Title	Forest Ecosystems of the Cryolithic Zone of Siberia : Regional Features, Mechanisms of Stability and Pyrogenic Changes
Author(s)	Abaimov, A. P.; Zyryanova, O. A.; Prokushkin, S. G. et al.
Citation	Eurasian Journal of Forest Research, 1, 1-10
Issue Date	2000-10
Doc URL	https://hdl.handle.net/2115/22118
Type	departmental bulletin paper
File Information	1_P1-10.pdf

Eurasian J. For. Res. 1: 1-10 , 2000

Forest Ecosystems of the Cryolithic Zone of Siberia; Regional Features, Mechanisms of Stability and Pyrogenic Changes

Abaimov, A.P.[1]*, Zyryanova, O.A.[1], Prokushkin, S.G.[1], Koike, T.[2] and Matsuura, Y.[3]

[1] V.N.Sukachev Institute of Forest, SB RAS,
Academgorodok, Krasnoyarsk 660036, Russia
[2] Hokkaido University Forests, Sapporo 060-0809, Japan
[3] Forestry and Forest Products Research Institute, Hokkaido Research Center, Sapporo 062-8516, Japan

Abstract

Cryolithic zone occupies about 40% of the forested area of Siberia. The most important tree species are *Larix sibirica* Ledeb., *L. gmelinii* (Rupr.) Rupr. and *L. cajanderi* Mayr. These larch species replace each other from the west to the eastward. Wild fires at high latitudes of Siberia are the major disturbing factors, which transform forest environments, biodiversity of forest ecosystems and their dynamics. Sparse forests of the cryolithic zone are characterized by low biomass productivity, weakened recovery potential, uneven-aged tree stands as well as by low species diversity and woody plant dominance. Adaptation mechanisms of larch species to extreme environments are developed at population, organismic, tissue, cellular, subcellular and biochemical levels. Adaptive reactions of larch roots to low positive temperatures of soil are provided by reconstruction of their structure, functions and nitrogen metabolism. The trends in and the rate of pyrogenic progressive successions are conditioned by fire power, environments transformation degree and biological features of Siberian larch species. Peculiar features of forest ecosystems of the cryolithic zone, regularities of their succession after forest fires as well as some mechanisms of stability to extreme northern environments are considered in this paper.

Key words: biodiversity, cryolithic zone, larch ecosystems, postfire transformation, Siberia successions

Introduction

Forest ecosystems of the high latitudes of Siberia are developed mainly in the cryolithic zone, which occupies about 40% of forested area of the region. Being of great biosphere and environment importance, these ecosystems provide a relative equilibrium of natural processes under the harsh climatic conditions (Utkin 1976;, Pozdnyakov 1986) and are characterized by a number of peculiar features (Abaimov *et al.* 1997). They are the indigenous peoples' habitats and their skill promotion as well. The most important tree species in this region are *Larix sibirica*, *L. gmelinii* and *L. cajanderi* These larch species replace each other from west to eastward of Siberia and form mono-specific larch forests (Abaimov *et al.* 1998a).

Wild fires are major disturbing factors, regularly affecting the northern forest ecosystems. About 1,5% of the total forested cryolithic area are damaged annually by forest fires (Sofronov *et al.* 1998). Prevailing in the region ground fires not only transform forest environments, but also change the cycling of mineral nutrition, the soil respiration rate (Schulze *et al.* 1995, Abaimov *et al.* 1998b, Matsuura and Abaimov 1998, Prokushkin *et al.* 1998), phyto-diversity of plant associations (Zyryanova *et al.* 1998, 1999) as well as the trends in and the rate of progressive successions (Abaimov 1997, 1999).

Global warming issue appears to be able to change fire frequency in the cryolithic zone and to disturb forest ecosystems in large scale.

This paper deals with the regional features of dense and sparse forests of the Siberian cryolithic zone, some adaptive mechanisms to the harsh environments and the resistance capacities of larch species to fire impacts.

Materials and Methods

1. Study sites:

We studied sparse and closed northern forests of three larch species (*Larix sibirica*, *L. gmelinii* and *L. cajanderi*) mentioned above. They characterize various stages of the postfire progressive successions. For the last 10 years, the observations have been taken in the permanent experimental plots established at Tura Experimental forest (64° 15' N 100° 13' E) (Table 1). The study sites were located in the higher latitudes of northern hemisphere where tree species are surviving under severe and peculiar environments. In the cryolithic zone of Siberia, air temperature amplitudes and negative

---

(Received; Mar. 15, 2000 : Accepted; June 16, 2000)

* Corresponding author: institute@forest.akadem.ru

Table 1. Characteristics of the experimental permanent plots (PP)

