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Author(s)	Zyryanova, Olga A; Yaborov, Victor T; Tchikhacheva, Tatiyana L et al.
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The Structure and Biodiversity after Fire Disturbance in *Larix gmelinii* (Rupr.) Rupr. Forests, Northeastern Asia

ZYRYANOVA Olga A.^{1,2*}, YABOROV Victor T.³, TCHIKHACHEVA Tatjyana L.¹, KOIKE Takayoshi⁴,
MAKOTO Kobayashi⁵, MATSUURA Yojiro⁶, SATOH Fuyuki⁴ and ZYRYANOV Vyacheslav I.¹

¹ V.N. Sukachev Institute of Forest SB RAS, Academgorodok, Krasnoyarsk, 660036, Russia.

² Siberian Federal University, Krasnoyarsk, 660041, Russia

³ Far Eastern State Agricultural University, Blagoveshchensk, 675005, Russia

⁴ Hokkaido University Forests, FSC, Sapporo 060-0809, Japan

⁵ Graduate School of Agriculture, Hokkaido University, Sapporo 060-8589, Japan

⁶ Forestry and Forest Products Research Institute, Tsukuba 305- 8687, Japan

Abstract

Larix gmelinii (Gmelin larch) is one of the most widespread larch species in northern Eurasia as a whole and in the Russian Federation dominating here in both the distribution area and the growing stock. Owing to high adaptability and ecological plasticity it occupies different sites within its range and performs well under continuous permafrost conditions. Over an immense area Gmelin larch forests differ in species composition, ecosystem structure and the features of natural regeneration. Ground fires are the main force driving larch forest development. Depending upon site conditions, fire intensity and periodicity, fire regimes determine forest age structure, species diversity, spatial-temporal dimensions of larch ecosystems as well as succession patterns in their trends and rates. Based on the results of long-term investigations we discuss Gmelin larch forest post-fire dynamics in the central part of their distribution in Siberia versus the southeastern part in Priamurye in the Russian Far East.

Key words: biodiversity, cryolithic zone, forest fires, larch ecosystems, Siberia

Introduction

Larch (*Larix* Mill.) is one of the most important elements of the boreal forests in the northern hemisphere as a whole and in northeastern Eurasia, in particular. The largest massives of the Russian larch forest are to be found in Siberia and the Russian Far East. Here, they cover the immense Siberian area with generally abundant pure or mixed larch forests from the Ural Mountains in the west to the Pacific Ocean in the east, as well as between the steppe zone (Lat. N 48°) in the south and the tundra zone in the north (Lat. N 72°) (Abaimov *et al.* 1998a). The larch forests occur even outside of Russia in China and Mongolia. Two larch species, *Larix gmelinii* (Rupr.) Rupr. (Gmelin larch) and *L. cajanderi* Mayr., - share the dominance over the vast territory of eastern Siberia with their distribution almost completely coinciding with the continuous and discontinuous permafrost area (Abaimov *et al.* 1998a).

Larch forests growing in Siberia are recognized to be of very high bio-spheric and ecological importance worldwide. They establish both the southern and the northern timberlines and carry out water- and soil conservation functions in mountain regions as well as being regarded as a large carbon sink (Shvidenko *et al.* 2003). Due to specific life strategies with respect to seed dispersion patterns and very high adaptability to the fires that often affect Siberian forests, these larch species occupy very successfully post-fire habitats (Abaimov *et al.* 1998a).

Forest fires are an important ecological factor

controlling both environments for vegetation establishment and vegetation succession in larch forests (e.g. Abaimov and Sofronov 1996, Makoto *et al.* 2007). Return fire intervals here can vary from 3-5 years to 40-100 years and even up to 200 years and are predictive of proper cycles in forest community development (Abaimov *et al.* 2000). Depending on site conditions, fire intensity and periodicity, fire regimes determine forest age structure, species composition and physiognomy, landscape diversity and succession patterns in their trends and rates (Abaimov 1999, 2005, Abaimov *et al.* 2002, Zyryanova *et al.* 2002). To make clear the important role of permafrost on the vegetation characteristics of Gmelin larch forests, we compare the physical and biological environments of this species in two contrasting larch forests in Siberia and the Russian Far East where we have frequent forest fires. We selected the two sites of Gmelin larch forests because we have carried out long-term monitoring studies. One forest is established in a well-developed permafrost zone and the other is established on seasonal frozen sites mixed with Scots pine and birch as well as partly with spruce.

