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Evidence of Evergreen Conifer Invasion into Larch Dominated Forests During Recent Decades in Central Siberia

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Abstract

Models of climate warming predict the migration of "warm-adapted" species to habitats of "cold-adapted" species. Here we show evidence of the expansion of "dark-needle" conifers (DNC: Siberian pine, spruce and fir) into the habitat of larch, the leader in adaptation to harsh climatic conditions in Asia. The studies were made along two transects oriented from the western and southern borders of a larch dominated forest to its center. The invasion of DNC into the historical larch habitat was quantified as an increase of the proportion of those species both in the overstory and in regeneration. Abundance and invasion potential were expressed using the following variables: (1) N_i and n_i – the proportion of a given species in the overstory and in regeneration, respectively, and (2) K_i – "the normalized propagation coefficient" defined as $K_i = (n_i - N_i) / (n_i + N_i)$. The results show that Siberian pine and spruce have high K_i values both along the margins and in the center of zones of absolute larch dominance even where their presence in the overstory is <1%. There is a tendency for K_i to increase for DNC and birch from south to north and from west to east. The age structure of regeneration showed that regeneration occurred mainly during the last 2-3 decades. In particular, warm winter temperatures promote the survival of regenerated Siberian pine. The results obtained indicate the climate-driven migration of Siberian pine, spruce and fir into traditional zone of larch dominance. Substitution of a deciduous conifer (larch) by evergreen conifers decreases the albedo and may provide positive feedback for temperature increases.

Key words: climatic change, forest succession, larch communities, permafrost, species migration, wildfires

Introduction

The larch (*Larix gmelinii, L. sibirica)* dominance zone (LDZ) extends from the Yenisey River in the west to the Pacific Ocean in the east, and from Baikal Lake in the south to the 73rd parallel in the north, where there is the world's most northward stand at Ary-Mas. In Central Siberia larch at its southern and western margins is in contact with "dark-needle" conifers (DNC: Siberian pine, *Pinus sibirica*, spruce, *Picea obovata*, fir, *Abies sibirica*), Scotch pine, *Pinus silvestris* and hardwoods (birch, *Betula pendula*, *B. pubescens*, and aspen, *Populus tremula*). Within the LDZ, larch competes effectively with other tree species due to its higher resistance to harsh climatic conditions. Larch surpasses the other tree species in water use efficiency and survives at a semi-desert level of precipitation (<250 mm/yr) (Kloeppel *et. al*., 1998). Moreover, larch can survive in the permafrost zone because its deciduous leaf habit and dense bark protect stems from winter desiccation and snow abrasion (Berg and Chapin 1994, Kharuk *et al*., 2003). The larch forest area, including the vast forest-tundra ecotone zone, is considered to be a carbon sink. However, as temperatures and precipitation increase at high latitudes (IPCC, 2001), the area could become a source of greenhouse gases. Better climatic conditions, in general, result in (1) larch expansion into the tundra on its northern and altitudinal borders, stand densification, and a growth increment increase (Payette *et al*., 2001, Sturm *et al*., 2001, Beniston, 2003, Walther, 2003), and (2) a decrease in the existing competitive advantage of larch in comparison with other species in its traditional dominance zone. The evidence for these responses has been published mainly for Europe and North America (Grace *et al*., 2002, Smith *et al*., 2003, Kullmann, 2007).

Although the most significant temperature changes are observed and predicted in Siberia (IPCC 2001, WMO, 2002, Zwiers, 2002), there are few published reports on the response of Siberian species to climate warming (Shiyatov, 2003, Kharuk *et al*., 2005b, 2006).

The purpose of this study is to answer the question: is there evidence for an invasion of DNC into the larch habitat? Regeneration is considered herein as an indicator of DNC invasion in terms of its abundance, species composition, age structure, and the proportion of the relevant species both in the overstory and in regeneration.

Materials and Methods

Study Area

The main part of the investigated area is situated on

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the Central Siberian plateau within the permafrost zone. The area is bounded on the west by the Yenisey Ridge, and on the north by the Putorana plateau (around 68°N 100°E). The climate is severe continental with an average annual temperature range of –8 to 14 °C. The mean annual precipitation level is 300-400 mm in the central part, 600-800 mm in the east and 400-500 mm in the south. Wildfires are typical for this territory with the majority occurring in late spring as ground fires due to low crown closure. The investigations were made during 2001-2004 field seasons along two transects: the "West-East" (WE, 91°E - 106° 30′ E, ~800 km length) and "South-North" (SN, 57° 30′N - 64°30′ N, ~ 420 km) (Fig. 1).