Plot No of PP	Location, Larch Association	Tree stand characteristics		Depth (cm)		Larch root capacity (g·dm^{-3})
		Composition Age	Mean: H (m) DBH (cm)	Soil Litter	Root layer	Root layer One tree
I-1	Bottom of the valley . Low bush-sphagnum	10 *L.g.*** 72-92	4.2 4.0	10-12 9-13	15-20	0.428 0.64±0.13
I-2	Surface of a socle terrace. Crowberry-bearberry	9*L.g.* 1*B* 72-92	6.1 6.2	0 2-4	50-70	0.930 1.32±0.20
I-3	Middle part of SW slope. Cowberry–green mosses	10 *L.g.* 72-92	8.2 6.6	7-10 2-3	25-35	0.690 1.35±0.18
I-4	Upper part of SW slope. Cowberry-*Ledum*-green mosses	10 *L.g.* 72-92	10.7 9.0	6-11 5-9	25-35	0.450 1.40±0.07
5	Surface of fluvial terrace. *Ledum*-Blueberry	10 *L.g.* rare *B* 41-285	8.9 9.1	8-12 3-5	25-40	0.584 1.50±0.33
6*	*Larix sibirica* plantation of 1978. Grass	10 *L.s.* 25-30	10.0 12.0	0 3-5	100-130	1.635 ***

Notes: * - PP is located in forest-steppe zone near Krasnoyarsk;
*** - L.g. – Larix gmelinii* (Rupr.) Rupr.; *L.s. – Larix sibirica* Ledeb., *B – Betula pendula*
*** - was not determined.

Table 2. Climatic characteristics of cryolithic zone of Siberia

N	Meteorological station	Air temperature (°C)			Frost-free period (days)	Annual precipitation (mm)
		Absolute		Average annual		
		min	max			
		I. West-Siberian plane region				
1.	Salekhard	-52	+30	-11.0	53	300
2.	Polui	-52	+29	-12.3	74	450
3.	Nadum	-50	+29	-9.5	60	480
4.	Taz	-50	+31	-11.8	56	550
		II. Central Siberian plateau region				
1.	Agata	-57	+33	-11.4	44	452
2.	Khatanga	-53	+34	-13.4	73	237
3.	Tura	-66	+35	-9.2	70	375
4.	Olenek	-65	+35	-15.0	46	289
5.	Zhigansk	-64	+33	-11.0	74	250
		III. Yana-Kolyma Mountains region				
1.	Verkhoyansk	-68	+34	-15.6	69	142
2.	Nera	-68	+33	-15.6	53	238
3.	Artyk	-70	+32	-17.1	-	260
4.	Darpir	-61	+35	-13.7	<30	226

annual temperatures are being increased from the west to the eastward (Table 2).

Plant species diversity (a number of species per area) was examined on the sample plots of 1 m^2, 10 m^2, 100 m^2 per each larch associations. Species compositions of the vascular plants, mosses and lichens as well as each species abundance (coverage in percentages) were calculated. The quantitative species participation was analyzed with the dominance-diversity curves (Wittaker, 1980).

To estimate the changes in the development of a forested stand, the cores of 20-30 larch trees as well as their height and diameter distributions were analyzed in each plot. Natural regeneration both under a shelterwood and on the burned areas was estimated with sample plots of 0,5, 1 and 4 m^2. Their number per larch stand ranged from 25 up to 60 and total area of estimation, namely from 30 up to 100m^2. Age of larch seedlings was determined counting the number of growth rings on stem discs. Young larch trees of 30-50 individuals were cut at the ground layer for this purpose. In case of need in forest inventory studies and data published by other researchers were used for analysis.

2. Plant Materials:

The seasonal dynamics of growth of fine roots were surveyed during the last four years in five different larch stands, which differ in temperature of the active soil horizon. First, roots were dug up from soil and placed on a chromatographic paper. Then, they were placed at the original location by covering it with the moss-lichen ground floor, which was removed at the time of root excavation. Measurements of root growth were carried out during the vegetative season for 5-10 day-interval. To eliminate the negative effects of water deficiency in July and in the beginning of August, moisture was supplied at two experimental sites by watering the soil around the roots every 3-5 days at the rate of 10 liter per m^2.

To estimate functional role of fine roots, soil monoliths of 5-7 profiles were taken in each stand. The fine roots, rinsed from soil, were divided depending upon their diameter into two fractions: 10-1.1 mm and 1.0 mm and less. Finest physiologically active roots were divided into the absorptive and growth roots.

For anatomical analysis, the main skeletal roots were used. In each experiment, we took from alive roots of 10 individual larch and made cross sections at 3-4 mm away the tips. The samples of cross sections were placed in glycerol and analyzed under the light microscope at x 200-1000 magnification. Each section was studied to reveal the root diameter, thickness and number of cell rows of the exodermis and bark parenchyma, their cell diameter as well as the size of intercellular space and the thickness of cell wall.

In biochemical analyses, we examined the content of total nitrogen and the nitrogen of protein, of free amino acids as well as of carbohydrates and organic acids (Yermakov *et al.* 1972). The quantitative and qualitative composition of these compounds can characterize the peculiar features of metabolic processes under the harsh cryolithic environments in Siberia.

Results and Discussion

1. Growth condition and characteristics of the northern Siberian forests

Duration of frost-free period is being reduced from 74 days in the northern part of Western Siberia up to 40-30 days in the north-easternmost of Yakutia. The timing of snow melting is essential for inhatins the formation of forming annual rings in whole Siberain region (Vaganov *et al.* 1998). Annual average precipitation has corresponding decreasing gradient from 550 up to 142 mm while index of continentality is being increased here from 55 up to 95-100% (Nazimova and Polikarpov 1996).