In this paper, we focused on the results of long-term investigations of Gmelin larch forest post-fire dynamics in the cryolithic zone of Siberia in comparison to the Priamurye region. Thus, we deal with larch forests in the center and at the southeastern edge of the *Larix gmelinii* range. We focus on changes in species diversity in a plant community and forest regeneration

patterns in a burnt area in terms of the characteristics of the site environments as well as in terms of the composition and structure of intact larch ecosystems.

We follow the nomenclature of Latin names of plant species established by Czerepanov (1985).

Gmelin larch (*Larix gmelinii*) distribution and general properties

Gmelin larch is widely distributed over northern Eurasia. This species has established the northernmost larch ecosystems in the world in the valleys of the Lukunskaya River (Lat. N 72° 45') (Kryuchkov 1972) and the Novaya River (Lat. N 72° 30') (Ary-Mas 1978). Forming the southern limit outside of Russia, *Larix gmelinii* reaches the 45th parallel in both northeastern Mongolia (Savin *et al.* 1978) and northeastern China (Shi *et al.* 2001, Wang 1995) as well as the southernmost location in the Korean Peninsula at 43° N (Shi *et al.* 1999). The western border of Gmelin larch distribution is rather complicated to describe while the eastern one coincides over large distances with the January isotherm -30°C (Abaimov *et al.* 1998a). In total, it makes up a large percentage of Asian forests both in area and in wood stock. It covers 1.9 million km² (Abaimov and Koropachinskiy 1984) while its growing stock encompasses about 23 billion m³ (Pozdnyakov 1975).

Within such a vast area *Larix gmelinii* occupies very different sites: watershed slopes of all exposures and degrees of steepness, plain areas, swamp-like lowlands as well as river valleys. The wide ecological range of larch can be explained by several of its ecophysiological features, such as an ability to take up water even from relatively cold soil, its anatomical

structure and the metabolic adaptation of the fine roots, its tolerance of very low winter temperatures, its shallow root system and the ability to develop adventitious roots above the root collar (Abaimov *et al.* 1996, 1997, 1998a, 2000, Dylis 1981). *Larix gmelinii* as well as *L. cajanderi* are adapted to permafrost conditions better than any other tree species of Siberia (Pozdnyakov 1986).

Growing in such different natural conditions as was mentioned above Gmelin larch differs obviously in morphological and ecological features (Abaimov *et al.* 1998a), something that gives rise to confusion over which *Larix* species occupies Priamurye (Dylis 1961, 1981, Bobrov 1972, 1978, Koropachinskiy and Vstovskaya 2002). Based on our own research we will try to make the situation on this matter clearer.

Location and the environments of the study sites

As we mentioned above the sites investigated are located in two different parts of the *Larix gmelinii* range. The geographical coordinates of Tura Experimental Forests (TEF) are 64°18' N 100° 11' E and the Svobodnenskiy region (SR; Priamurye) plots 51°30' N 127° 30' E. Owing to such different geography the climatic patterns of the research sites are rather different from each other (Table 1).

The Gmelin larch species dominates absolutely at TEF where it has no competitors and forms large massives of pure forests of different densities (Photo 1). *Picea obovata* forms tree stands only in river valleys and on flat watersheds, the warmest sites of the area. Thus, this research site belongs to the forests of the boreal zone. In the Svobodnenskiy region, the presence of temperate species such as *Quercus mongolica*,

Table 1. Climatic patterns of the study sites.

Patterns	Sites	Tura Experimental Forests (Evenkiya)*	Svobodnenskiy region (Priamurye)**
Mean temperature, °C:			
	annual	-7, -9	-2.8
	of January	-36.8	-28.0
	of July	16.3	19.0
Annual precipitations, mm		269-342	400-600
Growing season, days		115	160
Snow depth (cm)		40-50	30
Duration of snow coverage per a year (days)		207	150
Frostless period, days		55-56	135-137

Note: Data are derived from * Abaimov et al. (1997) and ** Ershov (1984).

Betula platyphylla, *Lespedeza bicolor*, and *Rhododendron dauricum* in larch ecosystems is a characteristic and peculiar feature (Photo 2). Here we have investigated mixed conifer-broadleaved forests recognized as a transition from typical boreal to typical cool temperate vegetation (The types., 1984).