The WE transect is oriented along a gradient of climate severity - from Yenisey ridge mixed forests (which are under the influence of Atlantic cyclones) into the middle of larch dominated forest. The southern part of the SN transect is an area of mixed forest in the Angara River region (Fig. 1).

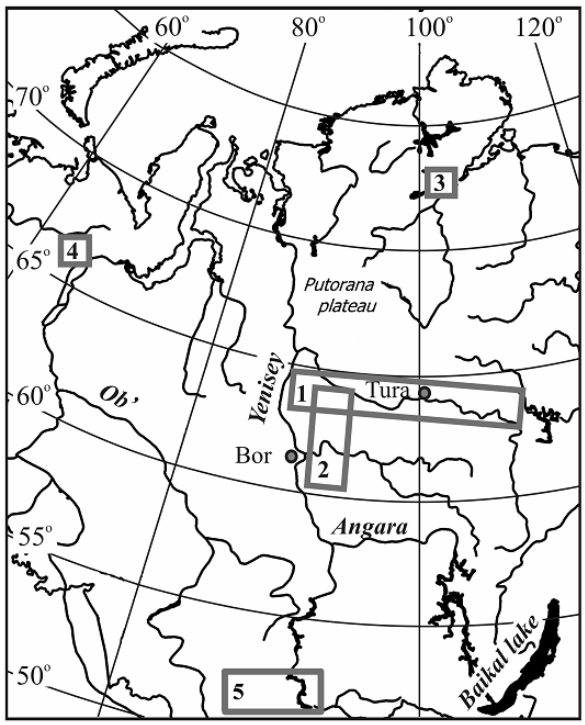

Fig. 1. The investigated area.
1 – WE transect, 2 – SN transect,
3 – the Ary-Mas site, 4 – the Polar Ural site,
5 – the Altai-Sayan Mountains site.

Plant species

The larch-dominated communities are composed mainly of larch (*Larix gmelinii*) with an admixture of birch (*Betula pendula*, *B. pubescens*). The western and southern transect margins are areas of a "larch-DNC ecotone" composed of larch with other conifers (Siberian pine, *Pinus sibirica*, pine, *Pinus silvestris*, spruce, *Picea obovata*, and fir, *Abies sibirica*) and hardwoods (birch and aspen, *Populus tremula*).

Methods

A total of 58 test sites (TS) along the WE transect and 51 along the SN transect were measured. For each TS (19.6 m in diameter) the following parameters were described: topography (height above mean sea level, slope aspect, slope steepness), vegetation cover type, forest stand structure (e.g., open, closed), tree diameters and heights, disturbance history (wildfire damage or logging), regeneration structure, description of shrub and ground cover, and soil type. Center point coordinates for each TS were also geo-referenced with ±15 m accuracy.

Regeneration studies were made on subplots of 10 x 10 m size (3 plots for each TS). For each subplot the density of trees with height ≤ 2.5 m and the plot age structure were calculated. The height limit was conventional, and agrees with Russian inventory rules. A description of the vigor of young trees was also made. Burn age was determined based on the age of post-fire regeneration. Preliminary to this, before the actual field work began, NOAA/AVHRR, Terra/MODIS and Landsat-7 images were used to detect burns.

The appearance of DNC into larch habitat was quantified as an increase in the proportion of DNC species both in the overstory and in regeneration. For the estimation of abundance and the species invasion potential, we employed the following variables: (1) N_i and n_i – the proportion of a given species in the overstory and in regeneration, respectively, and (2) K_i – "the normalized propagation coefficient" defined as $K_i = (n_i - N_i) / (n_i + N_i)$. The normalized data is easier to interpret and to present in comparison with absolute or non-normalized data (for example, a simple ratio index): the K_i values vary within +1 (in the case of the absence of *i-th* species in the overstory) to -1 values (in the opposite case), and are equal to 0 when $n_i = N_i$. Non-parametric Kolmogorov-Smirnov statistics and Fourier-analysis were used in the data analysis (StatSoft, Inc. 2003).

Temperature and precipitation data were taken from the Bor and Tura weather stations (Fig. 1). The period from June to August was conventionally taken as "summer," and the period from September to May was considered as "winter." An available forest inventory map was also used in this study (State Forest Committee, 1990).

