

FLORISTIC CHARACTERISTICS, TYPES AND ECOLOGY OF LARCH FORESTS OF THE MIDDLE SIBERIA OF NORTHERN BOREAL SUBZONE

Leonid V. Krivobokov¹, Andrei A. Zverev², Liudmila V. Mukhortova¹

¹V.N. Sukachev Institute of Forest, Siberian Branch of Russian Academy of Sciences, 50, Bld. 28, Akademgorodok, Krasnoyarsk, 660036, Russia

²Tomsk State University, 36 Lenin Prospekt, Tomsk, 634050, Russia

Abstract

The widespread types of larch forest of the Middle Siberia of Northern Boreal Subzone near the Tura settlement were singled out. Leading ecological factors forming diversity of forest types were examined by means of DCA-ordination. Floristic composition and structure of forest communities were studied using IBIS-software. The completed study showed that poor floristic composition, leveling influence of fire impact and soil permafrost insignificantly influenced both alpha-diversity and beta-diversity.

Key words: *larch forest, Middle Siberian plateau, classification of forest communities, ordination of plant communities, analysis of floristic composition*

1. INTRODUCTION

The study of the floristic composition and the structure of plant cover is a question of great importance for identification of plant community's diversity and territorial complexes of vegetation both separate landscape districts and vast geographical regions. Likewise, there is important part for development of scientific methodology of native ecological zoning and for investigation of modern dynamics processes in the ecosystems. Larch biome occupy vast territory in the Northern Eurasia, there ultra-continental climatic conditions and soil permafrost are basic ecological factors of vegetation forming. Mainly Eastern areas of Siberia and Far East had been included of the generalizing botanical-geographical investigations of boreal larch forest ecosystems so far (Krestov et al. 2009). The aim of our study is to expose phytocoenological and floristic diversity of forest vegetation of Central Evenkia near the Tura settlement. Therefore, the system of ecophytocoenological classification had been elaborated and ordination of forest types had been carried out on the main axes of environmental gradients. In addition, the general floristic composition had been identified and the traits of forest type coenofloras (floristic composition of specific type of forest, which term is consistent with contemporary tenets of comparative floristics (Yurtsev 1987; Bulokhov 1993)) had been analyzed comparatively. The floristic investigations had been done earlier on the Middle Siberian plateau by Vodopyanova (1984) and Zyryanova and co-authors (2009).

2. MATERIALS AND METHODS

Studied region is situated on the Middle Siberian plateau (64°N 100°E). Relief of study area is erosive and low mountainous with gentle slopes within 120–600 m above sea level. Paleozoic effusive basic bedrocks, such as trapps and basalts, are a base of soil formation. The soils of study area are developed on continuous permafrost. The soil cover is generally consisted of crysoils and podburs, which are formed on the loamy eluvium. Climate of study region is continental and temperate humid. The annual average temperature is -8.9°C, the average temperature of January is -36°C and the average temperature of July is +16°C. The sum of temperatures for the period with temperatures above 10°C are 1000°C. The annual amplitude of temperature is 52°C. The annual amount of precipitation is 369 mm. There is comparatively even seasonal distribution of precipitation. Snow cover thickness changes within 50–60 cm. The frost-free season is 70–80 days. The climate conditions vary depending on altitude due to climatic inversions in the foot and summit of mountains (Climatic Atlas 1960; Gerasimov 1964).

We described the flora and vegetation of V.N. Sukachev Institute of Forest Evenk Experimental Station permanent study area in 2011. To characterize the vegetation, 47 detailed relevés (descriptions of plant community samples) were done along transects stretching from local watersheds to river valleys. Classification of plant communities was carried out with help of phytocoenological approach in Russian tradition, when dominant species are playing a certain role for delimitation of plant communities (Sukachev 1972). The processing of floristic and geobotanical data was made by software IBIS (Integrated Botanical Information System) (Zverev 2007).

