting the dynamics of its advancement along the height gradient with climate warming (Fig. 4a). The cohort of young trees includes rapid- and slow-growing specimens; the latter have localized mainly on the upper growth limit,

Table 2. Characteristics of sample plots

Area	Transect	Length, m	Altitude difference, m	Number of sample plots	Altitude (max–min)	Direction, °
No. 1	K1	190	58	7	1368–1310	60
	K2	200	50	6	1340–1290	250
	K3	110	16	4	1313–1297	300
	K4	110	19	5	1315–1296	100
No. 2	K5	140	30	4	1390–1360	240

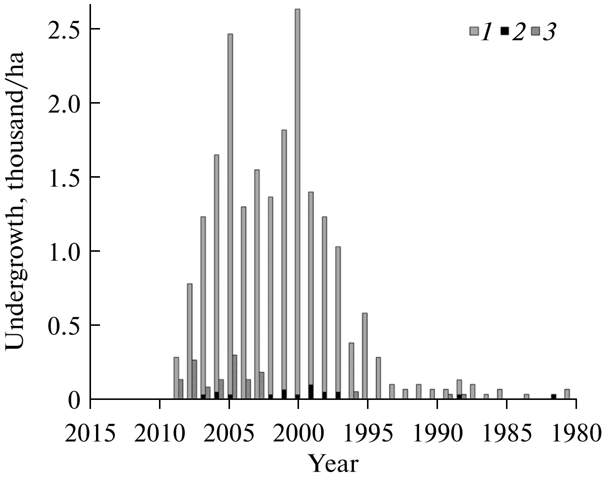

Fig. 3. Number and age structure of young trees in Area 1. (*1*, *2*) Cedar (*1* viable and *2* nonviable), (*3*) larch.

as well as in areas most vulnerable to the impact of wind. The growth dynamics of these trees was similar to that of "refugial" trees (Fig. 4b). Since the growth dynamics of larch groups mentioned in the above text was high (r = 0.82–0.92), a generalized chronology was developed for them.

Elfin forms of all the studied species transformed into vertical ones. However, cedar and fir on the upper growth limit were represented by elfin forms and larch by vertical forms.

Dendrochronological Analysis

Comparative characteristics of the averaged chronologies are given in Table 3. The dynamics of radial growth in the studied tree species was synchronous with the dynamics of air temperature (Fig. 5). The correlation analysis provided the following results:

The growth of *Abies sibirica* correlates with the duration of vegetation period (the number of days with an average daily temperature >+5°C) (r_{ach} = 0.41–0.46, $p < 0.01$). Negative correlation is observed with precipitation in May (r_{ach} = 0.33, $p < 0.05$). In fir from Area 1, the highest correlation coefficient was between the average annual temperature and averaged chronology (r = 0.48, $p < 0.01$, Fig. 5a). Applying the 5-year moving average to the obtained data made it possible to increase the climatic signal (r_{ach} = 0.86, $p < 0.01$). Subsequent analysis demonstrated that the growth of trees is limited by either winter or summer temperatures, depending on the season. Thus, from the 1940s up to the late 1980s, the total amount of average monthly temperatures during the cold period was the main factor influencing the radial growth (November–March, r_{ach} = 0.83, $p < 0.01$). In the early 1990s, the total of temperatures in May–June becomes the limiting factor (r_{ach} = 0.78, $p < 0.01$). A similar model is observed in fir from Area 2 (Fig. 5b): the correlation coefficient between the averaged chronology and average annual temperature equals 0.79 (r_{ach} = 0.79, $p <$ 0.01). Up to the mid-1980s, the total amount of temperatures during the cold period (r_{ach} = 0.62, $p < 0.01$) remains the main limiting factor, after which it is replaced by that during the warm period (r_{ach} = 0.66, $p < 0.01$).

