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# Expansion of Evergreen Conifers to the Larch-Dominated Zone and Climatic Trends

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**Abstract**—The expansion of so-called evergreen conifers (EGCs), including Siberian stone pine, spruce, and fir, along the transect oriented from the boundary of the larch-dominated zone (LDZ; mixed forests of the Yenisei Ridge) to its center has been studied. The normalized dispersal coefficient calculated as $K_i = (n_i - N_i)/(n_i + N_i)$, where $n_i$ and $N_i$ are the relative numbers of the *i*th species in the undergrowth and the upper layer, respectively, serves as an indicator of the expansion. It has been found that the $K_i$ values for EGCs (and birch) are higher than the $K_i$ of larch even in the zone absolutely dominated by larch, where the relative numbers of EGCs in the upper layer is less than 1%. The EGC undergrowth has mainly been formed during the past 20–30 years, which is correlated with the trend of summer temperatures The spread of EGCs in the LDZ depends on the frequency of forest fires. The decrease in the time intervals between fires in the 20th century to 65 years (versus 100 years in the 19th century) may have prevented the expansion of competing species in the LDZ. The results obtained indicate that EGCs and birch penetrate into the zone traditionally dominated by larch, which is related to climatic changes during the past three decades. At the same time, tree stand density is increasing in the forest–tundra ecotone, and larch is spreading further into the tundra zone.

*Key words*: larch forests, successions, climatic trends, forest fire sites, permafrost.

The larch-dominated zone (LDZ) extends from the Yenisei Ridge to the Pacific Ocean and from the Angara River basin to the 73rd parallel, where larch forms the northernmost tree stands in the world (the Ary-Mas and Lukun regions of the Taimyr Reserve). *Larix gmelinii* is the dominant larch species in central Siberia; in western and southern regions, there is an admixture of *L. sibirica*; hybrid forms of these two species are found in their contact zone. In the west (the Yenisei Ridge) and the south, mixed tree stands, which are most prevalent there, consist of larch and the spruce *Picea obovata* with admixtures of the Siberian stone pine *Pinus sibirica*, the fir *Abies sibirica*, and the Scotch pine *P. sylvestris*, as well as small-leaved trees (*Betula pendula, B. pubescens*, and *Populus tremula*). Larch successfully competes with other conifers due to its higher resistance to severe climate: at the margin of its species range, larch survives at an average annual temperature of –14°C and an absolute minimum temperature of –68°C. Larch exceeds other species in the efficiency of water use (Kloeppel *et al.*, 1998) and survives at an annual precipitation corresponding to that of the semidesert zone (<250 mm). The improvement of site conditions due to the predicted increase in air temperature and precipitation at high latitudes (Kondrat'ev, 2002; *IPCC…*, 2001) may lead to the expansion of larch into tundra; an increase in the density and productivity of forests bordering on tundras (Hughes *et al.*, 1999; Sturm *et al.*, 2001; Shiyatov, 2003; Kharuk *et al.*, 2003); and a decrease in the competitiveness of larch as a species adapted to severe climatic conditions, which will lead to its expansion to the zone dominated by other forest-forming species (Kharuk *et al.*, 2002a).

Here, we estimated the expansion of evergreen conifers (EGCs) to the LDZ caused by climatic changes during the past decades. The numbers, species composition, and age structure of larch undergrowth and the species ratios in the undergrowth and the upper layer are used as indicators of this expansion.

## REGION

The study region is located mainly on the Middle Siberian Plateau with elevations varying from 200 to 700 m, mostly in the permafrost zone. The region borders on the Yenisei Ridge (with maximum heights of approximately 1000 m) in the west and the Putoran Plateau (with maximum elevations of approximately 1700 m) in the north. The greater part of the region is a plateau with maximum elevations of approximately 900 m. According to forest zoning, the region studied belongs to the Angara–Tunguska Province of taiga forests. In the Lower Tunguska Region of light northern taiga forests, more than 80% of forested area is covered with *L. gmelinii* belonging to quality class 5 (the rest is covered with birch forests). The climate is cold conti-