The research sites differ in the permafrost conditions. For example, the permanent permafrost layer temperature at the depth of 5-10 m in TEF is equal to -3, -5°C (Glaciation., 1986), while in Priamurye, seasonal permafrost represented by the ice lenses rarely occurs resulting in wetland soil conditions (The types., 1984). Permafrost leads to the development of cryogenic microtopography (Photo 3, 4), which results from frost action and provides the patterned environments of the forest sites. In TEF we faced a few forms of microtopography: spot hillock-depressions and small hillocks developing on flat surfaces with linear ridge-depression forms usually occurring on the slopes (Zyryanova 2004, Zyryanova *et al.* 2002). Such microtopography at a continuous permafrost area is responsible for the patterned hydrothermal and edaphic conditions of forest habitats as well as for the spatial mosaic of the ground vegetation and its post-fire changes (Abaimov *et al.* 1997, 1998b, Zyryanova 2004, Zyryanova *et al.* 2002, 2006).

Results and discussion

1. Forest structure and species composition of intact larch ecosystems

Larix gmelinii completely dominates in TEF. As examples, tree stand characteristics under different topography conditions are represented in Table 2. From these parameters, we have concluded that larch forests in TEF are rather sparse, and of low productivity; the trees have small height and DBH (Photo 1).

Species richness in different larch associations ranges between 22 and 59 plants per 100 m² with its maximum values in the sites with expressed microtopography (Zyryanova 2004, Zyryanova *et al.* 2002, 2006). Soil temperature on the hillocks is always 3-5°C (Abaimov *et al.* 1999) or even 5-8°C (Kajimoto *et al.* 1998) higher than in micro-depressions. The western and southern micro-slopes are warmer and wetter compared to eastern and northern ones (Abaimov *et al.* 1999). Such patterned environments lead to an increase in the number of ecological niches in the forest site. As a consequence, boreal forest (*Cypripedium guttatum*, *Dactylorhiza cruenta*, *Vaccinium vitis-idaea*, etc.), forest-tundra (*Empetrum nigrum*, *Salix boganidensis*, *Vaccinium uliginosum*, etc.) and tundra (*Betula nana*, *Ptilidium ciliare*) species coexist in one plant association on different elements of microtopography (Photo 5) (Abaimov *et al.* 2000,

Table 2. Tree stand characteristics of research sites.

Plant association	Age, years	Mean		Canopy closure	Growing stock (m ³ ha ⁻¹)
		Height(m)	DBH, (cm)		
Tura Experimental Forests (Siberia)					
<i>Larix gmelinii</i> - <i>Duschekia fruticosa</i> - <i>Ledum palustre</i> + <i>Vaccinium vitis-idaea</i> - <i>Pleurozium schreberi</i> (without microtopography)	87	10.7	9.0	0.3	61.7
<i>Larix gmelinii</i> - <i>Vaccinium vitis-idaea</i> + <i>V. uliginosum</i> - <i>Pleurozium schreberi</i> + <i>Cladina rangiferina</i> (spot hillock-depression microtopography)	192	7.4	7.8	0.3	53.0
<i>Larix gmelinii</i> - <i>Duschekia fruticosa</i> - <i>Ledum palustre</i> + <i>Vaccinium uliginosum</i> - <i>Pleurozium schreberi</i> + <i>Cladina</i> sp. (linear ridge-depression microtopography)	225	6.0	5.0	0.3	32.0
Svobodnenskiy region (Russian Far East)					
<i>Betula platyphylla</i> + <i>Larix gmelinii</i> - <i>Rhododendron dauricum</i> - <i>Carex</i> sp. + <i>Calamagrostis langsdorffii</i>	B	B	B	0.2	140.0
	70	18	22		
	L	L	L		
	100	23	32		

Zyryanova et al. 1999). Thus, cryogenic topography provides for an increase of plant species diversity in forest ecosystems (Zyryanova and Bugaenko 2004).

Generally, vascular plants of Gmelin larch intact forests in TEF belong to 25 families. Such families as *Ericaceae*, *Salicaceae*, *Cyperaceae*, *Rosaceae*, and *Asteraceae* are the most numerous in the number of plant species. Woody plants (28%) and perennial grasses (37%) dominate among life forms (Zyryanova 2004). The share of the mosses and lichens (35%) is also significant. In SR the Gmelin larch in the stands is accompanied by *Betula platyphylla* (Photo 2). Tree canopy is also rather sparse, but the forest is of high productivity and both larch and birch trees are tall and have a large diameter (Table 2). *Quercus mongolica* of 7-8 m in height rarely occurs.