Complexes of species distinguished based on species coenotic role (belt-zonal groups), humidification (ecological groups) and life form (biomorphological groups) applied to estimate ecological-coenotic modifications in plant community of different forest types. The belt-zonal groups of species were determined according to Malyshev and Peshkova (1984): LC – forest light coniferous, DC – forest dark coniferous, PB – forest preboreal, MM – mountain, HM – hypoarctic-mountain, TM – tundra-high mountain, AM – alpine-mountain, MD – meadow, FS – forest-steppe, MS – mountain-steppe. The ecological groups by humidification were determined according to Pykhalova, Boikov and Anenkhonov (2007): X – xerophyte, MX – mesoxerophyte, XM – xeromesophyte, M – mesophyte, HM – hygromesophyte, MH – mesohygrophyte, H – hygrophyte. The biomorphological groups were determined according to Serebryakov (1962): TR – taproot plants, SR – short rhizome plants, LR – long rhizome plants, LT – loose tuft plants, DT – dense tuft plants, B – bulbiferous plants, A – annual plants, T – trees, SH – shrubs, USH – undershrub, SSH – subshrub, DSH – dwarf subshrub.

For the taxa (species, genera and families) of the coenoflora the activity indices were determined according to B.A. Yurtsev (1968). Accordingly, the activity was calculated as, $R = \sqrt{AB/N}$, where R – a taxon's activity, A – a sum of cover scores of the taxon in a given forest type, B – the occurrence frequency of this taxon, and N – the number of relevés.

Species names follow the list of vascular plants of the former USSR (Cherepanov 1995), the check-list of mosses of East Europe and North Asia (Ignatov, Afonina & Ignatova 2006) and “A check-list of the lichen flora of Russia” (2010).

3. RESULTS AND DISCUSSION

According to the forest vegetation zoning system (Korotkov 1994), the study area is located in the Middle Siberian Plateau forest zone. The forest area near the middle part of the Lower Tunguska River occurs in Lower Tunguska forest district found, in turn, within Angara-Tunguska forest province. The vegetation in this area is largely represented by northern taiga light conifer forests of *Larix dahurica* Turcz. ex Trautv. at different post-fire regeneration stages. The fire interval averages 200 years here (Sukachev 1972). We identified the following forest types (Fig. 1).

Larch-herb-lichen (Forest Type 1) open stands growing on outcropped bedrock of steep to gentle slopes varying in aspect (150–250 m a.s.l.). These were uneven-aged *Larix dahurica* 7–15 m high stands with different canopy closure. The cover of the well-developed 0.5–3.0 m deep tall shrub layer consisting of 7–11 shrub species and dominated by *Rosa acicularis* Lindl. or *Juniperus communis* L. was 5–15% of the stand area. The herb-small shrub layer covered 10–15% of the area, was 5–20 cm deep, and was made up by *Vaccinium vitis-idaea* L. and by an average of 20–23 herbal petrophyte species. The moss-lichen layer had a cover of 35–45% and was composed of about 20 moss and lichen species dominated by *Rhytidium rugosum* (Hedw.) Kindb. and different species of *Cladonia* P.Browne. The understory species characteristic of this forest type appeared to be *Lonicera caerulea* L., *Ribes nigrum* L., *Gymnocarpium jessoense* (Koidz.) Koidz., *Viola brachyceras* Turcz., *Dryopteris fragrans* (L.) Schott., *Potentilla inquinans* Turcz., *Rubus matsumuranus* Levl. ex Vaniot, *Sorbus sibirica* Hedl., *Chamaenerion angustifolium* (L.) Holub., and *Ribes triste* Pall.