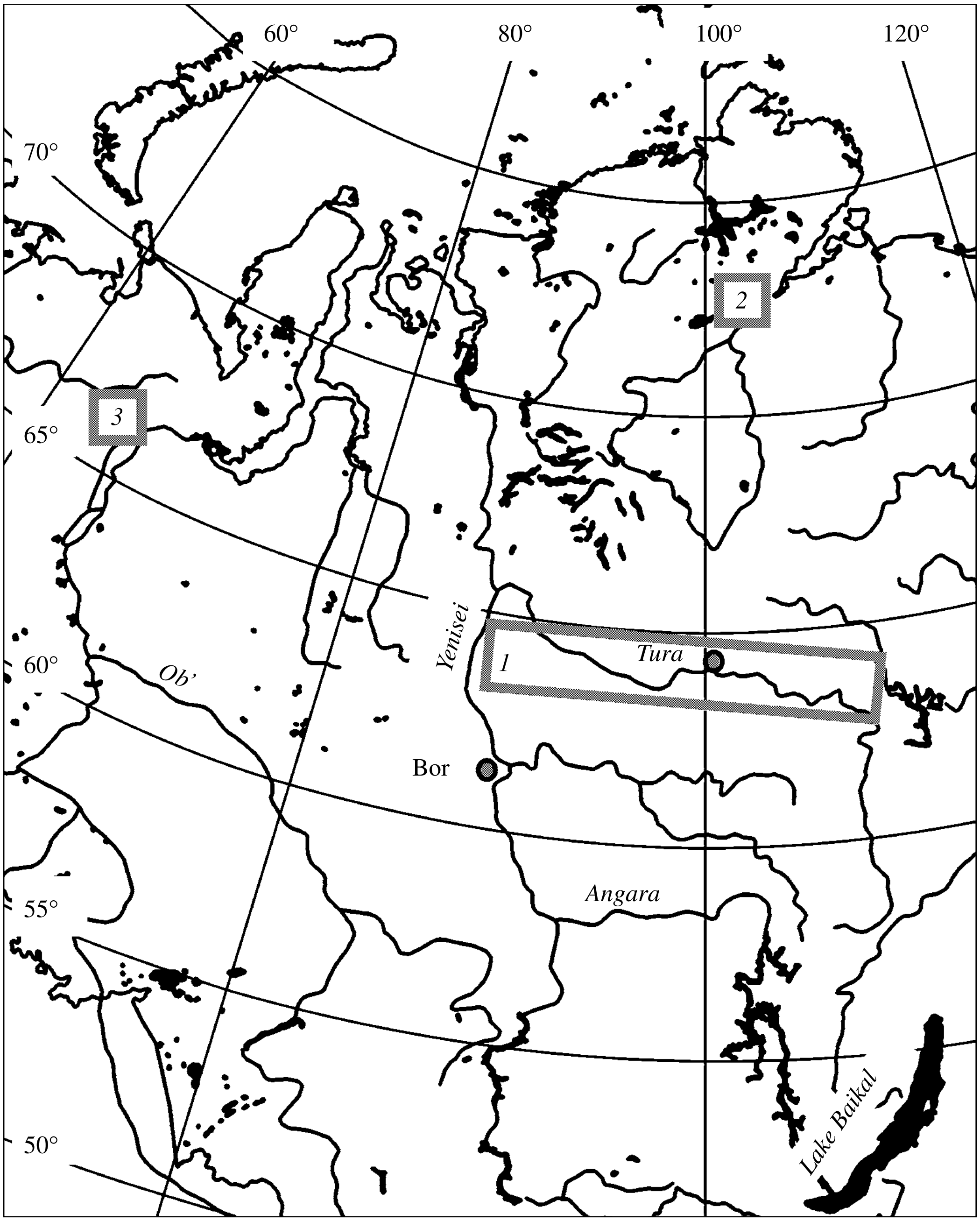

**Fig. 1.** Map of the study region: (*1*) the west–east transect; (*2*) the Ary-Mas plot; (*3*) the Polyarnyi Ural plot.

nental; the annual precipitation is 300–400 mm in the center, 600–700 mm in the west, and 400–500 mm in the south. Land studies were performed along the west–east transect oriented along the "gradient" of the contribution of larch to the upper layer. The transect was ~800 km in length (from 91° to 106°30′ E) (Fig. 1).