Results

The regeneration distribution along the transects

The charts in Figures 2 and 3 represent a "snapshot" of mature tree species, regeneration, and the values of the propagation coefficient, K_i, along the WE transect. The data on regeneration abundance are presented in Figures 2B and 3B. Figure 2A and 3A data were generated using a "sliding window" (10 x 150 km) of the forest inventory map (State Forest Committee, 1990), which provides mean values of the species distribution in the overstory. These data correlated with the on-ground data along the transects (r=0.58 for the WE transect). The regeneration data for Siberian pine were of special interest, since this species is the most wide-spread DNC along the transects; data for spruce

and fir on the chart were combined for better graph visualization (Figs. 2B, 3B). Fir was eliminated from the overstory at about 63°N latitude since this species has a minimal resistance to harsh climatic conditions. In general Scotch pine, fir and aspen did not significantly penetrate into the LDZ other than as local stands growing on warmer south facing slopes.

The changes along the SN transect in general are similar to those along the WE transect, although not as dramatic (Fig. 3). This is because the SN transect is two times shorter, and extends along the Yenisey Ridge, an area experiencing the impact of Atlantic cyclones, with a gradual south-north climate gradient.

The West-East transect was oriented from the mixed taiga on the east macro-slope of the Yenisey ridge to the interior of the larch dominated area. This corresponded to an increase in climatic severity: in the west part of the transect annual temperatures and precipitation were minus 3.7°C and 560 mm, respectively, whereas in the area of larch domination (Tura Weather Station) the parameters were minus 9.0°C and 353 mm. Climate variables were considered for the whole period of instrumental observations (1934-2003). Larch increased in proportion in the overstory and in regeneration (Fig. 2A) towards the transect's eastern end.