Larch- shinleaf- cowberry-feather moss (Forest Type 2) stands found on light loams (podzolized brown soils) on high terraces along the Kochechum River floodplain, at elevations of 120–140 m a.s.l. These stands had a canopy closure of 0.5–0.7, overstory of *L. dahurica* trees 10–20 m high, and a subcanopy layer of *Betula pendula* Roth trees 7–10 m high. The trees ranged 100–250 and averaged

50 years of age, respectively. The undergrowth was weakly developed, had a cover of 5–15% of the stand area, consisted of 7–10 species that included larch seedlings 1–3 m high, and was dominated by *Duschekia fruticosa* (Rupr.) Pouzar or *Salix saposhnikovii* N. Bolschakov. The grass-small shrub layer covered 35–45% of the area and consisted of a canopy and a sublayer. The sublayer of 5–15-cm-high cowberry and shinleaf was under the canopy of ledum and grasses 30–40 cm high. The moss-lichen layer was of a patched distribution, covered 5–30% of the area, and consisted of 2–5 species, with the dominant species being *Pleurozium schreberi* (Brid.) Mitt. and *Hylocomium splendens* (Hedw.) Schimp. The characteristic understory species of this forest type were *Pyrola rotundifolia* L., *Lonicera caerulea*, *Salix saposhnikovii*, *Sorbus sibirica*, *Chamaenerion angustifolium*, *Ribes triste*, *Equisetum pratense* Ehrh., *Vicia cracca* L., *Orthilia obtusata* (Turcz.) Jurtzev, *Rubus arcticus* L., *R. humilifolius* C.A. Meyer, and *Betula pendula*.



Fig. 1. The forest types of studied area: A – Larch-herb-lichen (Type 1); B – Larch- shinleaf-cowberry-feather moss (Type 2); C – Larch-ledum-feather moss (Type 3); D – Larch-cowberry-feather moss (Type 4); E – Birch-bog bilberry-cowberry-feather moss (Type 5).

Larch-ledum-feather moss (Forest Type 3) stands found on heavy, stony loams (cryogenic soil with raw humus) at 140–250 m a.s.l. on gentle north-facing slopes, where permafrost was located at a depth of 30–40 cm. These were 100–300-yr.-old larch stands with tree height ranging 6 to 13 m and a canopy closure of 0.2–0.3. Tall shrubs covered 2–15% of the stand area, were 1–3 m high, and consisted mainly of *Duschekia fruticosa*, with 3–5 species, mainly willows, being minor components. The ground vegetation cover was 20–35% and consisted of 10–20 species, with the dominants being *Ledum palustre* L. in the canopy and *V. vitis-idaea*, *Empetrum nigrum* L. and *Carex globularis* L. in the sublayer. The moss-lichen layer covered 100% of the area, was 10–15 cm deep, and consisted of 10–16 species, the dominants being *Pleurozium schreberi* and, less commonly, *Hylocomium splendens* or *Aulacomnium* sp., with *Cladonia rangiferina* L. (Web.) and *C. stellaris* (Opiz) Pouzar et Vezda found as co-dominants. The characteristic understory species of this forest type were *Salix saposhnikovii*, *Poa sergievskajae* Probat., *Arctagrostis latifolia* (R.Br.) Griseb., and *Carex vaginata* Tausch.

Larch-cowberry-feather moss (Forest Type 4) stands growing on sunlit gentle slopes at 160–220 m a.s.l. The soil cover was made up by heavy loamy cryogenic and lithogenic soils. Nearly all larch stands of 100–200 years of age, 8–18 m high and with a canopy closure of 0.25–0.5 had minor components of *Betula pendula* and *Picea obovata* Ledeb. The tall shrub layer was well-developed, 1–3 m deep, covered 5–30% of stand area, and consisted of 5–7 species, with the dominants being *Duschekia fruticosa* or *Spiraea media* Franz Schmidt, less commonly *Betula exilis* L. The ground vegetation was composed of 15–25 species and its canopy layer was cowberry 10–15 cm high, with *Pyrola rotundifolia* and *Arctous alpina* (L.) Niedenzu being the co-dominants. The moss-lichen layer averaged 50% in cover and contained 8–15, with *Rhytidium rugosum* and *Pleurozium schreberi* being the most common dominants. The understory species characteristic of this forest type were *Pyrola rotundifolia*, *Lonicera caerulea*, *Juniperus communis*, *Betula pendula*, *Picea obovata*, *Spiraea media*, *Carex reventa* V. Krecz., and *Cypripedium guttatum* Sw.