When having a dense canopy these ecosystems found in SR develop scattered shrubs of *Rhododendron dauricum*, *Betula fruticosa*, *Lespedeza bicolor*, etc. with *Vaccinium vitis-idaea* and *V. uliginosum* dominants on the ground floor. Under felling or fire thinning the shrub species mentioned as well as *Spiraea media*, *S. salicifolia*, *Rosa acicularis*, *Alnus hirsuta* form a very dense layer of 60-70% coverage. *Calamagrostis langsdorffii* accompanied by *Carex* sp. are the main dominants of the ground vegetation in this case. Thus, in intact larch forests of SR the distribution of the main tree dominant, not the local environments as in TEF, provides the spatial mosaic of the ground floor. Species richness in such a mosaic ecosystem is equal to 57 per 100 m². Such families as *Asteraceae*, *Rosaceae*, *Apiaceae*, *Liliaceae* and *Ericaceae* are the most

numerous in the number of species here. The share of woody plants (26%) is almost equal to that in TEF while the amount of perennials (67%) increases considerably. Mosses and lichens sharply decreased in species number by 7%.

2. Natural regeneration in intact larch forests

The larch forests of TEF are characterized by a weakened recovery potential (Abaimov 2000). The total amount of young larch growth rarely exceeds 2-3 thousand trees per hectare in different forest types (Table 3). Some reasons have been considered to explain such poor natural regeneration. These are rare abundant seed crop years, low seed quality, the thick moss-lichen cover which hampers the germinating seeds from reaching the soil as well as severe root competition for the elements of mineral nutrition and available moisture in the active soil horizon limited by the permafrost (Abaimov et al. 1997, Pozdnyakov 1975, Vipper 1975).

In Priamurye, on the contrary, an abundant seed crop occurs every 2 years (Yaborov 2000). The total number of larch saplings is also significant and is 3-10 and even 50 times greater than that in TEF (Table 3). Natural regeneration would be successful in intact forests here if a part of larch regrowth could attain seed production age. But the fires, occurring every 3-5 years, kill larch saplings and seedlings, resulting in changes in tree species composition and even the replacement of larch forests by secondary *Betula platyphylla* forests (Zyryanova et al. 2005).

Table 3. Natural regeneration in different larch ecosystems.

Larch ecosystems and their groups	Growing stock, (m ³ ha ⁻¹)	Regrowth, thou pcs. (ha ⁻¹)
Tura Experimental Forests (Siberia)		
<i>Larix gmelinii</i> - <i>Salix myrtilloides</i> + <i>Betula nana</i> - <i>Ledum palustre</i> + <i>Vaccinium uliginosum</i> - <i>Sphagnum</i> sp.	8.2	0.0
<i>Larix gmelinii</i> - <i>Empetrum nigrum</i> + <i>Arctostaphylos uva-ursi</i>	12.3	0.6
<i>Larix gmelinii</i> - <i>Vaccinium vitis idaea</i> + <i>Ledum palustre</i> - <i>Pleurozium schreberi</i>	71.8	0.9
<i>Larix gmelinii</i> - <i>Duschekia fruticosa</i> - <i>Ledum palustre</i> + <i>Vaccinium vitis idaea</i> - <i>Pleurozium schreberi</i>	61.7	1.0
Svobodnenskiy region (Russian Far East)		
<i>Betula platyphylla</i> + <i>Larix gmelinii</i> - <i>Rhododendron dauricum</i> - <i>Vaccinium vitis-idaea</i> + <i>Calamagrostis langsdorffii</i>	90-170	5.0-25.0
<i>Quercus mongolica</i> + <i>Larix gmelinii</i> - <i>Rhododendron dauricum</i> - <i>Carex</i> sp.+ <i>Calamagrostis langsdorffii</i>	60-250	0.5-30.0

3. Recovery of forest vegetation after fire disturbance

3.1. Sites with expressed microtopography in TEF

Various microtopography conditions provide different burning characteristics and consequently affect the restoration of larch trees and ground vegetation. Under conditions of spot hillock-depression microrelief a steady ground fire of middle intensity destroyed, first of all, the vegetation of the micro-depressions. This happened due to the large amount of organic matter fuel that had accumulated on the bottoms of the depressions and due to *Ledum palustre* and *Vaccinium uliginosum* dominating, two species which are the most fire-prone species in the permafrost area. The difference between the top of a hillock and the bottom of a depression was about 40-50 cm (Photo 3). The vegetation on the tops of the hillocks in part was preserved at least one year after the fire until the microtopography began to change. Total number of species decreased 2.5-fold as compared to that in unburned associations (Zyryanova *et al.* 2002).