The growth of *Pinus sibirica* correlates with the duration of the vegetation period (r_{ach} = 0.36, $p < 0.01$), the total amount of average monthly temperatures during the cold period (r = 0.52, $p < 0.01$), and the average annual temperature (r = 0.50, $p < 0.01$). This set of data was also smoothed with the 5-year filter. Upon filtration, the correlation coefficients increased to 0.82 and

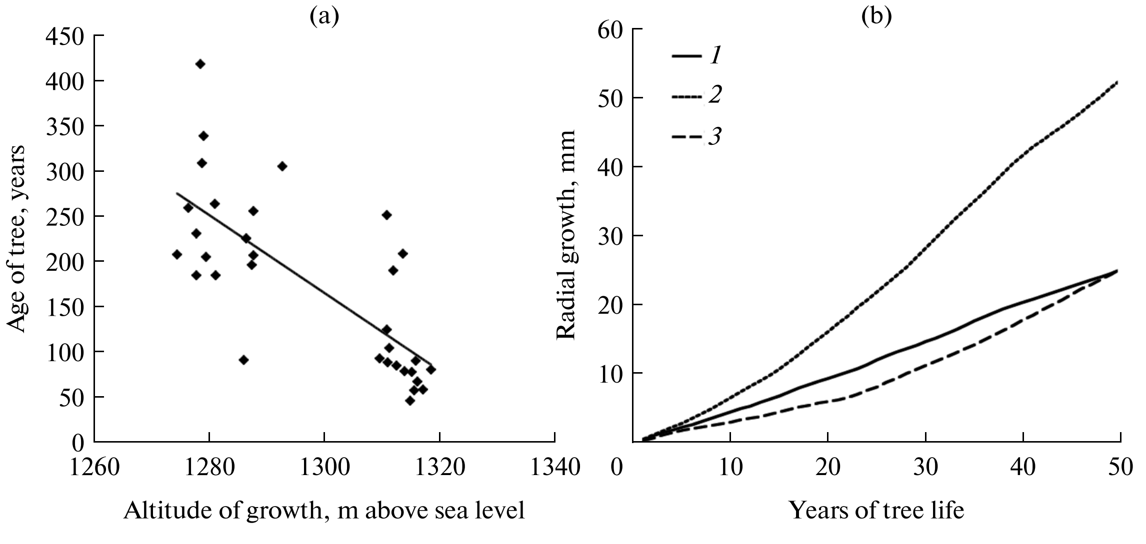

Fig. 4. (a) Dependence of larch age on growth altitude. (b) Integral curves of larch growth: (*1*) old (A > 200 years) trees; (*2*) rapidly growing and (*3*) slowly growing "young" trees (A ~ 80 years).

Table 3. Characteristics of averaged chronologies of the studied species over the period of 1940–2012

Species	Average TRW (Tree-Ring Width)	Maximum TRW	Standard deviation	Autocorrection	Sensitivity
Abies sibirica (Area 1)	0.63 mm	1.17 mm	0.22	0.79	0.18
Pinus sibirica	0.72 mm	1.01 mm	0.18	0.83	0.12
Larix sibirica	0.70 mm	1.29 mm	0.26	0.55	0.28
Abies sibirica (Area 2)	0.75 mm	2.28 mm	0.53	0.93	0.21

0.83 ($p < 0.01$) for the temperature during the cold period and average annual temperature, respectively.

The growth of *Larix sibirica* correlates positively with the temperature in June ($r_{ach} = 0.28$, $r_{gch} = 0.44$, $p < 0.05$) and negatively with that in April ($r_{ach} = -0.33$, $r_{gch} = -0.34$, $p < 0.05$) and precipitation in May ($r_{ach} = -0.32$, $p < 0.05$).

There is strong correlation between the sunshine duration (SSD) in May–June and the growth indices of *Pinus sibirica* ($r_{ach} = 0.33$, $p < 0.05$ and $r_{gch} = 0.46$, $p < 0.01$) and *Abies sibirica* ($r_{ach} = 0.42$, $p < 0.01$, $r_{gch} = 0.32$, $p < 0.05$ in Area 1; $r_{ach} = 0.31$, $p < 0.05$, $r_{gch} = 0.47$, $p < 0.01$ in Area 2). SSD was not related to the chronologies of larch.

The growth rate of all conifers correlates highly with the concentration of CO_2 in the atmosphere ($r = 0.42$–0.84; $p < 0.01$).