Birch-bog bilberry-cowberry-feather moss (Forest Type 5) stands of *Betula pubescens* Ehrh., always with larch and somewhere with spruce as minor components, found at 530–580 m a.s.l. on hill tops. They were supported by heavily loamy and stony cryogenic soils, below which permafrost occurred at 30–45 cm depth. Birch and larch trees ranged 30 to 70 and 100–200 years of age, respectively. The general stand canopy closure was 0.3–0.5 and tree height was 4–11 m. The tall shrub layer consisted of 4–7 species including 1–4 m high *Duschekia* covering 10–40% of stand area. The grass-small shrub layer had a canopy and a sublayer and consisted of 10–18 species. Bog bilberry (30–50 cm high) and cowberry (5–15 cm high) dominated, whereas *Calamagrostis lapponica* (Wahlenb.) Hartm. and *Rubus arcticus* occurred as the minor components. The moss-lichen layer had 40–100% cover and was composed of 12–15 species, among which *Hylocomium splendens* and *Pleurozium schreberi* were the dominants and *Cladonia* species co-dominated. The understory species characteristic of this forest type were *Betula pubescens*, *Lycopodium annotinum* L., and *Vaccinium myrtillus* L.

DCA-ordination resulted in a clear dependence of the forest type distribution along a complex gradient of moisture and continentality (Fig. 2) controlled by topography and elevation above sea level, of which gradient axis 1 may be interpreted as a reflection. Forest Type 1 found on bedrock outcrops appeared to be the most xerophilous, whereas hill tops with Forest Type 5 had the highest moisture and least continentality due to deep snow cover and winter air temperature inversions. Axis 2 may be interpreted as a summer heat gradient. The warmest were the sites with Forest Type 1, which were followed by river terraces with Forest Type 2 and south-facing slopes with Forest Type 4, and, finally, by the coldest north-facing slopes with Forest Type 3, with Forest Type 5 occupying the intermediate position.

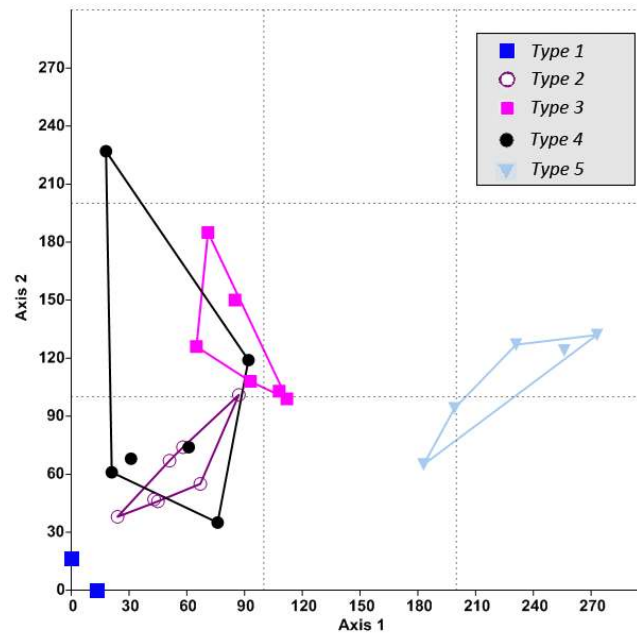


Fig. 2. DCA-ordination (axes 1 and 2) of forest types of studied area: Type 1 – Larch-herb-lichen; Type 2 – Larch- shinleaf- cowberry-feather moss; Type 3 – Larch-ledum-feather moss; Type 4 – Larch-cowberry-feather moss; Type 5 – Birch-bog bilberry-cowberry-feather moss.