## MATERIALS AND METHODS

We established 58 test plots (TPs) along the west–east transect during land studies performed in 2001–2003, as described in the (*Instruktsii…,* 1995). In each TP, we described the relief, the types of vegetation and the phytocenosis, the species composition of the tree stand, the average diameter and height of trees, exogenous factors (fires and felling), the shrub layer, the dead and live soil covers, and the soil type. The center of the TP was determined using GPS. The undergrowth was studied in 10 × 10 m squares (three squares per TP). We counted the total abundance of undergrowth (no more than 2.5 m in height), determined the age of each tree, and assessed its reliability. Data on temperature and precip-

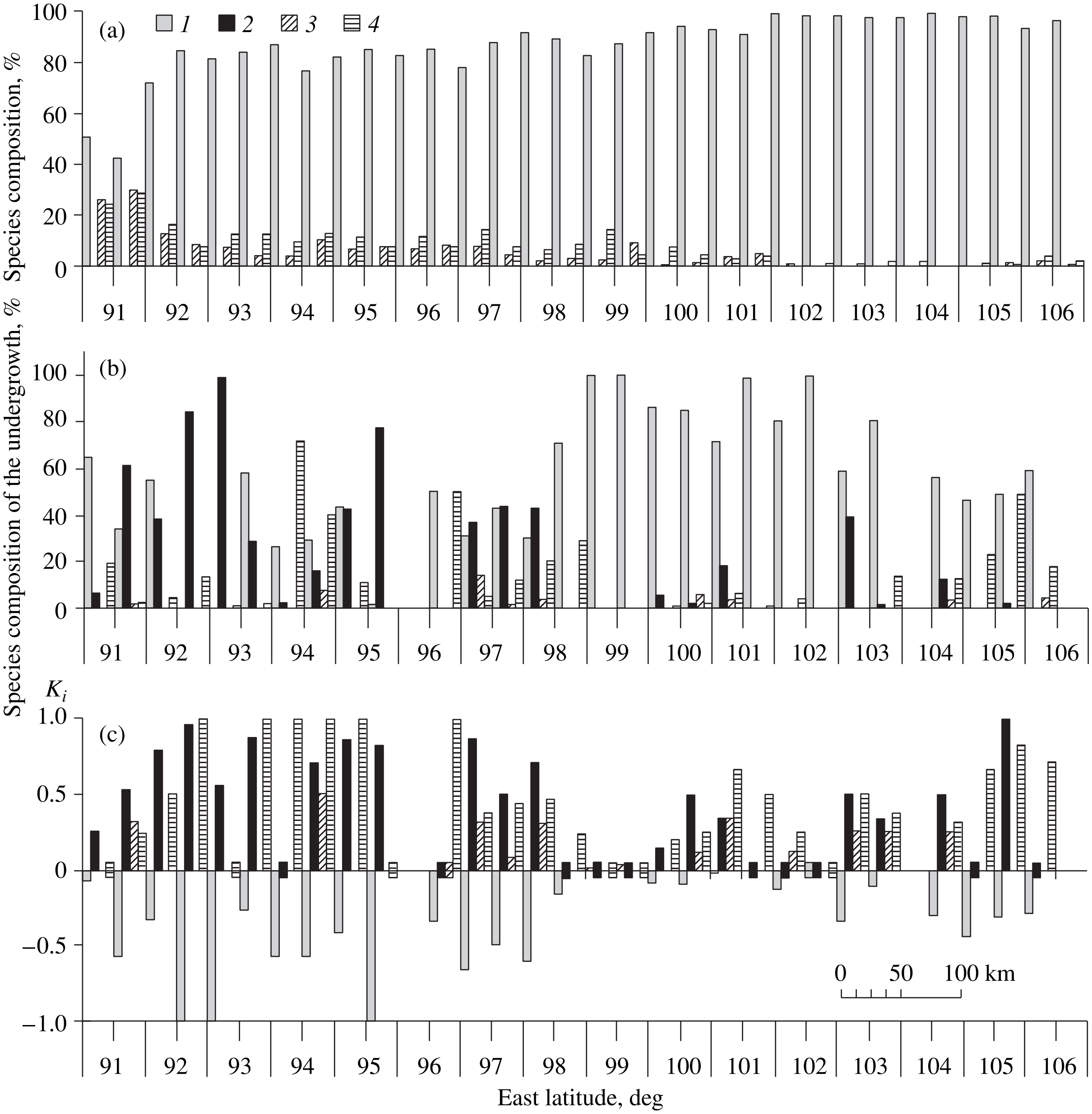

**Fig. 2.** West–east transect: the proportion of woody plants in the (a) upper layer and (b) undergrowth. (c) Normalized reproduction coefficient. Designations: *1*, larch; *2*, Siberian stone pine; *3*, spruce + fir; *4*, birch.