Over the period from 1990 to 2010, compared to the earlier similar period (1950s–1970s), the growth became ~40 and ~35% higher in cedar and larch, respectively. The growth rate of fir was 60 and 210% higher in Area 1 and 2, respectively. The latter is associated with the transformation of elfin forms into vertical ones. In 1990–2010, the total amount of temper-

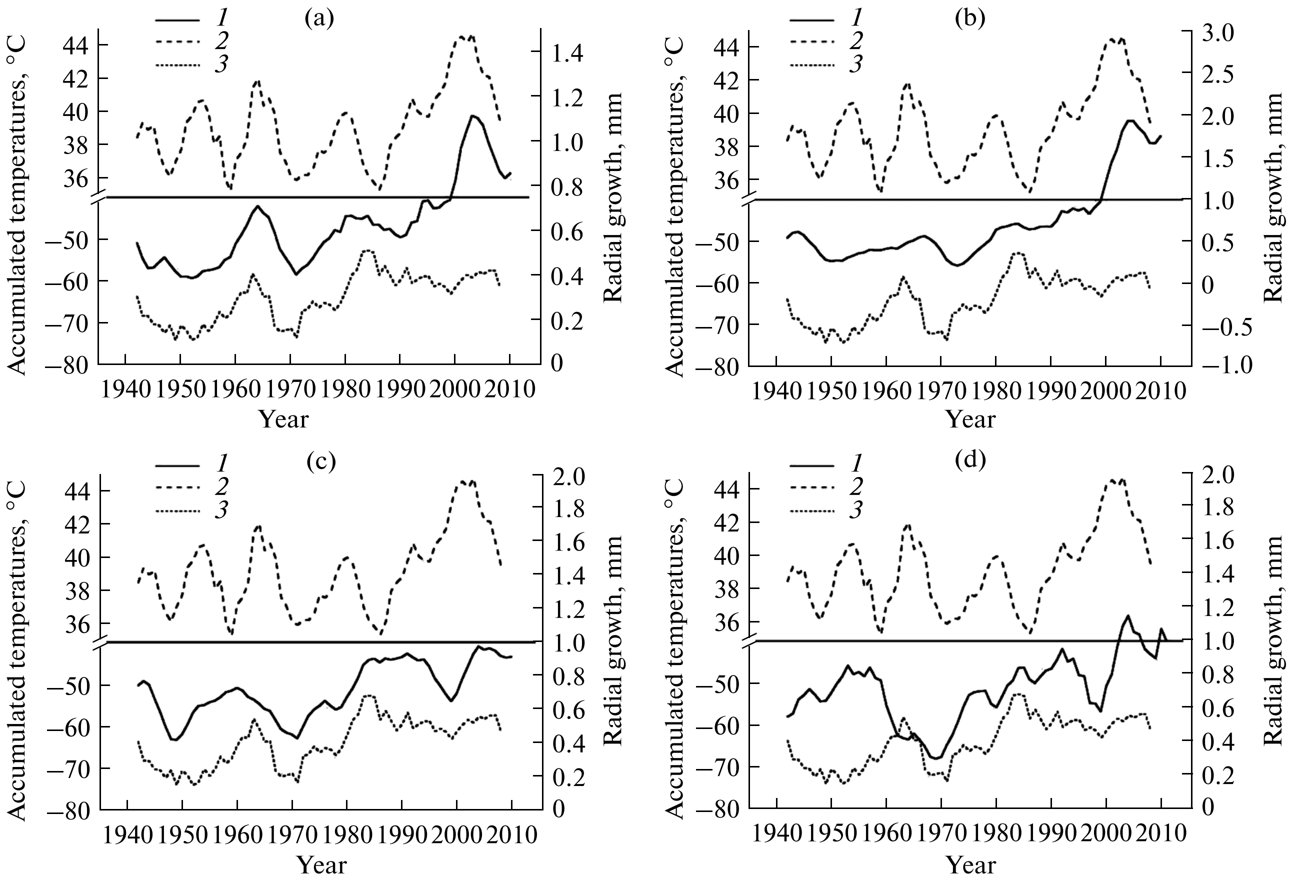

Fig. 5. Comparison of averaged chronologies with climatic factors: *Abies sibirica* ((a) Area 1; (b) Area 2), *Pinus sibirica* (c), *Larix sibirica* (d). (*1*) Chronology, (*2*) accumulated temperatures during the warm period, and (*3*) accumulated temperatures during the cold period.