The analysis of floristic composition of the plant communities may give very important ecological and geographical information about them. Composition of partial forest flora near Tura settlement involved 132 species from 87 genera and 40 families. Many families were presented by one genus (25–62.5 %) and by one (16–40 %) or two (10–25 %) species. Such ratio is characteristic for floras that are developing in the severe living conditions (Tolmachev 1974). In the family-species spectrum, first six families are ordered typically for boreal forest floras (Table 1): *Poaceae*, *Asteraceae*, *Rosaceae*, *Cyperaceae*, *Salicaceae*, *Ranunculaceae*. The leading genera of flora are *Carex*, *Salix*, *Betula*, *Poa*, *Viola*, *Saxifraga*. The weighted spectra showed absolutely different proportion, where weight of family or genus is sum of of taxon's occurrences and abundance in the all plant communities (activity of taxon). In the family-species weighted spectrum, first six families are ordered as following: *Ericaceae*, *Rosaceae*, *Poaceae*, *Betulaceae*, *Salicaceae*, *Pinaceae*. In the genus-species weighted spectrum, the leading genera of flora are *Vaccinium*, *Salix*, *Calamagrostis*, *Larix*, *Betula*, *Equisetum* and *Rosa*. The weighted spectra show actual phytocoenotic role of taxa in studied communities. According to these spectra studied flora is transitional from northern boreal to forest-tundra (Yurtsev 1966).

Table 1. Floristic spectra of larch forest communities.

| Family-species spectrum | | | | Genus-species spectrum | | | |
|-------------------------|-------------------|-------------------|------------------|------------------------|-------------------|--------------------|-----------------|
| Ordinary spectrum | | Weighted spectrum | | Ordinary spectrum | | Weighted spectrum | |
| Family | Number of species | Family | Weight of family | Genus | Number of species | Genus | Weight of genus |
| Poaceae | 13 | Ericaceae | 325 | Carex | 9 | Vaccinium | 186 |
| Asteraceae | 12 | Rosaceae | 233 | Salix | 8 | Salix | 129 |
| Rosaceae | 11 | Poaceae | 231 | Betula | 5 | Calamagrostis | 99 |
| Cyperaceae | 9 | Betulaceae | 171 | Poa | 4 | Larix | 96 |
| Salicaceae | 8 | Salicaceae | 131 | Viola | 4 | Betula | 94 |
| Ranunculaceae | 8 | Pinaceae | 120 | Saxifraga | 4 | Equisetum, Rosa | in 92 |

Comparative analysis of coenofloras on the belt-zonal (Fig. 4), biomorphological (Fig. 5) and ecological groups (Fig. 3) was carried out in order to confirm ecological traits of forest types. Analysis of ecological groups by humidity was the most informative.

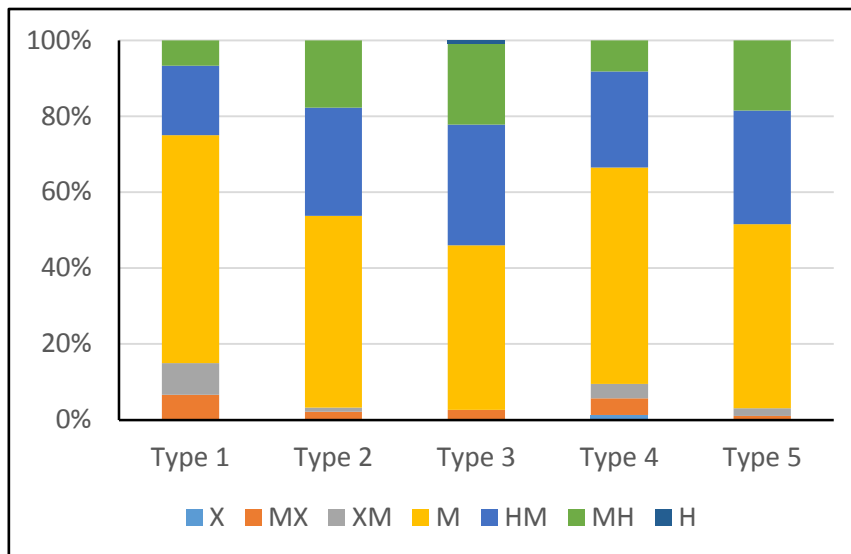


Fig. 3. The spectra of ecological (humidification) groups of species of forest types.