itation were obtained from the Tura and Bor meteorological stations (Fig. 1). We conventionally divided the year into three summer months (from June to August) and nine winter months (from September to May). Data from the national forest inventory (*Lesa SSSR*, 1990) were used in the study. The abundance of EGC undergrowth (trees per hectare), the age structure of the undergrowth, and the normalized dispersal coefficient served as indicators of the expansion. The coefficient was calculated as $K_i = (n_i - N_i)/(n_i + N_i)$, where $n_i$ and $N_i$ are the relative numbers of the *i*th species in the undergrowth and the upper layer, respectively; $K_i$ was equal to +1 if the *i*th species was absent in the upper layer and present in the undergrowth of the given TP, –1 if the situation was opposite, and 0 if $n_i = N_i$. The nonparametric Kolmogorov–Smirnov statistics (*StatSoft, Inc.*, 2003) were used for data treatment.

## RESULTS

**The distribution of undergrowth along the west–east transect.** Figure 2 shows the relative numbers of tree species in the upper layer, the species composition of the undergrowth, and $K_i$ values. The data shown in Fig. 2b were obtained by scanning a map of forests of the Soviet Union (*Lesa SSSR*, 1990) with a window

Undergrowth abundance, trees per hectare

| Parameter | All TPs | | | | TPs with $n > 0$ | | | |
|---|---|---|---|---|---|---|---|---|
| | Siberian stone pine | Larch | Spruce | Birch | Siberian stone pine | Larch | Spruce | Birch |
| Number of TPs | 58 | 58 | 58 | 58 | 36 | 50 | 29 | 33 |
| Undergrowth abundance | 1080<br>(0–3200) | 37150<br>(0–530000) | 210<br>(0–2000) | 3390<br>(0–62130) | 1740<br>(167–3200) | 43100<br>(17–30000) | 430<br>(17–2000) | 5960<br>(67–62130) |

15 × 150 km in size to determine average values for the upper layer. These values were correlated with the results of ground-based observations along the transect ($R = 0.58$). The data on undergrowth are shown in Fig. 2b and the table. The data on the *P. sibirica* undergrowth are shown separately, because it was the most common species along the transect; the data on spruce and fir have been pooled for easier perception of the graphic material. Fir disappeared from the renewal pool and the canopy at approximately 63° N: this species is more sensitive to site conditions than any other conifer studied. In general, pine, fir, and aspen were rare in the LDZ; they grew fragmentarily on southern and western slopes.

The west–east transect was oriented from the mixed taiga of the eastern macroslope of the Yenisei Ridge to the LDZ. In this direction, the climate became more continental: annual average temperature and precipitation were –3.7°C and 560 mm, respectively, in the western part of the transect (the Bor meteorological station) and –9.0°C and 353 mm, respectively, in the LDZ (the Tura meteorological station). The data were averaged over the entire period of instrumental observations (1934–2003). As the climate became more continental, the proportion of larch in both the tree stand and the renewal pool increased (Fig. 2a).

The distribution of undergrowth along the transect did not replicate the distribution of tree species in the upper layer: the undergrowth of EGCs was more prevalent than that of larch on a considerable part of the transect (Fig. 2b). This is especially obvious from the dispersal coefficients for different species: the $K_i$ values of the EGC (and birch) undergrowth were higher than those for larch even in the zone absolutely dominated by larch, where the proportion of EGCs in the upper layer was less than 1% (Fig. 2c). These data indicate that EGCs expanded to the typical larch area.