Besides climatic conditions, the permafrost is of great importance for the northern forest vegetation. The permafrost provides low temperatures of active soil horizon and peculiar hydrological regime, which is characterized by intensive elution of nutrients from forest soils into aquatic ecosystems along water proof frozen layer (Prokushkin A.S. *et al.* 2000). On the other hand, the permafrost just makes convenient environments for woody vegetation in the beginning of vegetative season when precipitation deficiency usually takes place (Berg and Chapin 1994, Abaimov *et al.* 1998).

On the base of published inventory and obtained data, we conclude the next peculiar features of the forests of cryolithic zone;

1) Low stand productivity: wood stock varies from 15-20 up to 60-90 m^3ha^{-1} in different geographical points and environments;

2) Absolute dominance in tree stand composition of *Larix* Mill. genera species which have the best adaptations to the permafrost among Siberian conifers;

3) Sparse tree canopy which eliminates a competition for light;

4) Small diameter trees prevailing in the stands (56-84%) resulted from their self-thining due to permafrost rise up and general change for the worse ring of site environments;

5) Uneven-aged tree stands without aged generations with age limits of trees in 200-250 years and more as resulted from aperiodic fires;

6) Weakened recovery potential (the number of shelterwood regrowth usually does not exceed 1.0-1.5 thouthound seedlings per hectare) which resulted from the competition of trees and ground vegetation for nutrients and moisture in active soil horizon;

7) Heightened sensitivity to external impacts among which wildland fires are of the most significance;

8) The lowest species diversity among forest ecosystems of the northern Eurasia.

Environmental factors apart the peculiarities mentioned above are provided by the geological youth of northern landscapes. As a whole, environmental, biospheric and social functions of the cryolithic forests are of grat importance in comparison to their resourse stock which accounts for nearly 10 billion m^3 (Pozdnyakov 1986).

2. Biodiversity

Plant species diversity of cryolithic larch ecosystems are characterized by a considerable share (56%) of woody plants: shrubs make up 32% and dwarf shrubs – 24% accordingly. *Duschekia fruticosa* (Rupr.) Pouzar (on well drained the middle steep slopes) as well as

Betula nana L. and *Salix myrtilloides* L. (under overmoistened conditions) can develop in the understory layer of the plant associations (Abaimov *et al.* 1997).

Subarctic and boreal species make peculiar combination in the northern forests. Their ratio in different larch associations makes up 53:47 – 58:42 in percentage. Both boreal (*Duschekia fruticosa, Arctostaphylos uva-ursi (*L.) Spreng., *Vaccinium vitis-idaea* L., etc.) and subarctic (*Salix bebbiana* Sarg., S. *boganidensis* Trautv., *Empetrum nigrum* L., *Vaccinium uliginosum* L.) species can dominate in the ground vegetation of larch forests.

Northern larch associations undamaged by wildfires for a long period have a community of high complexed structure. There are 4-8 species groups in them which differ in the degree of dominance. As a result, the dominance-diversity curves assume a multi-step shape (Fig. 1) as indicated by Zyryanova *et al.* (1998, 1999).

Such species composition has resulted from the cryogenic microrelief as well as from non-uniform hydrothermal and edaphic conditions of the sites.

Rare frequency of climax plant associations characterizes the forest vegetation of the cryolithic zone. It appears to be dependent on slope denudation caused by forest fires. Due to this disturbing factor, northern plant associations lack long self-development. Wildfires depending upon their power or degree and the duration provide unique series of plant associations which approach fire climax, but never reach it. According to our data, fire frequency in one site of cryolithic zone can vary from 40-100 up to 200 years predicting proper cycles in the forest association development.

3. Differentiation of larch species native to Siberia

Among many mechanisms which determines stability of northern forest ecosystems, superdominance of larch species is of the most importance. *Larix* species occupy a wide range of ecological niches in the cryolithic zone including the northern timberline. They can also successfully restore their dominant positions after the catastrophic damages of forest fires. Relative distribution of forested area could covere by dominant treespecies in different regions of Siberian cryolithic zone (Table 3),