Forest Types 3 and 5 were similar as very humid types of studied area because about half of species of their coenofloras were presented by hygromesophytes and mesohygrophytes. Forest Type 1 occurred as very arid because basic part of species of its coenoflora were mesophytes and 15 % were presented by xerophytes (such as *Carex reventata* V. Krecz., *Potentilla inquinans* Turcz., *Campanula rotundifolia* L., *Thalictrum foetidum* L., *Pulsatilla flavescens* (Zucc.) Juz., *Saxifraga spinulosa* Adams) that are typical for bedrock ecotopes. Similar spectrum of species was revealed in Forest Type 4 occurring on the southern slopes. Forest Type 2 occurring on the loamy-sandy alluvial deposits was placed intermediate position between humid and arid Forest Types.

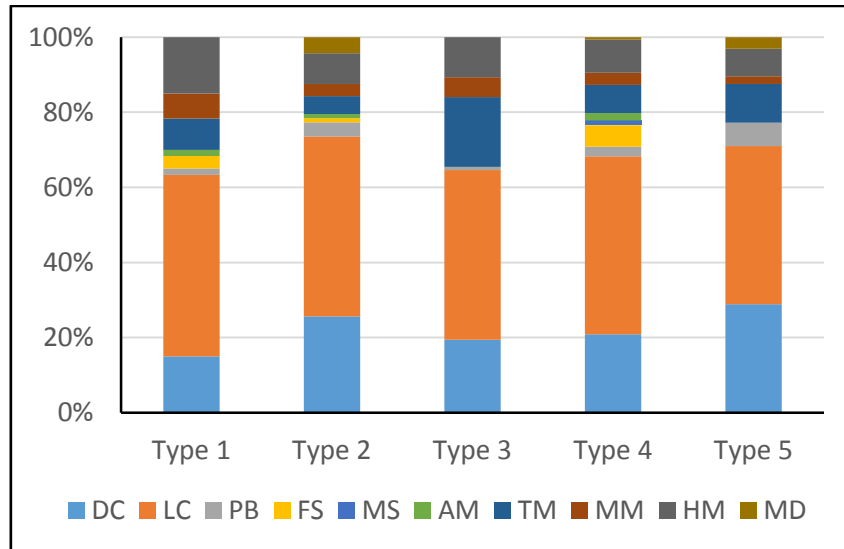


Fig. 4. The spectra of belt-zonal groups of species of forest types.

On the whole, spectra of belt-zonal species groups of forest types differ insignificantly. Species of forest dark coniferous group and forest light coniferous group compose more than two thirds of species number in all communities. However, certain features of ecology of forest types may be singled out according to contribution of species of little groups. The few species of forest-steppes group take part in warmer Forest Types 1 and 4 (such as *Vicia nervata* Sipl., *Galium boreale* L., *Campanula glomerata* L., *Sedum telephium* L., *Tephrosieris integrifolia* (L.) Holub, *Viola arenaria* DC). Forest Type 5 (birch forests on hill tops) is the least continental among all Forest Types and contains some species from forest preboreal group (such as *Betula pubescens* Ehrh., *Sambucus sibirica* Nakai). The coldest Forest Type 4 and the rockiest Forest Type 1 (on the stony soils and bedrocks) contain at the most number of mountain, hypoarctic-mountain and tundra-high mountain species (such as *Calamagrostis lapponica* (Wahlenb.) Hartm., *Valeriana capitata* Pall. ex Link., *Carex vaginata* Tausch, *Arctagrostis latifolia* (R. Br.) Griseb., *Dryopteris fragrans* (L.) Schott, *Stellaria peduncularis* Bunge, *Trisetum agrostideum* (Laest.) Fries, *Potentilla stipularis* L.).