Regeneration distribution along the transects did not

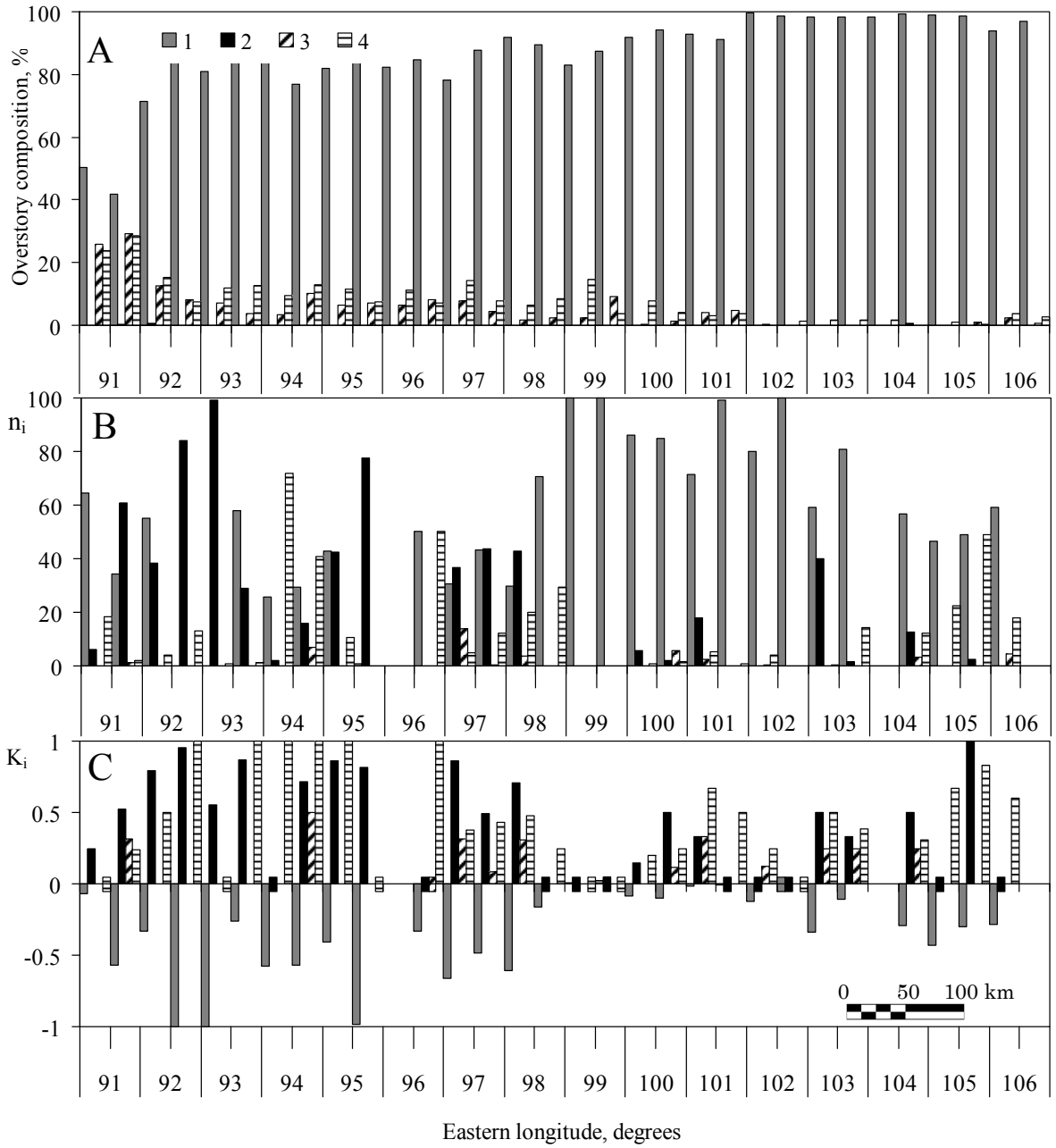

Fig. 2. WE transect. A. Overstory. B. Regeneration. C. Propagation coefficient.
1 – larch, 2 – Siberian pine, 3 – spruce+ fir, 4- birch.

replicate species distribution in the overstory. For example, DNC regeneration predominated over a significant part of the WE transect (Fig. 2B, 3B). This effect is more pronounced for the propagation coefficient values. *Ki* for DNC regeneration (and birch regeneration) was higher than for larch even in zones of absolute larch domination where DNC presence in the overstory was < 1% (Fig. 2B). These data support the idea of DNC propagation into typical larch habitat zones.

Siberian pine regeneration has appeared mainly during the last three decades (Fig. 4), and, according to field records, 90% of it is of good vigor. The regeneration mortality for the last 30 years was about 10 %. This was determined by counting dead saplings, since under climatic conditions of high latitude they can be identified for decades.