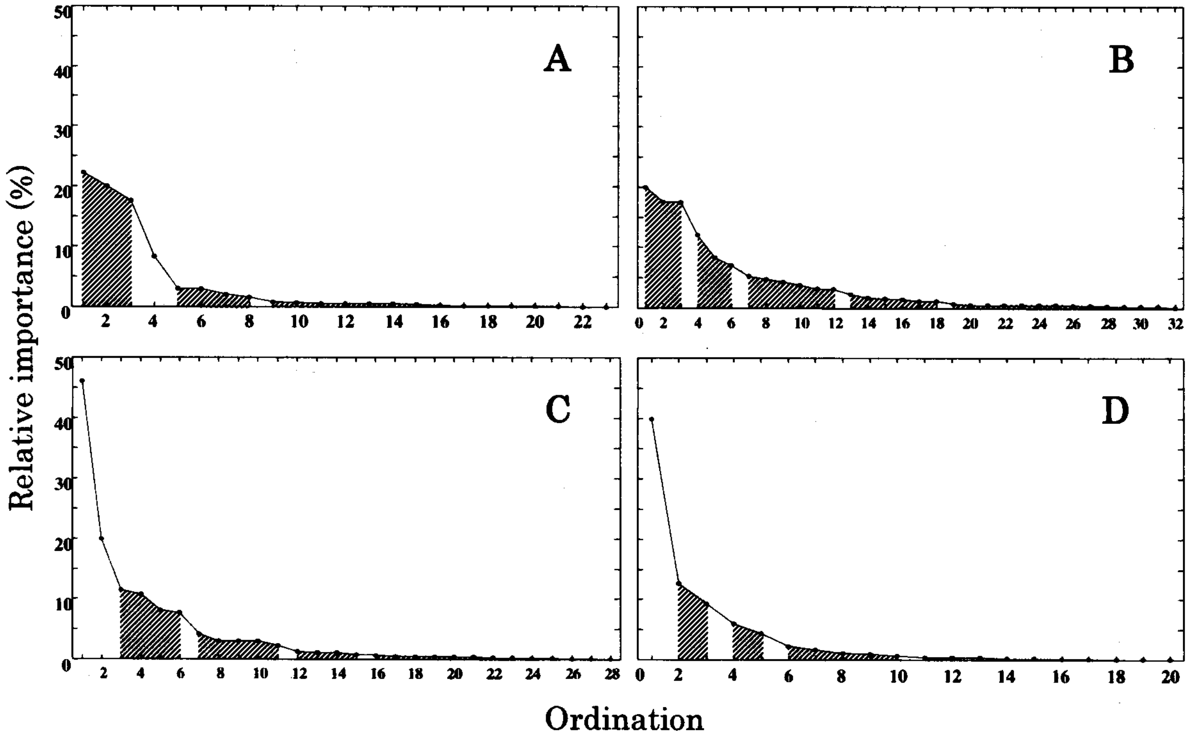

Fig. 1. The dominance-diversity curves of four *Larix gmelinii* associations.

A–crewberry-bearberry;
B–dwarf shrub-sphagnum with willow and dwarf birch understory;
C–cowberry-ledum green mosses;
D–blueberry-cowberry-crewberry green moss-lichens.

which shows that the share of larch trees increases continualy from north to the eastward

In the north of Western Siberia, larch forests of *Larix sibirica* make up 34.8% of forested area. At the high latitudes of central Siberia, the share of *Larix gmelinii* forests rises up to 81-90% of forest cover there. Behind Verkhoyansk Range, in the east of Yakutia, in Magadan and Chukotka districts, *Larix cajanderi* is the only tree species. It is obvious that, during the evolution, Siberian larch species have made a number of environmental and biological hereditable features which provide their dominant role in cryolithic zone. They are manifested in seed production of larch species, their high ecological plasticity and in a wide range of adaptive mechanisms to extreme cryolithic conditions and fire effect (Abaimov 1998).

Table 3. The distribution of forested area covered by dominant tree species in different regions of Siberian cryolithic zone, % (Filimonov *et al.* 1995)

No	Administrative unit	Tree species						
		Pine	Spruce	Larch	Siberian cedar	Birch	Aspen	In total
1.	Yamalo-Nenets Autonomous Area	28.1	12.7	34.8	14.3	10.0	0.1	100.0
2.	Taimyr Autonomous Area	-	10.9	86.0	-	3.1	-	100.0
3.	Evenki Autonomous Area	7.5	2.5	81.3	3.4	5.2	0.1	100.0
4.	Republic of Sakha (Yakutiya)	7.8	0.3	90.0	0.3	1.5	0.1	100.0
5.	Magadan district	-	-	99.8	-	0.2	-	100.0
6.	Chukot Autonomous Area	-	-	100.0	-	-	-	100.0

Table 4. Composition of the major plant families ranked by species number in unburned larch association and its burned area on the initial stages of progressive successions in central Evenkiya region

Family	Number of plant species				
	Unburned association	Burned area			
		1995	1996	1997	1998
Cyperaceae	4	–	1	2	3
Ericaceae	4	4	4	4	4
Poaceae	3	1	3	3	3
Asteraceae	3	1	2	2	3
Salicaceae	2	1	2	3	3
Orchidaceae	2	2	2	2	2
Caprifoliaceae	2	1	1	2	2
Pinaceae	2	1	1	1	1
Rosaceae	1	2	2	4	2
Onagraceae	1	1	1	2	2
Scrophulariaceae	1	1	1	1	2
Caryophillaceae	1	1	1	1	1
Valerianaceae	1	1	1	1	1
Polemoniaceae	1	1	1	1	1
Campanulaceae	1	–	1	1	1
Betulaceae	1	–	1	2	2
Pyrolaceae	1	–	1	1	1
Equisetaceae	1	–	1	1	1
Empetraceae	1	–	–	–	–
Cupressaceae	1	–	–	–	–
Saxifragaceae	–	–	1	1	1
Ranunculaceae	–	–	–	2	2
Apiaceae	–	1	1	1	1
Grossulariaceae	–	–	–	1	1
Primulaceae	–	–	–	1	1
Gentianaceae	–	–	–	–	1
Vascular plant number	34	19	29	40	42
Mosses	15	1	4	9	9
Lichens	11	–	–	5	1
Total number of species	60	20	33	54	52