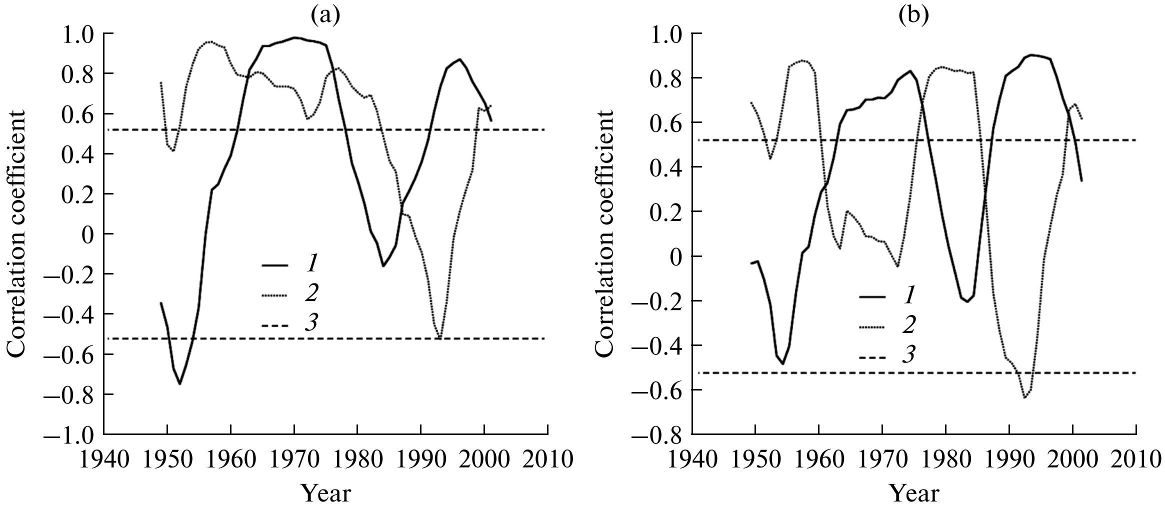

Fig. 6. Moving 11-year functions of the response in chronologies of fir trees from Area 1 (a) and 2 (b). (*1*) Correlation with accumulated temperatures during the warm period, (*2*) correlations with accumulated temperatures during the cold period, and (*3*) confidence interval ($p < 0.05$).

atures during the warm and cold periods became +2.5 and +7°C higher, respectively.

DISCUSSION

The growth rate of all conifers in the forest-tundra ecotone has significantly increased in recent decades: positive correlations are observed with the temperatures of both warm and cold periods. A periodical limitation of the radial growth in fir by winter and summer temperatures is found which was observed three times over the studied period (since 1940) (Fig. 6). When the total amount of winter temperatures exceeds the average long-term ones by +2°C, the growth was mainly determined by summer temperatures (r = 0.8–0.9). When the winter temperatures were 7°C below the average long-term ones, it led to an increase in the correlation with the temperatures of the cold period (r = 0.8–0.9; Fig. 6). The effect of periodicity is due to the dependence of desiccation on temperature: it is known that low temperatures in the synergy with wind caused the damage and death of needles and apical growth and promote the development of elfin forms. Among conifers, fir is distinguished by the lowest resistance to cold: in cedar and larch this effect has not been identified.

