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Effect of Climatic Changes on Radial Increment and Age Structure Formation in High-Mountain Larch Forests of the Kuznetsk Ala Tau

P. A. Moiseev

Institute of Plant and Animal Ecology, Ural Division, Russian Academy of Sciences, ul. Vos'mogo Marta 202, Yekaterinburg, 620144 Russia

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Abstract—The relationship between growth indices and renewal rates of the Siberian larch (*Larix sibirica* Ledeb.) stands that have grown at the timberline in the Kuznetsk Ala Tau mountains during the past 350 years was analyzed. The age generations of larch were formed in the 1640s, 1660s, 1680s, 1700s, 1720s, 1740s, 1760s–1770s, 1800s–1810s, 1850s, 1870s–1880s, 1900s, 1920s, and 1930s–1940s. It was shown that the formation of these age generations coincided with 10- to 30-year periods of increased growth of larch and improved temperature conditions in summer.

Key words: *Larix sibirica*, Kuznetsk Ala Tau, forest renewal, growth indices, climate change.

In recent years, the dynamics of subgoltsy and forest–tundra ecosystems has been of special interest to the world scientific community in view of the expected and already occurring global warming (*Global Change…*, 1992). However, the reconstruction of past climatic conditions and the prediction of future conditions have been mainly based on indirect sources of information, such as the analysis of tree rings, varved clays, glaciers, and lake and sea peat sediments (*The PAGES Project…*, 1992). To date, the effects of climatic factors, including air temperature and precipitation, has been studied in greater detail. However, dendroclimatic data alone do not permit determination of changes in the structure of ecosystems and populations. To accomplish this task, dendroclimatic data should be analyzed together with the responses of other components of ecosystems, such as changes in the species and spatial structures of the vegetation.

In the 1970s–1990s, a number of studies on forest renewal at the timberline in the 20th century were carried out. Considerable regrowth and increase in the closeness of canopy in subalpine light forests slightly below the upper timberline have been reported for Canada (Kearney, 1982), various regions of the United States (Taylor, 1995; Jakubos and Romme, 1993; Woodward *et al.*, 1995), northern Europe (Kullman, 1986), Russia (Shiyatov, 1983), and New Zealand (Wardle and Coleman, 1992). Only a few studies dealt with the dynamics of the quantitative and spatial characteristics and the altitudinal location of subalpine light forests as related to climatic fluctuations on a decade to century scale (Shiyatov, 1967; Denton and Karlen, 1977; Shiyatov, 1993; Lloyd and Graumlich, 1997), although this information is more important for understanding the possible ecological consequences of drastic global warming.

The renewal rate in subalpine Siberian larch (*Larix sibirica* Ledeb.) forests in the Kuznetsk Ala Tau mountains was studied as related to climatic changes during the past 350 years reflected in the changes in growth indices.

MATERIALS AND METHODS

The study area is in the southwestern Kuznetsk Ala Tau (between 53°38′30″ N and 54°03′30″ N, and 88°19′30″ E and 89°15′30″ E), which is a part of the Salair–Kuznetsk region of the Altai–Sayan highlands. The area included the slopes of Tigertysh, the highest ridge, with elevations of about 2000 m above sea level and a considerably broken stony terrain. On these slopes, several altitudinal vegetation belts may be distinguished: dark taiga (up to 700–800 m a.s.l.); mountain taiga (up to 1300–1440 m); subgoltsy or subalpine belt (up to 1500–1600 m); and mountain tundra (up to 2100–2200 m).

In the upper part of the ridge, the monthly average air temperatures in June, July, and August are 8–11, 11–15, and 8–12°C; the sum of above-zero temperatures varies from 600–800 to 1000–1200°C; and the maximum annual precipitation is 3000–3500 mm (Shpin', 1980). The proportion of days with precipitation is 50–60%; it increases to 70–80% in some months. The annual dynamics of precipitation has two peaks, in spring (or early summer) and autumn. In the warm season, there are thick clouds, frequent fogs, and prolonged periods of bad weather, which considerably decrease the mean temperatures of summer months.