4. Root system developmet of larch on the permafrost region

Negative radiation balance and low temperature in the active soil horizon are the major limiting factor on the plant growth in the cryolithic zone. Warmth deficiency provides both organic matter accumulation on soil surface and the development of thermal insulation litter. The latter not only accumulates atmospheric moisture and prevents its penetration into mineral soil, but also favour the appearance of moisture-lowing dwarf shrubs and mosses. As a result, the permafrost rises and hydrological conditions as well as ambient environments as a whole are getting worse. In this connection, roots faced to severe hydrothermal conditions of rhizosphere have an extremely important role in adaptation of larch trees in the cryolithic zone. The tolerance of roots to low positive temperatures in the soil may be provided by the changes of their structure and activity at subcellular, cellular, tissue, organismic and population levels of adaptation (Fig. 2). Our study of Gmelin larch roots in the central Evenkia has revealed the next important features of their seasonal growth. Growth of fine roots start in June when the rhizosphere temperatures of about +1 to +3℃ and terminated in the beginning of September, already after needle shedding and the transition of aboveground larch organs to the dormant condition. At the same time, it was found that on the permafrost soils, despite the excessive moisture in the lower soil horizons, the growth of roots in the top-soil could be limited not only by temperature, but also by water deficiency (Berg and Chapin 1994, Abaimov *et al.* 1998). In this connection, dynamics of the root growth in bionic soil layer showed three periods of root activity (Fig. 3).

The first period was early summer (middle – end of June), when growth is insignificant, and, mostly, it is provided by the low rhizosphere temperature. The second one was the middle of vegetation period (July – mid-August), when growth of roots at high temperature is limited by the moisture stress of active soil layers. The third was at the end of vegetation (the end of August - the beginning of September) and is characterized by the intense growth of roots at sufficient temperature (+1 – +2℃) and adequate moisture condition of the active soil layer. The last period showed maximal root increment, which ranges from 1.5-2.0 mm in the dwarf shrub-sphagnum larch up to 15-20 mm under optimal conditions.

Larch root system also has demonstrated sufficient changes in its structure when it is exposed to the permafrost. Superficial root system with well-developed thick skel*etal* roots has resulted from the permafrost and low temperature in the active soil layer. Furthermore, Gmelin larch seems to have an ability to generate adventitious roots when the permafrost rises up (Kajimoto *et al.* 1999). We suppose that these morphological mechanisms in the root system provide larch dominance and stability in the forest ecosystem at high latitudes of Siberia.

The study of the anatomic structure of fine roots has shown its distinct reaction to the change of thermal conditions in the rhizosphere. Accordingly, the various degree of rhizosphere

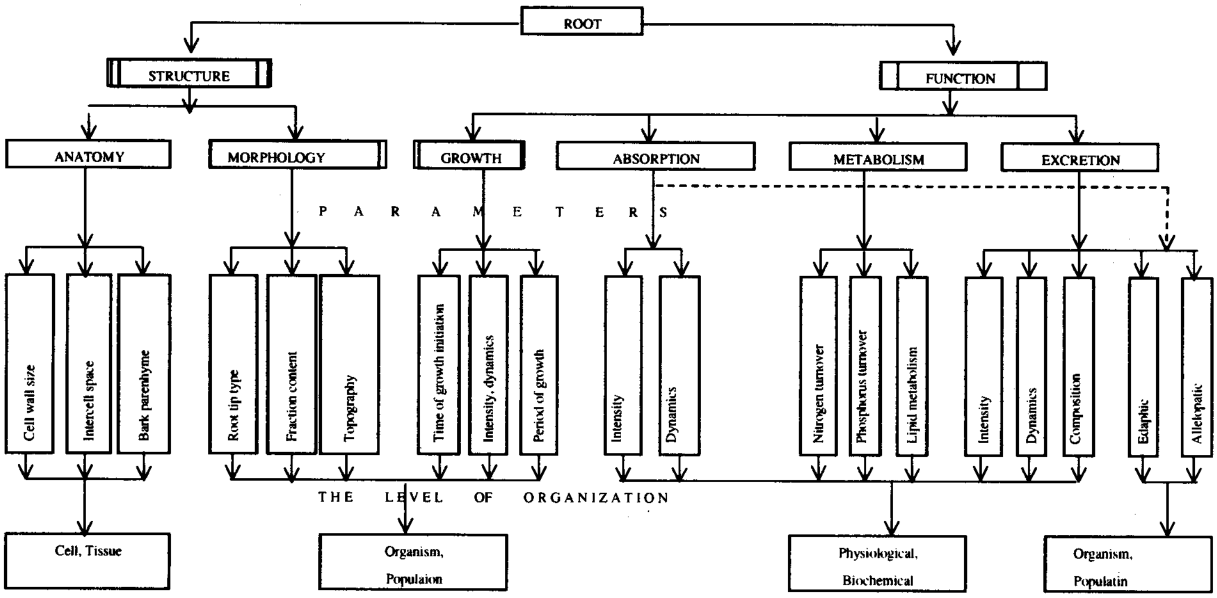

Fig. 2. Structural and functional adaptations of roots to low positive temperature of substrate at different levels.