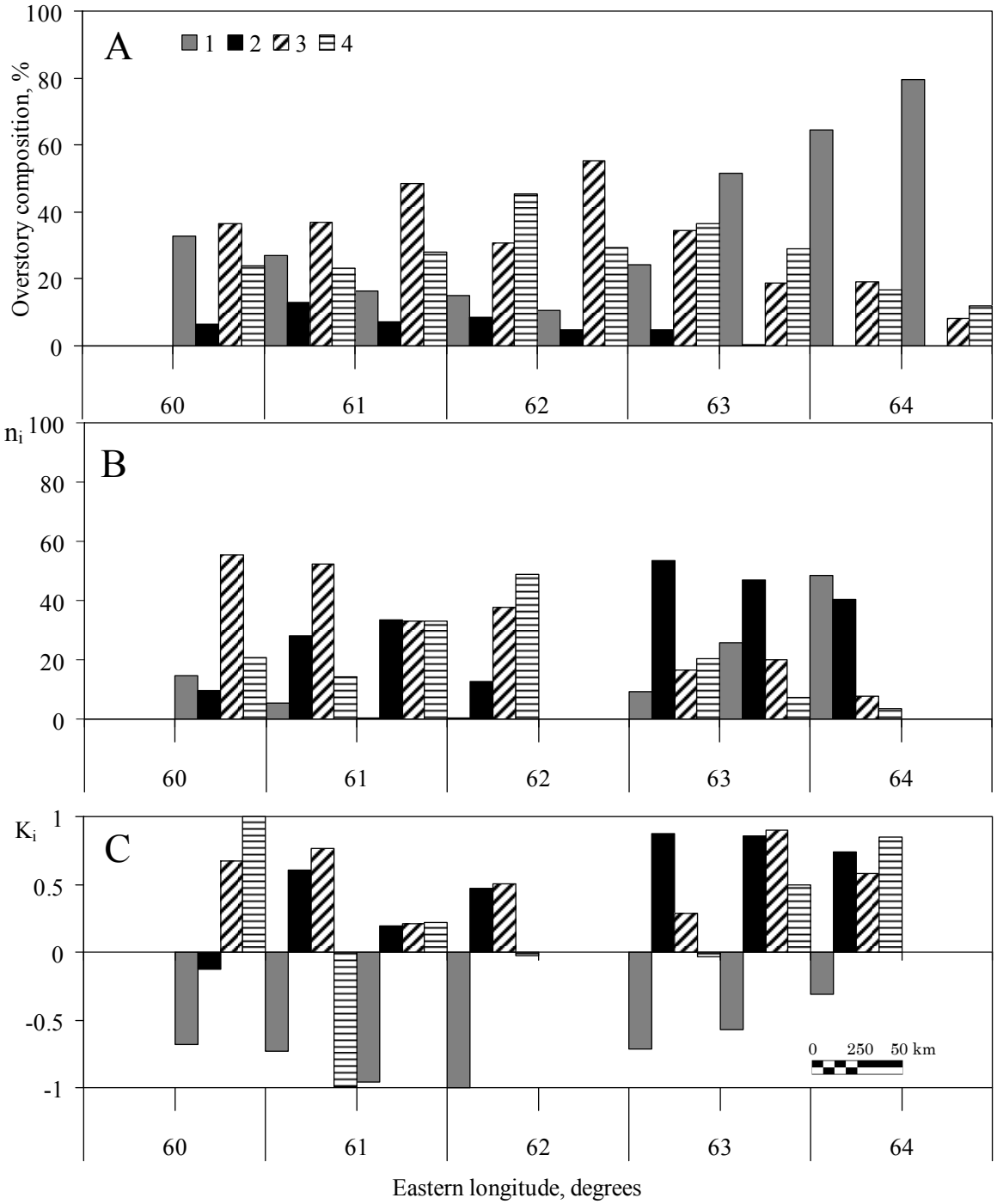

Fig. 3. WE transect. A. Overstory. B. Regeneration. C. Propagation coefficient.
1 – larch, 2 – Siberian pine, 3 – spruce+ fir, 4- birch.

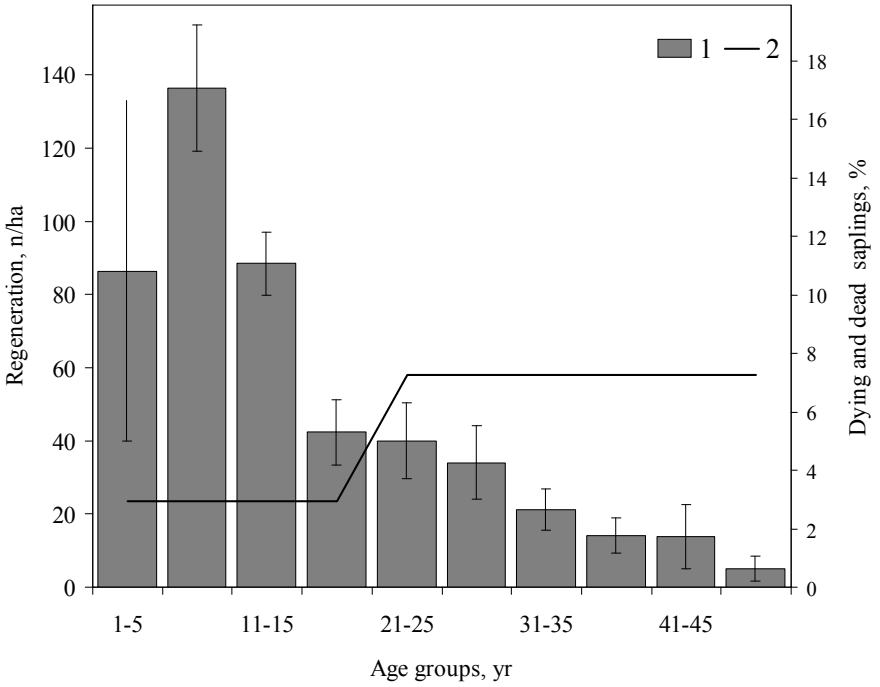

Fig. 4. Siberian pine regeneration age structure.
1 – living Siberian pine saplings;
2 – dying and dead Siberian pine saplings.