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The monthly average wind velocity is maximum in the cold season and, most often, in transition seasons, when wind velocities on the mountaintops are often higher than 25–30 m/s.

Six micropopulations of *L. sibirica* were described near the sources of four rivers on the slopes of Tigertysh in July and August of 1994–1997 (Moiseev *et al.*, 1999). Earlier, only one site of larch growth in the Kuznetsk Ala Tau was reported, with the note that, "due to the highly humid climate, its upper limit is located below the timberline" (Sedel'nikov, 1979). Conversely, all larch micropopulations that were found during this study were either located above the upper limit of closed-canopy forests (1270–1580 m a.s.l.) or partly preserved within the Siberian stone pine and fir stands expanding from below.

The ground vegetation of mountain larch forests in the Kuznetsk Ala Tau is formed by alternating lichen–crowberry, moss–blueberry, moss–dwarf birch, and herbage–woodreed communities, depending on local conditions (Moiseev *et al.*, 1999). The lichen–crowberry communities are typical of relatively dry detrital and stony places, whereas the herbage–woodreed communities are more typical of habitats with a well-developed soil layer and moderate moisture supply. The proportions of these communities in the ground cover gradually change with a decrease in elevation in the order indicated above.

Four of the six larch micropopulations were studied along the altitudinal gradient, from the lower to the upper limit of their growth. Sixty test plots with a total area of 8 ha were laid along four main and two auxiliary profiles. Their sizes depended on stand closeness and averaged 20×40 m; the area varied from 400 to 1400 m^2. On each plot, the height and diameter of the trunk and the width, length, and shape of the crown were recorded for trees thicker than 8–10 cm in diameter. Site conditions were estimated by describing the ground vegetation (coverage and height of main dominants) and measuring average soil depth with a metal probe. When necessary, a general geobotanical description of the vegetation on the plot was made. The trees thinner than 8–10 cm in diameter were regarded as undergrowth and were recorded by half-meter height classes. To construct tree-ring chronologies and analyze the age structure of light larch forests, core samples were taken from every other tree at a height of 20 to 40 cm, as close to the original vertical growth point as possible by the method of perpendicular boring in proximity to buttress flares.

The year of formation of the oldest tree ring in each of 557 core samples was determined by means of cross-dating. If the corer reached the center of the trunk, then the age of the tree at a height of 20 to 40 cm from the trunk base was assumed to be equal to the difference between the year of sampling and the year of the oldest tree ring formation. If the corer did not reach the center because of eccentricity of the trunk growth or a focus of rot, then the distance to the center was first calculated from the radius of a template circumference that fitted the shape of the arc formed by the oldest tree rings of the core sample. In this case, the number of years in the last segment of the sample equal to the calculated radius was taken to be the number of years that had to be added to obtain the age at a height of 20 to 40 cm.

To construct the tree-ring chronology of the maximum length, the samples older than 180–200 years were selected from the total set of samples for each profile. All samples were divided into groups according to the elevation: elevations of 1270–1390 and 1400–1580 m corresponded to the lower and upper plots, respectively. For each sample, the widths of tree rings were measured to an accuracy of 0.01 mm using the LINTAB-III measuring complex with TSAP version 3.5 software. Individual chronologies were cross-dated with one another with the aid of the TSAP graphic package. Individual tree-ring width series were standardized by means of approximation with an exponential function or a spline function with the use of Trend software (Riemer, 1991). A generalized tree-ring chronology was obtained by averaging 91 individual series of growth indices. The variations of growth indices from year to year were smoothed by the five-year moving average method, and smoothed curves of growth indices were constructed for the period from 1640 to 1997.