**Age structure of the undergrowth and changes in temperature and precipitation.** Data on the age structure of *P. sibirica* undergrowth (Fig. 3) show that it has mainly been formed during the past 20–30 years, with >90% of the undergrowth being reliable, and the loss was <10% during that period. The loss was assessed from the amount of dead trees, which are preserved for several decades at high latitudes. Note that the abundance of *P. sibirica* undergrowth has been increasing parallel to the increase in temperature and precipitation during the past several decades (Figs. 4a, 4b). Meteorological parameters were treated in two variants; we calculated (1) the deviations from the mean value for the entire period of instrumental observations (1934–2003) and (2) the differences between the deviations from the mean value for the past 30 years (1970–2003) and the preceding period (1934–1969). Both temperature and precipitation have increased at both meteorological stations during the past 30 years. In the case of precipitation, the differences were significant at $p > 0.95$. Although the differences in temperature were nonsignificant, we found significant temperature trends ($p > 0.95$ and $p > 0.93$ for the Tura and Bor stations, respectively). The age structure of the undergrowth during the past three decades correlated with winter temperature anomalies ($R = 0.83$ and $R = 0.78$ for the Tura and Bor stations, respectively; $p > 0.95$). The correlation with summer temperature was nonsignificant. This fact indicates that winter temperatures are an important factor in the survival of *P. sibirica* undergrowth. The undergrowth abundance peaked within the past 10–15 years; note that the last decade of the 20th century was "the warmest" of the past millenium (*IPCC*, 2001; Kondrat'ev, 2002).

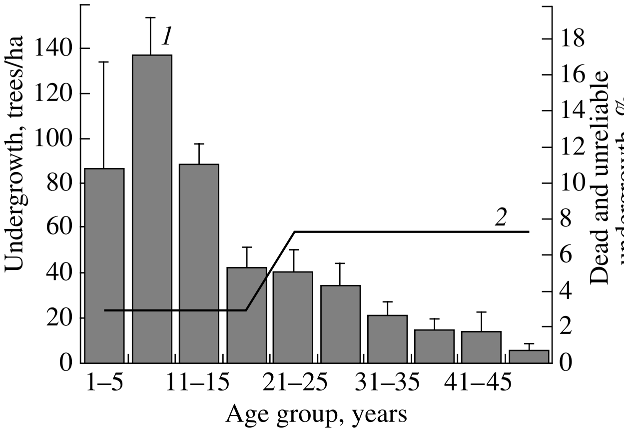

**Fig. 3.** Age composition of the Siberian stone pine undergrowth (confidence intervals are shown for α = 0.05): (*1*) *P. sibirica* undergrowth; (*2*) dead and uncertain undergrowth.