During the two following years due to soil thermal melioration the microrelief of the site began to be destroyed and the hydrological and thermal regimes were changed considerably (Abaimov *et al.* 1999). By the fourth year after the fire ground vegetation following such environment changes developed a secondary grass-moss association dominated by *Calamagrostis lapponica*, *Chamaerion angustifolium*, *Marchantia polymorpha* and *Ceratodon purpureus* (Photo 6). Young larch trees were abundant on the burned area: the number of seedlings amounted to 558.5 per ha (Abaimov *et al.* 1998b). In 3 years after the fire, the number of vascular plants on the burned area was 1.2 times as many as in a mature plant community. The total number of species was 1.1 and 1.2 times as many as in unburned associations by the 5th and 6th post-fire years. Since the 5th post-fire year the plant species composition of ground vegetation had become more similar to that of unburned larch associations due to restored pre-fire species such as *Duschekia fruticosa*, *Empetrum nigrum*, *Juniperus sibirica*, and *Tomenthypnum nitens* (Zyryanova *et al.* 2002). New species (*Atragene sibirica*, *Galium boreale*, *Potentilla inquinans*, etc.) continued to occupy free ecological niches. The invasion of the new species in the sites with spot hillock-depression microtopography lasted for 9 years after the steady ground fire of middle intensity.

Linear ridge-depression micro-relief (Photo 4) provides for stripped burning out of the ground vegetation and its subsequent regeneration (Zyryanova *et al.* 2002). In 4 years after a running ground fire all the main dominants (*Duschekia fruticosa*, *Vaccinium vitis-idaea*, *Ledum palustre*, *Hylocomium splendens*) of the understory and ground vegetation were restored from preserved refugia of these species on the linear depressions. Ridge parts of the ecosystem strongly damaged by the fire have been covered now with the patches of *Vaccinium vitis-idaea*, *Equisetum scirpoides*, *Rubus arcticus*, *Dryopteris fragrans*, etc. (Photo 7). The restoration of the ground floor is not uniform and its rate is rather low.

On the contrary, small hillocky microtopography (the difference between the top of the hillock and the bottom of the depression was about 15-20cm) led to the total destruction of ground vegetation by a strong running fire. Eight years after the fire *Ceratodon purpureus*, a typical cryolithic area fire specialist species, occupied about 80% of the burned area and prevented both successful restoration of the pre-fire plant species and the invasion of new ones. Only *Vaccinium vitis-idaea*, *Vaccinium uliginosum* and *Ledum palustre* began their regeneration near larch stems. Thus, small hillocky microtopography is responsible for the uniform burning out of the ground vegetation and the slackening of its subsequent restoration.

3.2. Sites without microtopography in TEF

Larch associations without microtopography are completely destroyed by strong running ground fires. Under such conditions 7 stages in the recovery of larch associations can be distinguished. The first 4 stages last 5 years and are characterized by secondary grass associations dominated in series by *Corydalis sibirica*, *Calamagrostis lapponica*, *Carex media* accompanied by fire specialist mosses (Photo 8a). Larch trees began to develop dense storey 6 years after the fire (Photo 8b). Shrub and dwarf-shrub stories are developing simultaneously. This process (the fifth stage of succession) lasts for 15-16 years. In 21 years after a ground fire the main stories of an intact larch forest have been restored (Photo 9).

The main pre-fire dominants *Larix gmelinii*, *Duschekia fruticosa*, *Ledum palustre*, *Vaccinium uliginosum*, *V. vitis-idaea*, *Empetrum nigrum*, *Aulacomnium turgidum*, *Cladina sylvatica*, *Cl. rangiferina*, *Cl. amaurocraea*, *Cl. alpestris*, *Cetraria cucullata*, *Cetraria islandica* have been restored only after 50 years (the sixth successional stage) (Photo 10). The regeneration of both original species richness and floristic composition has been completed by 90-100 years after a strong ground fire (Photo 1). This is the seventh, final stage of progressive succession, which represents an intact ecosystem.