RESULTS AND DISCUSSION

Analyzing the relationships between individual tree height, diameter, and age, two groups of trees were distinguished with regard to their growth rates. These groups were divided into subgroups of the trees that grew in the lower and upper zones of the altitudinal range of larch (1270–1390 and 1400–1580 m, respectively). The trees were regarded as rapidly or slowly growing if their vertical growth rates were higher or lower than 6.8 cm per year; the highest and the lowest growth rates were 30.2 and 3 cm per year, respectively (Fig. 1). In our sample, there were 388 (69.7%) and 169 (30.3%) rapidly and slowly growing trees, respectively. Comparative analysis of the ratios between trunk diameter and tree age in rapidly and slowly growing trees (Fig. 2) showed that a slow vertical growth was accompanied by a low radial increment; hence, in the slowly growing trees, the trunk volume also increased more slowly.

To determine the causes of differentiation in growth rate between the groups of trees, the structure of ground vegetation under tree crowns (average coverage, soil depth, and the percentage of ground surface covered with stones) was analyzed in each group (table). The results of this comparative analysis indicated that site conditions had no noticeable effect on the distribution of trees into the slowly and rapidly growing groups, as the parameters used as indicators of these conditions were more similar under the trees of different groups growing at the same elevation than under the trees of

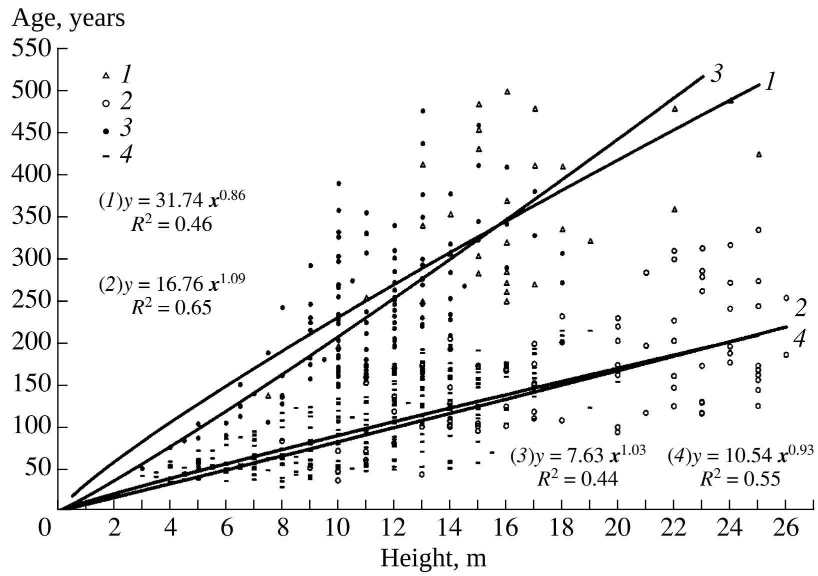

Fig. 1. The relationship between tree age at a height of 20–40 cm and tree height in groups of Siberian larch trees with different vertical growth rates in the subalpine zone of the Kuznetsk Ala Tau: (*1*, *2*) slowly and rapidly growing trees, respectively, in the lower parts of the slopes; (*3*, *4*) slowly and rapidly growing trees, respectively, in the upper parts of the slopes.