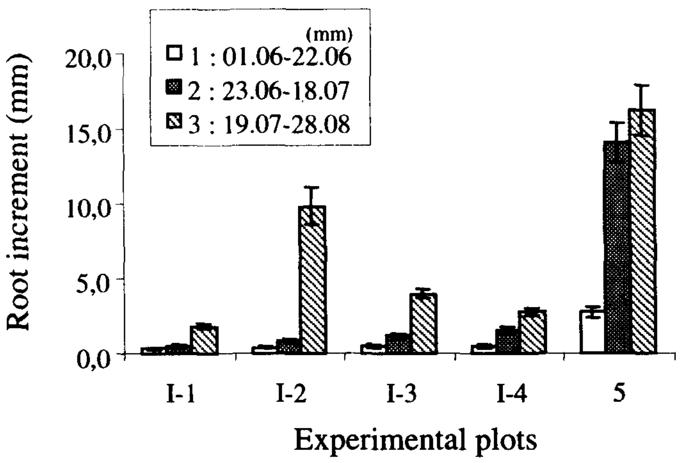

Fig. 3. The growth of *Larix gmelinii* roots during vegetative season.

heating, even within the borders of research region, is responsible for the changes of root diameter, size of root cells, intercellular spaces etc. In particular, larch fine roots collected in dwarf shrub-sphagnum larch stand, which was characterized by the lowest temperature of rhizosphere among the investigated communities, have shown significant increase of their diameter, bark parenchyma cell size and size of intercellular space as well as bark parenchyma thickening. Simultaneously, the decrease of cell number had led to the thinning of root exodermis. Besides, we have found that fine root cells under the continuous permafrost conditions have had thin cell walls. By contrast, thickening of the cell wall of fine roots has been characteristic of only over-moistened habitats.

5. Physiological ecology of rhizosphere

The adaptation of larch roots to low positive temperatures in the active horizon of the soil was also traced on the metabolic level. In comparison with the other regions, during the period of maximal activity of fine roots in cryolithic zone, carbohydrates reaching 30-80 mg.g^{-1} of a.d.w. are revealed to be prevalent substances in their tissues. Irrespective of environments, mostly insoluble storage forms (e.g. starch) represented carbohydrates. Among soluble carbohydrates monomer forms prevailed, while the content of olygosaccharides was insignificant. Improvement of hydrothermal conditions in rhizosphere has considerably increased the content of various soluble carbohydrates in the roots (Prokushkin *et al.* 1996).

The composition of organic acids in tissues of larch fine roots was almost independent of soil temperature and moisture conditions, but their amount considerably increased under favorable hydrothermal conditions. Maximum increase (4100-4700 mg.g^{-1} of a.d.w.) has had in larch stands with the highest temperature of active soil horizon (Abaimov *et al.* 1999). Among the identified acids (galacturonic, citric, malic, succinic, oxalic and fumaric), malic and succinic ones have had the highest concentrations. Other acids have been presented, however, in the trace amounts.

The biosynthesis of amino acids and proteins in roots is well known to be related with organic acids turnover and intensity of nitrogen uptake. Therefore, nitrogen metabolism may reflect the key point of larch root physiological adaptations to low rhizosphere temperatures. Special attention was focused on amino acid turnover in tissues of larch fine roots during the period of their intensive growth.

There were identified 22-24 kinds of amino acids (Prokushkin *et al.* 1996). The aliphatic group has have the highest concentration, while aromatic and heterocyclic amino acids have been presented in trace amounts. It was considered, that primary assimilation and transformation of the absorbed nitrogen has proceeded through pools of glutamate-glutamine, glutamate-γ-aminobutirate and cystine-cysteic acid. Fine roots inhabited lower temperature soils, according to our earlier data, contained about 1240-1730 (mg.g^{-1}) of amino acids per gram of the dry mass. It was 1.5-2.0 times more as compared to that of optimal environments. One of the main reasons of this increase is weak use of free amino acids in the protein synthesis. It was partly proved by data on total contents of protein nitrogen, reduced by 25 % in comparison with larch stands of higher productivity.

Thus, larch resistance to low temperatures in rhizosphere is provided by essential changes of morphological and anatomical features of its roots. They are the development of the superficial root system, different ratios of root types, various periods and rates of root growth, etc. In combination with the other mechanisms of adaptation such as physiological and biochemical ones they ensure successful functioning of Siberian larch species even near the border with the latitudinal and mountain tundra.

6. Adaptation characteristics of larch communities in the permafrost region

Resistance capacity of the larch populations of the cryolithic forest ecosystems at both local and regional levels can be provided by a stability of heat-exchange in the cryosphere. Its disturbance by wild fires, tree harvesting and other anthropogenic influences not only transform the forest ecosystems and influence subsequent forest successions, but also give impetus to the cryogenic processes. Such major processes as thermocarst and melting processes are followed by the degradation of landscape or forest-cover.

Wild fires in the cryolithic zone can be of both positive and negative significance depending on their power and duration. Mineralization of soil organic matter by fires provides not only the rise of the soil active layer the 5-7℃ increase in the summer rhizosphere temperatures and the increase in the available mineral nutrient content, but also the decrease in the acidity. Moderate fire mineralization and heat amelioration of the cryolithic soils favor for the successful larch regeneration. After holdover and middle fires the vigorous trees ranging from 1-2% up to 80% of pre-fire density provide reforestation and keep up larch dominant position. According to our data (Abaimov *et al.* 1997) the number of seedlings at initial stages of postfire forest succession can reach 500 thousand trees per one hectare and even more.