DNC propagation into LDZ and wildfires

Wildfires in the LDZ may interfere with DNC invasion into larch habitat. The majority of fires in LDZ were classified as ground fires, and are mainly of lightning origin, whereas on the southern and western borders of LDZ they are primarily of anthropogenic origin (Kovacs *et al*., 2004). Fires, though, may promote an invasion of DNC since firescars provide a starting place for "southern species" invasion since better thermal and soil conditions, enriched biogenic element content, increased soil thawing depth and drainage are present after fires (Fig. 5). On the other hand, larch (and birch) regeneration persists more consistently after fires than DNC because fires tend to eliminate DNC saplings, and of course there was a higher post-fire presence of larch trees in the overstory. Birch, as is known, can effectively regenerate by sprouts. The data in Figure 6 show that Siberian pine regeneration is more abundant in old burns in comparison with fresh ones, whereas larch preferably occupies fresh firescars, since there are more mother trees of larch in the areas adjacent to firescars than DNC trees.

Discussion

The observed differences in the regeneration number and overstory for DNC and larch, as well as the differences in the regeneration coefficient (*Ki),* indicate that DNC species are expanding into the traditional larch dominated region. The background of this phenomenon are winter temperatures and precipitation increases. The correlation between regeneration age structure (i.e. stems/ha for a given age class) for the last three decades and winter temperature anomalies was found to be R = 0.78- 0.83 ($p < 0.05$), whereas correlations with summer temperatures were not significant. This shows the importance of winter temperatures for regeneration survival because low temperatures (in synergy with winds) caused stem damage. Similar observations on Scotch pine seedlings in Swedish Scandia were reported by Kullmann (2007).

Higher precipitation is also favorable for Siberian pine invasion into the larch dominated area justifying the slang name "tree of fogs" for Siberian pine. Deeper snow cover promotes seedling survival, since the critical period of development is the time when the seedling height exceeds that of the snow cover forcing them to face snow and ice abrasion during snowstorms which results in the death of the tops of seedlings and the dying back of saplings, or their transformation into prostrated forms. Trees that effectively exceed this barrier have a typical crown shape: "tree-in-skirt" (Fig. 11). Larch, due to its dense bark (up to >20% of stem volume) surpasses the other tree species in winter desiccation resistance. In general, wind impact (in combination with low temperatures) is a principal factor affecting tree survival.

Climate-induced species migration into LDZ may interfere with increasing fire impact: in the zone of larch dominance the fire return interval (FRI) decreased one third in the 20th century in comparison with the 19th century (from 100 to 65 yr) (Kharuk *et al*., 2005a). The increase in climate-induced fire frequency may limit the southern species invasion into LDZ, because fires are inherent to larch forests and are necessary for their maintenance. Larch is a pyrophyte (i.e. fire-dependant)

species: the light larch seeds need the mineralized surface of fresh burns for germination (Fig. 7), whereas competitor species (Siberian pine, spruce) are more abundant on old burns (Fig. 6). Moreover, larch is protected by thick bark (Fig. 12) whereas dark-needle conifers are not. On the other hand, since wildfires cause an increase of seasonal thawing depth (by factor of 3 to 5, according to our observations), decreasing FRI will have a synergetic effect with climate-induced permafrost thawing, accelerating conversion of LDZ from a sink to a source of greenhouse gases. Thus, the problem of climate-driven fire frequency changes needs more investigation.

Along with climate impact, there are also natural fluctuations in Siberian pine regeneration numbers (and, to a lesser extent, other conifers). Fourier-analysis revealed that Siberian pine regeneration cycles with a 3.5 year period, which is similar to the reproduction cycle of this species. Since this cycle is much less than the analyzed time interval (~30 years), it did not impact on the reliability of results obtained.

The observed results of higher Siberian pine abundance in the LDZ in comparison with spruce and fir can be attributed to two main causes. 1) Siberian pine saplings surpass spruce and fir in their resistance to permafrost. Their root system can develop in the moss layer underlied by permafrost (Fig. 8). 2) The seed dispersal of this species is facilitated mainly by the "cedar bird" (*Nucifraga caryocatactes*). Consequently, Siberian pine regeneration was found at distances up to 1-2 km from the seed sources. In general, for all southern species the hydro-net is the principal way of invasion into larch habitat. Northern rivers valleys are wind-protecting, have a higher seasonal thawing depth,

Fig. 5. Siberian pine saplings appearing on the burn in the LDZ (east end of WE transect).