3.3. Sites in Svobodnenskiy region

In the Svobodnenskiy region (Priamurye), all experimental plots are located on the gentle north-east-facing upper slopes of the uplands. Here secondary white birch forests of different ages represent a kind of pyrogenic chronosequence in its initial stages. Birch ecosystems evidence their origin from mixed conifer-broadleaved forests by the presence of mature *Larix gmelinii* and *Betula platyphylla* trees distributed sporadically over the territory and by the numerous fire scars in the lower parts of the stems.

A seven-year-old birch association at the site has rather dense shrubs, among which *Rhododendron dauricum* completely dominates as in an intact forest. This shrub species as well as *Vaccinium vitis-idaea*, *V. uliginosum* and *Ledum palustre* were not killed by, at least, two running ground fires as we have concluded from the observation of the fire scars and preserved stumps. The groups of young white birch trees 2.5 m in

height accompanied by *Populus tremula* and *Quercus mongolica* regrowth developed a rather closed woody layer (Photo 11a). *Calamagrostis langsdorffii* of 60-70% abundance together with the fire specialist moss *Ceratodon purpureus* cover the ground surface.

A twenty four-year-old birch stand includes trees of 14 m mean height and 10 cm mean DBH with Gmelin larch being infrequent (Photo 11b). New shrub species composition resulting from a few running fires was seen with rare *Spiraea salicifolia*, *S. media* and *Rosa acicularis*. *Calamagrostis langsdorffii* also prevails in the ground vegetation of this association sharing dominance with the tall herbs *Filipendula palmata*, *Thalictrum simplex*, *Cimicifuga* sp.

The trees of a 35-year-old birch stand have larger mean height and diameter: 15 m and 14 cm, respectively, compared to those of the previous forest (Photo 11c). But *Alnus hirsuta*, *Vaccinium uliginosum*, *Pyrola rotundifolia*, *Orthilia secunda* and the other pre-fire species appear in the floristic composition of the association. They usually occur under the canopies of the mature larch trees although *Calamagrostis langsdorffii* still keeps its position as a dominant species.

In all the secondary birch forests running ground fires periodically kill larch saplings and seedlings. Owing to high sprouting ability only white birch, trembling poplar and Mongolian oak can regenerate under such conditions. Further reconstruction of forest development requires new research steps.

3.4. Conclusions and perspectives

The vast geographical area of *Larix gmelinii* shows the large ecological plasticity of this species and its high adaptability to the different natural conditions found in the boreal Eurasian zone and in transition to typical temperate forests. This assertion, though, requires strict evidences of which species we recognized in the site studied. In a previous report we hypothesized that Gmelin larch was the main tree species in Priamurye (Zyryanova et al. 2005). Since that time we have investigated larch cones collected in both TEF and Priamurye. Analyzing such important identification characteristics as cone form in open state, cone width/length ratio, angle of seed-scale, form of seed-scale upper edge we have concluded that all cones belong to the same species - *Larix gmelinii*. Indeed, all mature, dry cones have ovate form, the width/length ratio varies from 0.62 to 0.96, the upper seed-scale edge is slightly hollow and the angle of seed-scale changes between 15 and 45° (Photo 12). This is in good agreement with the data published (Abaimov et al. 1998a). Thus, we have first proved the distribution of Gmelin larch in Priamurye.

Intact larch ecosystems of TEF and Priamurye are different in species composition and growing stock as well as in the species diversity of plants. Boreal, subarctic and arctic species dominate in TEF while boreal and temperate species share the dominance in Priamurye. Spatial forest structure depends on the environment. In Siberia this was the cryogenic microtopography. On the other hand, in Priamurye the

distribution of mature trees may regulate the mosaic features of the ground vegetation.

Fires are the main forces driving postfire regeneration and forest development in both sites within the *Larix gmelinii* range. In Priamurye, ground fires, occurring every 3-5 years, result in the decrease of larch stand productivity and in the development of very dense shrub and herbal cover. Such dense ground vegetation combined with the fires hampers natural larch regeneration and promotes white birch invasion. Owing to fast vegetative propagation on burned sites birch forests gradually replace intact larch forests for a long period of time.

The fire return interval in Gmelin larch forests in TEF ranges in years from 30-40 up to 80-90. Ground fires change the species diversity of larch ecosystems. The dominant species of intact larch and postfire associations are different in the early successional stages. Representatives of the *Calamagrostis*, *Carex* and *Chamaerion* genera as well as the fire specialist species *Marchantia polymorpha*, *Ceratodon purpureus*, *Leptobryum pyriforme* are common for postfire regeneration of burned areas in Siberia and Central Alaska (Rees and Juday, 2002). Forest regenerative processes appear to have similar trajectories in the global permafrost area.