Ecological and biological features of Siberian larch species condition the trend and the rate of progressive successions. For instance, *Larix gmelinii* is keeping a part of viable seeds in the cones for 3-4 years. This specific adaptation allows to have permanent reserve of seeds in the stands and provides reservation of the occupied ecological niche even after catastrophic fires and consequent dying of all trees. Development of young tree stands on the burned areas has usually been completing for 10-15 years (Abaimov *et al.* 1997, 2000).

Larix cajanderi disperses all seeds just after ripening in autumn (Pozdnyakov 1986). Due to this reason, no seed reserve is kept in the stands in low-yield years. If larch stands are annihilated by the fires during this period sparse, they are replaced by a steady shrub community of *Duschekia fruticosa* and *Betula nana*. If a part of the trees is kept alive on the burned areas,postfire sparse forests of *Larix cajanderi* are developed in a few decades.

Larix sibirica, as mentioned above, develops large areas of sparse forests in the north of western Siberia where interrupted permafrost is located. This species is not a dominant, but makes up a share in mixed stands. Postfire recovery of *Larix sibirica* tree stands has been completed in 50-100-years. Similar scenarios sometimes take place in Gmelin and Cajander larch populations at the southern border of cryolithic zone. But here birch species compete successfully against conifers at well-heated plane watersheds.

7. The role of forest fires on the maintenance of species diversity

Ground fires considerably change plant species composition of larch associations. In 3-4 years after the fire, the number of vascular plants is 1.2-1.3 times more as compared with that of primary larch association (Table 4). Both the appearance of new species and even new families as well as the restitution of the before-fire plants are responsible for high species diversity on the initial stages of progressive successions. Primary species diversity of vascular plants will be recovers by the fourth year while that of mosses and lichens will be completed only in 30-40 years. Without repeated fires, larch trees develop adventitious roots during the period of the rising of the permafrost, while larch growth conditions worsens.

Catastrophic fires, which usually happen in dry years completely destroy forest sites. Annihilation of vegetation, litter and soil organic matter disturbs heat-exchange, and activates cryogenic processes. Solifluction usually takes place on the slopes while the thawing of fossil ice lenses and development of thermocarst lakes happen on watershed areas and plain surfaces of river valleys. Forest communities and their environmental functions on such disturbed areas appear to recover in many centuries

8. Summary of larch forest developed on the permafrost region.

A wide range of peculiar features, which make the larch forests differ from the typical boreal forests and are conditioned by unfavorable environments, characterizes forest ecosystems of cryolithic zone.

1) During the evolution Siberian larch species (*Larix sibirica*, *L. gmelinii*, *L. cajanderi*) have developed a number of adaptive mechanisms to the permafrost and other extreme environments

at different levels.

2) Stability of cryolithic forest ecosystems and their environmental, biospheric and social functions are provided by heat-exchange stability in cryosphere.

3) Wild fires at high latitudes of Siberia are the major external factors, which transform phytodiversity of forest ecosystems, the trends in and the rate of progressive successions.

4) To retain stability of cryolithic forests traditional approaches to forest management should be revised, especially in reference to the new economic situation in Russia.

The refuge network, ground and remote monitoring of northern forests as well as modelling and forecast of their structure and dynamics under Global Warming should be developed.

Acknowledgements

We thank all of our Russian and Japanese colleagues for their collaboration during the fieldwork and discussions. This paper was supported in part by Russian Federal Program «Integration» (grant No. 0023) and in part by joint grant of Russian Fund of Fundamental Investigations and Krasnoyarsk Scientific Fund (N 99-04-96008), Japan Environment Agency (by Dr. G. Inoue) and Japanese MESSC (Int. 11691162).

References

Abaimov, A.P. (1999) Modern tendencies and peculiarities of forest dynamics process in cryolithic zone. *In:* Proc. Forests and forest formation process in the Far East. Eds. Yu.I. *et al.*, Institute of biology and soil Science FEB RAS, Vladivostok, Russia, pp. 11-13.

Abaimov, A.P. (1998) Siberian larch species and their evolutionary adaptation to wildfire stress. *In:* Larix-98: World Resources for Breeding, Resistance and Utilization. IUFRO Interdivisional Symposium. Krasnoyarsk, Russia, pp. 18.

Abaimov, A.P. (1995) The larches of Siberian permafrost zone and their species peculiarities in progressive successions. *In:* Martinsson, O. ed Larch Genetics and Breeding: Research Findings and Ecological-Silvicultural Demands. Swedish University of Agricultural Sciences, Sweden, pp. 11-15.

Abaimov, A.P., Bondarev, A.I., Zyryanova, O.A. and Shitova, S.A. (1997) Polar forests of Krasnoyarsk region. – Novosibirsk, Nauka. Sib. Enterprise RAS, 208 p. (in Russian with English summary).

Abaimov, A.P., Erkalov, A.V., Prokushkin, S.G., Matsuura, Y., Osawa, A., Kajimoto, T. and Takenaka, A. (2000) The conservation and quality of Gmelin larch seeds in cryolithic zone of Central Siberia. *In*: Proc. Eighth Symposium on the Joint Siberian Permafrost Studies between Japan and Russia in 1999: Tukuba, Japan, pp. 3-9.