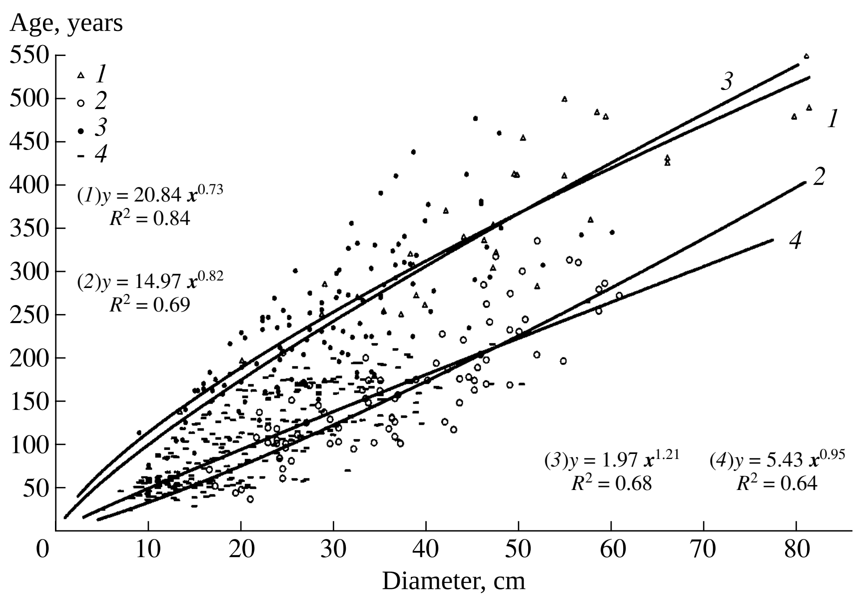

Fig. 2. The relationship between tree age at a height of 20–40 cm and trunk diameter in groups of Siberian larch trees with different vertical growth rates in the subalpine zone of the Kuznetsk Ala Tau: (*1*, *2*) slowly and rapidly growing trees, respectively, in the lower parts of the slopes; (*3*, *4*) slowly and rapidly growing trees, respectively, in the upper parts of the slopes.

the same group growing at different elevations. Apparently, more general factors, such as climatic conditions in the period when the seedlings of these trees emerged or some genetic features, have determined the differentiation of trees into groups. This is also confirmed by the similar ratios between the numbers of slowly and rapidly growing larch trees in the upper and lower altitudinal zones (31.5 : 68.5% and 26.2 : 73.8%, respectively).

I propose two different explanations of the observed differentiation of trees in larch populations. However, both explanations are not conclusive, and additional special studies are required. The first explanation is as follows. Some seedlings emerge in an extremely unfavorable (e.g., very cold) period and manage to survive but grow very slowly in the following few years. Such plants continue to grow relatively slowly, both in height and in diameter, for the rest of their life. They can survive subsequent unfavorable climatic periods and reach an age of 500–700 years. Other seedlings emerge in a relatively favorable period; they are numerous, and

Main parameters of slowly and rapidly growing tree groups and features of corresponding sites in the subalpine zone of the Kuznetsk Ala Tau

Average parameters	In lower plots		In upper plots	
	slowly growing	rapidly growing	slowly growing	rapidly growing
Number of model trees	32	90	137	298
Trunk diameter, cm	47 ± 3	36 ± 1	28 ± 1	21 ± 1
Trunk height, m	15.8 ± 0.7	18.5 ± 0.5	10.8 ± 0.2	10.5 ± 0.2
Age at trunk base, years	348 ± 17	160 ± 7	232 ± 7	99 ± 3
Vertical growth rate of the trunk, cm/year	4.7 ± 0.2	13.1 ± 0.5	4.9 ± 0.1	11.9 ± 0.3
Radial increment of the trunk, mm/year	1.36 ± 0.05	2.54 ± 0.01	1.22 ± 0.03	2.19 ± 0.05
Crown width, m	7.6 ± 0.6	8.0 ± 0.4	5.5 ± 0.2	4.6 ± 0.1
Distance from the ground to the crown, m	3.1 ± 0.3	2.9 ± 0.2	1.4 ± 0.1	1.4 ± 0.1
Elevation above sea level, m	1344 ± 8	1352 ± 6	1445 ± 11	1463 ± 6
Soil depth, cm	29 ± 2	28 ± 2	19 ± 1	20 ± 1
Coverage, %:				
Stones	1.6 ± 1.1	0.7 ± 0.4	13.0 ± 1.5	8.4 ± 0.9
Alder (*Alnus fruticosa* Rupr.)	8.4 ± 3.1	6.8 ± 1.8	2.0 ± 0.8	1.1 ± 0.4
Fir (*Abies sibirica* Ledeb.)	5.5 ± 2.0	8.9 ± 4.6	5.2 ± 1.1	2.9 ± 0.5
Ground birch (*Betula rotundifilia* Spach)	0.2 ± 0.1	1.5 ± 0.5	21.7 ± 2.0	24.9 ± 1.4
Blueberry (*Vaccinium myrtillus* L.)	22.6 ± 4.1	25.5 ± 2.4	19.5 ± 1.8	16.1 ± 1.3
Crowberry (*Empetrum nigrum* L.)	0.0	0.0	4.0 ± 1.1	4.9 ± 0.8
Cowberry (*Vaccinium vitis-idaea* L.)	0.4 ± 0.3	0.2 ± 0.1	5.5 ± 0.9	3.5 ± 0.5
Bergenia (*Bergenia crassifolia* (L.) Fritsch.)	4.6 ± 1.8	4.7 ± 1.2	7.6 ± 1.0	6.8 ± 0.8
Reedgrass (*Calamagrostis langsdorffii* (Link) Trin.)	13.7 ± 3.4	17.5 ± 1.9	5.5 ± 1.0	4.8 ± 0.7
Spleenwort (*Athyrium distentifolium* Tausch ex Opix)	3.7 ± 1.9	4.3 ± 1.1	0.0	0.0