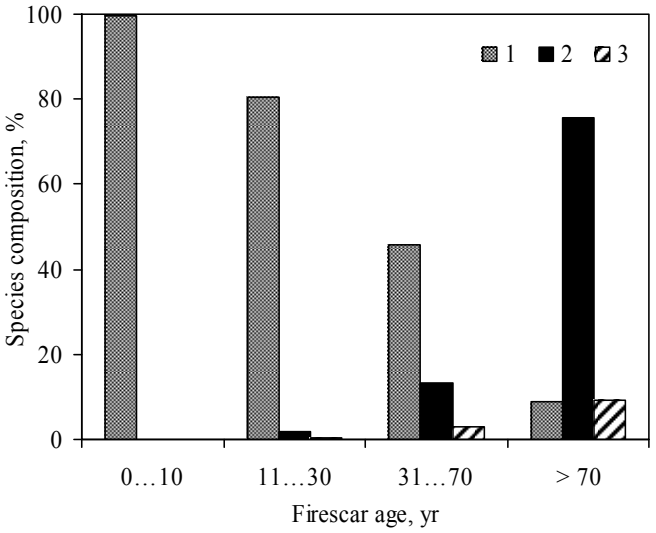

Fig. 6. Proportion of tree species vs. burn age. Data averaged for the WE transect. 1 – larch, 2 – Siberian pine, 3 – spruce.

Fig. 7. Larch regeneration on a fresh burn. Fire-caused soil mineralization is beneficial for seed germination (eastern part of WE transect).

Fig. 8. Siberian pine seedlings can grow while roots are within a thick (>40 cm, insert) moss cover. Mid of WE transect.

Fig. 9. Larch and alder regeneration on burn in the middle of WE transect.

Fig. 10. Birch regeneration on burn (mid-part of the SN transect).

Fig. 11. Trees-in-skirt: lower branches indicate snow height; between them and upper part of the crown trunks are without branches due to snow abrasion (northern part of the SN transect).

Fig. 12. Thick bark protects larch mother trees against ground fires (northern end of SN transect).

Fig. 13. Siberian pine regeneration forming a second layer under the larch canopy (western margin of WE transect).

and impart better soil drainage. As we can see the strips of "alley forest" along the rivers provides an example of what may happen with species composition in the LDZ with improvement of climatic conditions.

The results obtained indicate an invasion of southern species into larch habitat. On the western and southern margins, DNC regeneration formed a second layer in the forest canopies that could eventually replace the larch in the overstory (Fig. 13). With stand densification Siberian pine received an additional advantage since larch is a shade non-tolerant species. The DNC invasion into the larch habitat is a part of the general phenomenon of the larch area shrinking. In the former epoch the larch dominated forest range extended to southern Siberia as well, where presently it can be found only in the Sayany and Altai highlands on drier slopes. In mixed forests where larch regeneration is negligible, larch survives due to its longevity. Larch can reach an age of 600 years in the south taiga, and ~1000 years in the northern taiga. For other conifers these values are lower: the maximum age is ~300 years for fir, ~250 for spruce, ~500 for pine, and ~600 years for Siberian pine.

The described climate-driven "dark-needle" conifer migration into LDZ is an element of the broader response of boreal forests to climate change. Larch is responding to climate trends by migration into the northern tundra zone and by stand densification, as was found on the key-sites "Polar Ural" and "Ary-Mas" (Fig. 1) (Kharuk *et al*., 2003, 2006, Shiyatov 2003, Ranson *et al*., 2004). The resulting effect of this process may be the expansion of larch forests to the Arctic shore, a phenomenon that has happened in the past (Kind and Leonova, 1998), whereas the traditional area of larch dominance will be transformed into mixed taiga forest. The formation of a DNC overstory will cause a decrease in albedo, because larch is deciduous and larch stands are less dense in comparison with dark-needle conifer stands, and because of higher dark-needle conifer absorption of light in the visible and near infrared spectral regions (Kharuk *et al*., 1992). Thus, increases in solar radiation absorption will provide positive feedback for warmer temperatures.

The other consequence of climate warming and DNC migration is the promotion of insect outbreaks, since Siberian pine and fir are preferred host species for the Siberian silkmoth (Kharuk *et al*., 2004). Finally, similar climate-driven species migration is being observed in the mountain forest-tundra ecotone in the Altai-Sayan Mountain system (Fig. 1). Our observations show that climate warming provides competitive advantages to Siberian pine in areas with high precipitation (north-west windward slopes), whereas larch, due to high drought and wind resistance, has advantages in areas with low precipitation (rain-shadowed slopes) and in the extreme area of the upper tree line (Kharuk *et al*., 2008). In conclusion, climate-driven species interaction, in this case larch versus dark-needle conifers, needs more investigation.

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