Elfin forms of all conifers were transformed into vertical ones. The exception is cedar and fir trees on the upper growth limit. The upper growth limit of fir is 10–20 m lower than that of cedar. Larch is represented by only vertical forms. The transformation of elfin forms in vertical ones began in the 1970. This date varies for different species. The transformation of larch (about 1970) and cedar (the early 1970s) was the earliest; the beginning of transformation of fir elfins in vertical form refers to the 1980s (Fig. 5). The transition to vertical forms was induced by less intense damage of apical growth by desiccation and snow abrasion: wind in combination with low temperatures is the main reason for the development of elfin forms (Holtmeier and Broll, 2010). The sequence of the mentioned transformation (larch–pine–fir) reflects the cold resistance of these species. The transformation of elfins of cedar, fir, and larch in vertical forms is also described for the mountain forest-tundra of the Altai and Western Sayan (Kharuk et al., 2008, 2009). It is noteworthy that the same time period was marked by the transformation of elfins in pine (*Pinus sylvestris*) in the west of Eurasia—in the mountain tundra of Scandinavia (Kullman, 2007).

Increased winter temperatures promote the advancement of conifers along the height gradient, as well as the survival of young growth in the last decades (Fig. 4); this effect is also described for other parts of the Altai-Sayan region (Kharuk et al., 2010). On the growth limit, the survival of undergrowth is highly dependent on the microtopography of relief: the undergrowth is found only on the leeward and sheltered from the wind elements of the relief.

The age distribution of larch indicates that its advancement along the height gradient began about 150 years ago, with warming after the Little Ice Age. An important role in this process belonged to old-aged ("refugial") trees as a source of seeds; the conditions near these trees were more favorable (protection against desiccation and accumulation of snow) for growth. The rate of larch advancement calculated by the age of larch in the area refugium and on the upper border of its habitat is estimated to be 1 m/10 years. Compared to other tree species, larch is characterized by the maximum advancement along the gradient of height; it is followed by cedar and fir. Climate warming resulted in increased radial growth of larch: the current growth of maturing (A ~ 50 years) larch trees is about 55% higher than that of the same age group 200 years ago. The ratio of the abundance of undergrowth in larch and cedar (Fig. 4) shows that cedar stands can develop under the canopy of larch and later displace it. The negative correlation between the radial growth of larch and temperature in April ($r_{\text{sch}} = -0.33$, $r_{\text{gch}} = -0.34$, $p < 0.05$) is probably caused by the promotion of larch vegetation in the presence of snow cover. Late frosts following the warming contribute to the damage of needles, both directly and as a result of water stress. The negative impact of early thaws on growth was also observed in the Baikal area of alpine larch forests (Glyzin, 1993).

The growth of *Pinus sibirica* and *Abies sibirica* was determined not only by temperature and precipitation, but also sunshine duration in May and June. For the deciduous *Larix sibirica*, this effect is not detected, which is probably due to the formation of needles, while the evergreen conifers are already able to photosynthesize. The correlation of the radial growth in cedar with winter precipitation ($r_{\text{sch}} = -0.46$, $r_{\text{gch}} = -0.44$) is probably due to the longer melting of snow and, accordingly, the reduction of the vegetation period.

Significant correlations between the concentration of CO_2 in the atmosphere ($r = 0.42–0.84$; $p < 0.01$) and the radial growth were established for all conifers and are probably not accidental. It is known that the concentration of carbon dioxide that has increased substantially (by 70 ppmv) over the last 50 years still did not reach the level of saturation for photosynthesis and is one of the factors limiting the growth (Norby et al., 2010). In addition, the limit of CO_2 in mountains is higher due to the fall of barometric pressure. Thus, the concentration of CO_2 in the studied area is ~25% lower than that in the foothills. Consequently, it is in the alpine-tundra ecotone where the highest response of trees to increased concentration of CO_2 should be observed. The presence of a correlation, obviously, does not prove the existence of a functional dependence; however, the data are consistent with the experiments on CO_2 limitation of growth in trees (Hoch and Körner, 2005; Canadell et al., 2007; Norby et al., 2010) and with research in situ (Souza et al., 2010; Kharuk et al., 2011).

In conclusion, it should be noted that the radial growth of cedar and fir increases in highlands under conditions of sufficient (>800 mm) precipitation, while midlands and lowlands of the Altai-Sayan region is where numerous cases of death and drying of dark coniferous stands have been described (Kharuk et al., 2013). The latter is induced by increasing aridity, frequency and intensity of droughts, as well as the impact of pests on trees weakened by water stress.

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