their growth in the first years of life is relatively rapid. These trees retain a high growth rate for the rest of their life but partially die off during the subsequent unfavorable periods, so that all of them perish within 300–350 years. The assumption concerning the high resistance and, especially, longevity of slowly growing larch trees is confirmed by the data obtained in this study: slowly growing trees account for more than 90% of larch trees over 300 years of age, whereas their proportion in the total sample is less than 30% (Figs. 1, 2).

The second explanation is based on the assumption that the observed differentiation is related to the genetic predisposition of trees to a rapid or slow growth. This predisposition is mediated by different concentrations of phytohormones affecting the mitotic activity of meristematic cells and, hence, growth rate (Lebedenko, 1969; Fedorova, 1977). This is in agreement with the fact that the ratios between rapidly and slowly growing larch trees in the lower and upper zones of the altitudinal range are similar (73.8 : 26.2 and 68.5 : 31.5%, respectively). If the differentiation was determined by climate (the climate is milder in the lower zones, and the proportion of slowly growing trees should have been significantly lower there) the ratios should be considerably different. Possibly, the rapid or low growth is determined by groups of alternative genes, the former being dominant and the latter, recessive, because the ratio between rapidly and slowly growing trees in each population is close to 3 : 1. The higher proportion of slowly growing trees in the upper zones may be due to directional selection: the survival rate of slowly growing trees is higher because of their enhanced resistance to unfavorable climatic conditions, which are typical of the upper zones of mountain slopes.

Analyzing the distributions among one-year age groups for every year between 1640 and 1960, I estimated the number of slowly and rapidly growing trees that reached the height of sampling (20–40 cm) in each year. Variations in the number of trees in each group were smoothed with the use of a five-year sliding mean, and smoothed curves of changes in the numbers of slowly and rapidly growing Siberian larch trees with time were constructed. Comparing the smoothed curves of the growth indices and numbers of trees in each group, I found a gradual shift of the maximum and minimum numbers of trees away from the maximum and minimum growth indices. As early as in 1967, Shiyatov studied the dependence of the age structure of

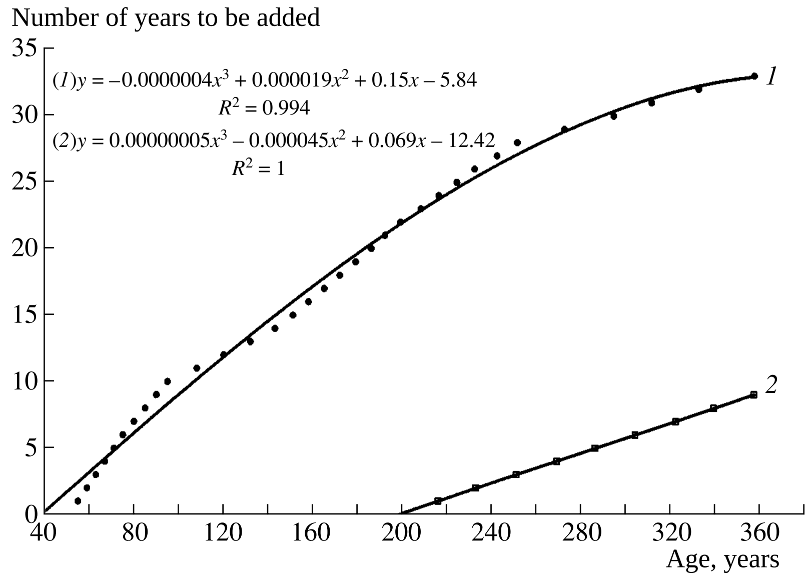

Fig. 3. The relationship between tree age at a height of 20–40 cm and the number of years that should be added to it to obtain the true age of the tree in groups of Siberian larch trees with different vertical growth rates: (*1*) rapidly growing trees; (*2*) slowly growing trees.