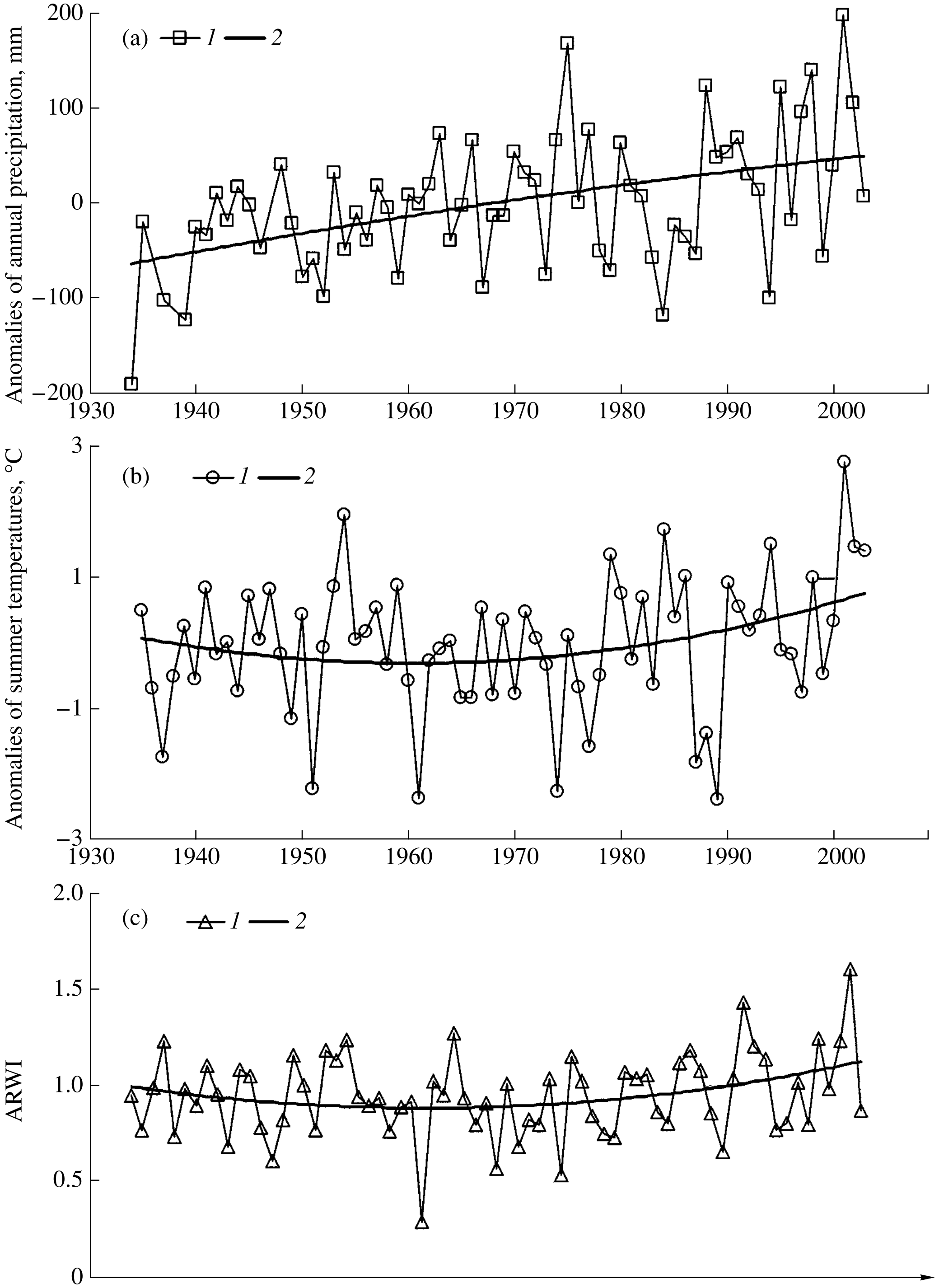

**Fig. 4.** Anomalies of (a) annual precipitation and (b) summer temperatures during the period of instrumental observations at the Tura meteorological station. (c) Annual ring width index (ARWI). Designations: *1*, original data; *2*, trends.

**EGC undergrowth and fires.** The expansion of EGCs to the LDZ depends on the frequency of fires. For "southern species," fire sites serve as "launching pads" (due to improvements in the thermal conditions and soil drainage, enrichment of soils with biogenic element, and increases in the depth of soil thawing). At the same time, the decrease in the intervals between forest fires in the 20th century (to 65 years, versus 100 years in the 19th century) (Kharuk *et al.*, 2003) prevents the expansion of species competing with larch. This is confirmed by our observations (Fig. 5): *P. sibirica* undergrowth is more abundant at old fire sites, whereas larch grows mainly at fresh fire sites because it is more abundant in the upper layer. Under favorable conditions (when a fire coincides with a year in which seed production is increased), the larch undergrowth abundance may be as large as 700000 trees/ha. Note that the alder *Duschekia fruticosa* also aggressively expands at fresh fire sites. At the southern and western margins of the LDZ, birch actively colonizes fresh fire sites (as much as ~1000000 trees/ha).

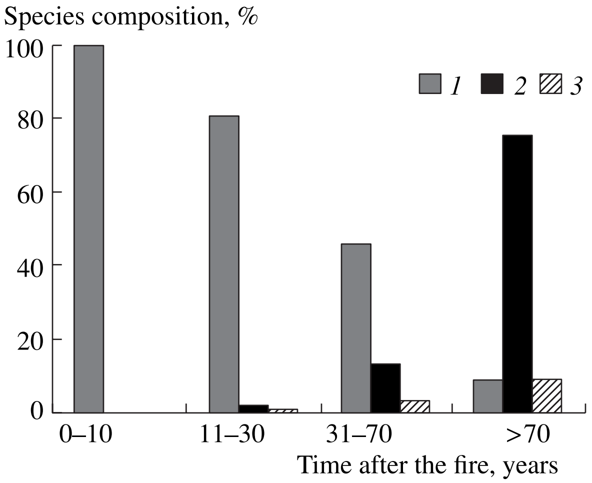

**Fig. 5.** The time course of the spread of conifer undergrowth at fire sites. Designations: *1*, larch; *2*, Siberian stone pine; *3*, spruce.