Abaimov, A.P., Lesinski, J.A., Martinsson, O. and Milyutin, L.I. (1998a) Variability and ecology of Siberian larch species. Swedish University of Agricultural Sciences. Department of Silviculture. Reports, No 43, 123 p.

Abaimov, A.P., Prokushkin, S.G., Matsuura, Y., Osawa, A., Takenaka, A. and Kajimoto, T. (1999) Wildfire and cutting effect on larch ecosystem permafrost dynamics in Central Siberia. *In*: Shibubya, M. *et al.* eds. Proc. Seventh Symposium on the Joint Siberian Permafrost Studies between Japan and Russia in 1998: Sapporo, Japan, pp. 48-58.

Abaimov, A.P., Zyryanova, O.A., Kanazawa, Y. and Osawa, A. (1998b) Estimation of *Larix gmelinii* (Rupr.) Rupr. regeneration on the burned areas in Central Siberia. *In:* Mori, S. *et al.* eds. Proc. Sixth Symposium on the Joint Siberian Permafrost Studies between Japan and Russia in 1997: Sapporo, Japan, pp.52-58.

Filimonov, V.K., Kukuev, Yu.A. and Strakhov, V.V. (1995) Forests of Russia. All-Russian Research and Information Centre for Forest Resources, Moscow, Russia. 280 p. (in Russian).

Matsuura, Y. and Abaimov, A.P. (1998) Changes in soil carbon and nitrogen storage after forest fire of larch taiga forests in Tura, Central Siberia. *In:* Shibuya, M. *et al.* eds. Proc. Seventh Symposium on the Joint Siberian Permafrost Studies between Japan and Russia in 1998: Sapporo, Japan, pp. 130-135.

Nazimova, D.I. and Polikarpov, N.P. (1996) Forest zones of Siberia as determined by climatic zones and their possible transformation trends under Global Warming. Silva Fennica. 30 (2-3), pp. 201-207.

Pozdnyakov, L.K. (1986) Permafrost forestry. Novosibirsk, Russia. Nauka Press. 192 p. (in Russian).

Prokushkin, A.S., Prokushkin, S.G., Koike, T., Mori, S. and Abaimov, A.P. (2000) Fluxes of water soluble organic carbon in larch ecosystems of the Northern part of Middle Siberia. *In*: Inoue, G. and Takenaka, A. eds. Proc. Eighth Symposium on the Joint Siberian Permafrost Studies between Japan and Russia in 1999: pp.135-142.

Prokushkin, S.G., Kaverzina, L.N. and Prokushkin, A.S. (1996) Productivity and root metabolism of the larch on permafrost soils of Central Siberia. *In*: Proc. International Conference Ecological and physiological aspects of xylogenesis in conifers. Krasnoyarsk, Russia, pp. 55-59.

Prokushkin, S.G., Korotkii, T.I., Mori, S. and Koike, T. (1998) Nitrogen metabolism of *Larix gmelinii* roots on the permafrost soils. *In:* Mori, S. *et al. eds.* Proc. Sixth Symposium on the Joint Siberian Permafrost Studies between Japan and Russia in 1997: Sapporo, Japan, pp. 18-22.

Schulze, E.D., W. Schulze, F.M. Kelliher, N.N. Vygodskaya, W. Ziegler, K.L. Kobak, H. Koch, A. Arneth, W.A. Kuznetsova, A. Sogatchev, A. Isaev, G. Bauer and D.Y. Hollinger. (1995) Above-ground biomass and nitrogen nutrition in a chronosequence of pristine Dahurian *Larix* stands in eastern Siberia. Can. J. For. Res., 25: 943-960.

Sofronov, M.A., Volokitina, A.V., Shvidenko, A.Z. and Kajimoto, T. (1998) On area burnt by wild land fires in the Northern part of Central Siberia. *In:* Mori, S. *et al.* eds. Proc. Sixth Symposium on the Joint Siberian Permafrost Studies between Japan and Russia in 1997: Sapporo, Japan, pp. 139-146.

Utkin, A.I. (1976) Forest biogeocoenosis of cryolithic district as peculiar ecosystems. Ecology, 3:15-22 (in Russian).

Wittaker, R.N. (1980) Plant communities and ecosystems. Moscow, Progress. 325p. (in Russian).

Yermakov, A.I., Arasimovich, V.V., Smirnova-Ikonnikova, M.I., Yarosh, N.P. and Lukovnokova, G.A. (1972) The methods of biochemical analysis of plants. 2nd edition. Ed. A.I. Yermakov. Leningrad, Kolos Press. 456p. (in Russian).

Zyryanova, O.A., Bugaenko, T.N., Bugaenko, N.N., Kanazawa, Y. and Matsuura, Y. (1998) Floristic diversity of Siberian larch ecosystems. *In:* Mori, S. *et al.* eds. Proc. Sixth Symposium on the Joint Siberian Permafrost Studies between Japan and Russia in 1997: Sapporo, Japan, pp. 92-100.

Zyryanova, O.A., Bugaenko, T.N., Bugaenko, N.N. and Matsuura, Y. (1999) Plant species composition dynamics on the initial stages of postfire progressive succession in Siberian cryolithic zone. *In:* Shibuya, M. *et al.* eds. Pros. Seventh Symposium on the Joint Siberian Permafrost Studies between Japan and Russia in 1998: Sapporo, Japan, pp.59-66.