tree stands in light larch forests on climatic fluctuations in the Polar Urals and discovered a fundamental relationship between forest renewal and climate. Shiyatov (1967) reported that the formation of age generations in light larch forests located at the timberline most strongly depends on favorable or unfavorable thermal conditions in each period, with their improvement or deterioration causing changes in the proportion of trees of the corresponding age, which is reflected in the age spectrum. Taking into account these relationships, I corrected the smoothed curve of the number of trees, including "extension" of the curve, so that most maximums and minimums of the curves coincided.

Ordinal numbers and precise dates of the places of inserts extending the smoothed curves of the numbers of slowly and rapidly growing trees were used to construct the curves and derive their formulas shown in Fig. 3. Summing up the numbers of years determined from core samples and calculated from the formulas, I determined the calendar year of appearance of each tree in the groups studied.

The obvious decrease in the number of years that should be added to the age determined at the height of sampling (20–40 cm) in order to calculate the actual age of each tree may be explained by the difference between climatic conditions in the region in the 14th to 18th and 19th to 20th centuries (colder and warmer periods, respectively) (Adamenko, 1978). The larch outgrowth reached this height in different ways in these periods. Also note that buttress flares of old trees increased in size with age and interfered with perpendicular boring at the appropriate height. Therefore, the point of sampling in these trees was farther from the original point of vertical growth. In addition, rapidly growing trees had a diameter almost twice that of slowly growing trees the same age; therefore, the point of sampling in the former was located considerably higher than in the latter. Apparently, this was the main cause of the striking difference between the numbers of years that had to be added to the age determined at the height of sampling in rapidly and slowly growing trees in order to calculate their true ages.

Summing up the numbers of trees of both groups in each one-year age class, I obtained a generalized curve of the number of trees; the total number of trees that emerged in each year was determined for every year from 1640 to 1960. Changes in the number of trees from year to year were smoothed by means of a five-year sliding mean, and a smoothed curve of changes in the number of Siberian larch trees with time was constructed.

The analysis of the smoothed curve of radial increment indices of Siberian larch (Fig. 4) revealed cycles of different lengths (from 21–24 to 100–110 years) reflecting the periods of favorable and unfavorable climatic conditions during the past 350–360 years. Distinct maximums of increment were found in 1640, 1660, 1680, 1700, 1720, the late 1760s and early 1770s, early 1780s, 1800s, late 1820s, 1850s, mid-1870s, late 1890s and 1900s, early 1920s, early 1930s, mid-1940s, 1950s, 1970s, and early 1990s. After the aforementioned correction, the periods of an increase in the number of trees became fairly coincident with these periods. The coincidence became especially good for the period after 1800, when there were only a few small discrepancies between the changes in increment indices and the numbers of new trees. For example, there was a distinct maximum of radial increment in the late 1820s and