The total number of species is 1.1 and 1.2 times as many as in unburned associations by the 5th-6th post-fire years in the sites with microtopography and by the 9th-10th years in the sites without it. The spot hillock-depression form provides for fast regeneration of plant species diversity and forest structure after ground fires while the small hillock and linear ridge-depression forms usually slacken this process. As we reported earlier, microtopography in northern forest sites totally sustains phytodiversity and the increase in species and family number (Zyryanova et al. 2002).

Plant species diversity restoration is a long-term process, which covers 7 successional stages (90-100 years). The percentage of pre-fire species usually regenerated 21 and 50 years after a fire is 48 and 71 %, respectively. Thus, even in a 50-year-old post-fire ecosystem, the total number of plant species and their composition differ from those in an intact larch association. This appears to be a global regularity. Similar data was obtained for the tropical forests of central Amazonia (Ferreira and Prance, 1999).

The regeneration of the forest stories is completed in 16-20 years after a catastrophic fire while the species of the association restore their shares in dominance only in 50 years. Final restoration of the original species diversity occurs in the period from 50 up to 90 years after the fire. Ninety- to 100-year-old larch associations in Siberian cryolithic area represent the ultimate structure of a plant community, the most stable, self-maintaining and self-reproducing stage of vegetational development. Plant species in them are co-adapted in their physical and temporal environment: they are niche differentiated due to interspecific competition (Zyryanova et al. 2006).

Generally, pyrogenic successions in Gmelin larch forests, growing in different parts of the Gmelin range,

follow different scenarios. In the continuous permafrost area of Siberia forest regeneration develops without tree species replacement and, as a rule, results in even-aged larch stands (Abaimov, 2005). In Priamurye, in the southwestern part of the Russian Far East, where only rare ice lenses of the permafrost occur and running ground fires are often, intact larch forests can gradually be replaced by white birch forests. This trend has been continuing since the beginning of the 20th century (Zyryanova *et al.* 2005).

In this paper, we have discussed only one scenario of the forest development after fire disturbances in central Priamurye without regard to the northern part of the district where larch boreal ecosystems dominate. Here, other trends of pyrogenic succession are likely to be found. For further understanding of the dynamics of the region, new joint research on *Larix gmelinii* forests in northeastern Asia should be carried out.

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Photo 1. Intact *Larix gmelinii* association with *Duschekia fruticosa* and dwarf-shrub species as an understorey vegetation (Photo by A.P. Abaimov).



Photo 2. Intact *Larix gmelinii* association with *Rhododendron dauricum* and different herb species as an understorey vegetation (Photo by O.A. Zyryanova).



Photo 3. Hillock – microdepression topography, Tura Experimental Forests (Photo by A.P. Abaimov).



Photo 4. Linear ridge-depression microtopography, Tura Experimental Forests (Photo by O.A. Zyryanova)



Photo 5. Boreal (*Cypripedium guttatum*) and subarctic (*Vaccinium uliginosum*) species coexist in one association (Photo by O.A. Zyryanova)



Photo 6. A hillock covered with *Calamagrostis lapponica* (top) and *Ceratodon purpureus* (down microslopes) (Photo by O.A. Zyryanova)



Photo 7. Small patches of regenerating *Vaccinium vitis-idaea*, *Equisetum scirpoides*, *Dryopteris fragrans* among the stones of the ridge (Photo by O.A. Zyryanova).



Photo 8. Initial stages of forest restoration: a) – sedge association; b) – dense larch seedlings in 12 years after the fire (Photos by O.A. Zyryanova (a) and A.P. Abaimov (b)).



Photo 9. Restoration of the forest storeys (Photo by A.P. Abaimov).



Photo 10. Restoration of the main dominants of beforefire association (Photo by A.P. Abaimov).



Photo 11. Secondary *Betula platyphylla* forests: a – 7-year-old, b – 24 year-old, c – 35-year-old (Photos by O.A. Zyryanova).



Photo 12. Typical cones of *Larix gmelinii*: a) from Tura Experimental Forest (Siberia), b) from Svobodnenskiy region (Primurye) (Photo by V.I. Zyryanov).