## DISCUSSION

The differences between EGCs and larch in the undergrowth abundance and the upper layer and the differences between these species with respect to dispersal coefficient indicate that EGCs are being expanding to the LDZ. The correlation between the age structure of *P. sibirica* undergrowth, temperature, and precipitation during the past decades indicates that this expansion is related to climatic changes. At the same time, the *P. sibirica* undergrowth abundance (and, to a lesser extent, other conifers) exhibits natural fluctuations. Fourier analysis of the age structure of *P. sibirica* undergrowth (Fig. 3) demonstrated that the main peak of the undergrowth appeared at 3.5-year periods, which was apparently related to the seed-production cycle. Since the period of this cycle was much shorter than the time interval analyzed (~30 past years), it did not affect the significance of the increase in *P. sibirica* undergrowth during the past several decades, although it decreased the correlation between the *P. sibirica* undergrowth abundance and meteorological parameters.

The aforementioned predominant expansion of *P. sibirica* compared to spruce and fir may be explained by two main factors: (1) *P. sibirica* is more resistant to permafrost, some trees being found at a latitude of ~65° N, and (2) a specialized bird species (*Nucifraga caryocatactes*) and certain mammals promote *P. sibirica* dispersal: its outgrowth is sometimes found several hundreds of meters away from the source of seeds. On the other hand, spruce may spread farther north than *P. sibirica* along drainage networks (on well-warmed banks of rivers and brooks). In general, the drainage network is the main pathway of the penetration of EGCs into larch forests, because the mesoclimatic conditions (protection from wind and higher humidity) along rivers and the better soil drainage in narrow (10–20 m) bank zones are favorable for "southern species." The increase in precipitation during the past several decades favors the expansion of *P. sibirica* in the LDZ: *P. sibirica* is sometimes called "the tree of fogs." The increase in winter precipitation also favors the survival of undergrowth: the time when tree height exceeds the snow cover thickness is the critical period of development. Snowstorm transfer in this zone leads to the dehydration and damage of shoots, drying of apical shoots, and the death of plants or the formation of dwarf forms. The crowns of trees that have overcome this barrier have a characteristic shape, with branches being absent in the snowstorm transfer zone (the so-called "skirt-wearing trees"). Wind conditions (combined with low temperatures) represent one of the main factors of the survival of trees at the northern treeline. The relatively high proportion of bark (>20% of the trunk volume) in larch gives it a competitive advantage over other conifers, protecting its shoots from desiccation. On the other hand, the increase in winter temperatures favors the survival of EGC undergrowth.

If the current climatic trends (increase in temperature and precipitation) continue, EGC undergrowth in the LDZ (Fig. 2b) will gradually form a second layer, which is currently the case at the western and southern borders of the LDZ. The formation of the tree canopy dominated by EGCs leads to a decrease in albedo and a corresponding increase in solar-radiation absorption. This creates a positive feedback, enhancing the greenhouse effect.

The changes observed in the species composition of undergrowth in the LDZ are related to the decrease in the larch species range. In previous epochs, larch dominated not only in the northern and middle taiga, but also southern Siberia, where dense larch forests are currently found only on "shadowed" macroslopes (with low precipitation) of the Sayan and Altai mountains. The preservation of larch in mixed tree stands where its undergrowth is not abundant is favored by the longevity of this species: the maximum life span of larch in southern taiga is 600 years, and some trees in northern taiga live as long as ~1000 years. The life spans of other conifers are shorter: spruces, firs, and pines (both *P. sylvestris* and *P. sibirica*) live as long as 300–350, 200–250, and 400–500 years, respectively.

The results obtained indicate the expansion of EGCs and birch to the zone traditionally dominated by larch and the relationship of this phenomenon with climatic changes that have occurred over the past three decades.

Larch has also responded to climatic trends of the past decades: its radial increment (measured by the annual ring width index; Fig. 4c) has increased, which was correlated with temperatures and precipitation in summer ($R = 0.5$ and $R = 0.43$, respectively; $p > 0.95$). Increases in larch stand density and the expansion of larch into the tundra zone (Kharuk *et al.*, 2002b) were observed at the border of the larch area (The Polyarnyi Ural and Ary-Mas plots; Fig. 1). As a result, larch expansion may reach the Arctic coast, which was the case in the Holocene (*Antropogen Taimyra*, 1982), whereas species characteristic of the middle and southern taiga zones will occupy part of the current LDZ.

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