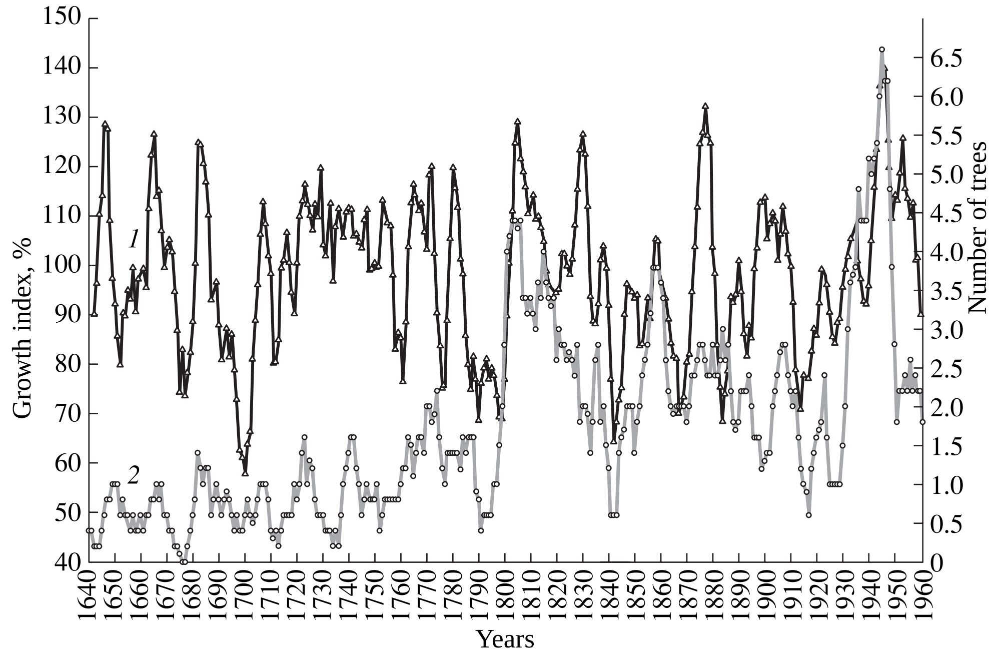

Fig. 4. The dynamics of smoothed five-year sliding means for (*1*) indices of radial increment and (*2*) numbers of Siberian larch trees that appeared in the subalpine zone of the Kuznetsk Ala Tau between 1640 and 1960.

early 1830s, whereas the rate of forest renewal remained almost unchanged. Before 1800, there were more of such discrepancies, which was probably related to an insufficient number of model trees, as their proportion in the sample was only 26.6%.

In general, conditions favored the formation of new generations in the 1640s, 1660s, 1680s, 1700s, 1720s, 1740s, 1760s–1770s, 1800s–1810s, 1850s, 1870s–1880s, 1900s, 1920s, and 1920s–1940s. The waves of increase in the numbers of trees were most pronounced in the first two decades of the 19th century and in the 1940s. The data on the undergrowth indicate that a similar increase has occurred in the past 30 years, which is expressed in the active renewal of larch forests in the upper zone of their altitudinal range.

I compared the indices of radial increment estimated in this study with relevant data on larch forests in the Altai Mountains reported by Adamenko (1978) and Panyushkina and Ovchinnikov (1999). The periods of increase and decrease in growth indices of larch trees growing at the upper boundary of subgoltsy larch forests in the Altai and Kuznetsk Ala Tau mountains were synchronous, although some of the periods in the two regions were shifted by one to three years relative to each other. Adamenko and Ivanov (1983) revealed a close association between these periods and the periods of increased air temperatures in summer (June and July) by comparing their data on radial increment in larch growing in the Kuznetsk Ala Tau over the past 150 years with the standard dendrological scale of the Altai Mountains constructed earlier (Adamenko, 1978). The latter exhibits a strong correlation with the pattern of changes in summer temperatures. Moreover, some discrepancies between the smoothed curves of changes in growth indices and numbers of trees may be explained on the basis of the aforementioned data on the Altai Mountains (Adamenko, 1978; Panyushkina and Ovchinnikov, 1999). For example, the cooling of the climate between 1813 and 1855 was more pronounced in this region; this probably led to a decrease in the survival of undergrowth, which is more sensitive to cold than growth processes in mature trees.

These results suggest that the periods of renewal in Siberian larch forests have been associated with periods of more favorable temperature conditions at the timberline in the Kuznetsk Ala Tau. This has affected the age structure of larch forests; specifically, the proportions of the trees that appeared and survived in the favorable periods are increased. This finding may be useful for more detailed studies on the relationships between climatic changes and forest regeneration rate, which is especially important for predicting the ecological consequences of global warming.

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