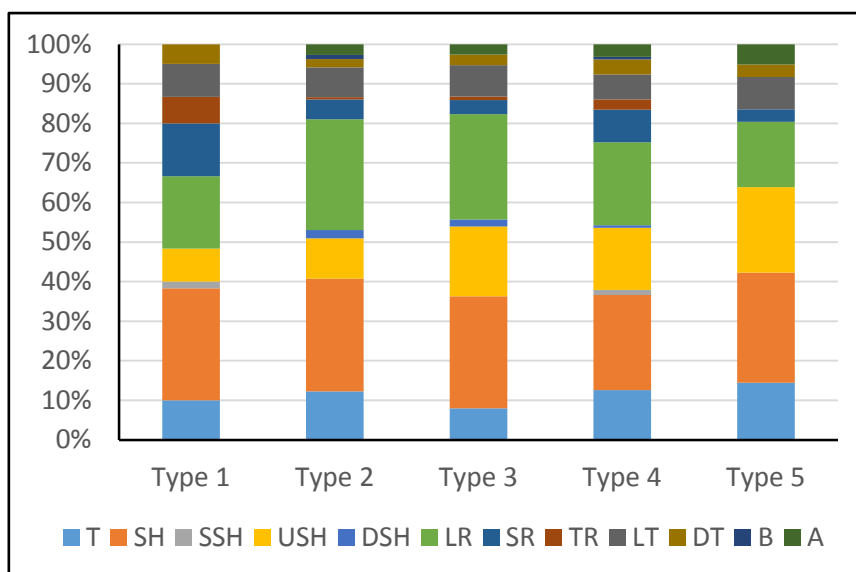


Fig. 5. The spectra of biomorphological groups of species of forest types.

All forest communities of studied area mainly are composed of four biomorphological groups, such as trees, shrubs, undershrubs and long rhizome herbs, which present 75–85 % of spectrum. Only Forest Type 1 (larch communities on the stony soils and bedrocks) differs from other Forest Types. In these communities, role of short rhizome herbs and taproot herbs increases (such as *Potentilla inquinans* Turcz., *Campanula rotundifolia* L., *Thalictrum foetidum* L., *Dryopteris fragrans* (L.) Schott, *Arnica iljinii* (Maguire) Iljin, *Polemonium boreale* Adams, *Lychnis sibirica* L.), while contribution of undershrubs and long rhizome herbs decreases, and annual plants are absent.

4. CONCLUSIONS

1. Our study showed that phytocoenotic diversity of Central Evenkia forests mainly depend on meso- and macroclimatical conditions, which may be transformed by relief. Fires have an insignificant and a short-term influence on the floristic composition, but they have a prolonged influence on the structure of plant communities. Poor floristic composition, leveling influence of fire impact and soil permafrost are factors of insignificant both alpha-diversity and beta-diversity.

2. All forest types have distinct ecological and floristic differences. Two belt of vegetation may be distinguished by elevation above sea level. First belt consisting of Forest Types 1–4 is placed from 100 to 300 m a.s.l. Second belt consisting of Forest Type 5 is placed from 450–600 m a.s.l. The boundary between belts is an ecotone within 300–450 m a.s.l. Factor of humidity (or continentality) including annual amount of precipitation and snow cover thickness is the basic cause of altitudinal differentiation of forest communities. Floristic differences are expressed in traits of ecological, belt-zonal and biomorphological spectra of groups of species. Each Forest Type is distinguished by original spectrum.

3. Comparative analysis of ordinary and weighted taxonomical spectra of flora of larch forest communities in northern boreal subzone near the Tura settlement (Table 1) showed which families and genera really take the most part in the composition of these communities. *Ericaceae*, *Rosaceae*, *Poaceae*, *Betulaceae*, *Salicaceae* and *Pinaceae* make most contribution in structure and composition of plant communities. Although *Asteraceae*, *Cyperaceae* and *Ranunculaceae* consist of many species, but activity of species of these families is insignificant. It is supported by genus-species spectrum, because genus *Vaccinium* prevail due to abundant presence of cowberry and bog bilberry in all studied forest communities.

5. ACKNOWLEDGEMENTS

The authors are very grateful to I.S. Savkina from V.N. Sukachev Institute of Forest of the Russian Academy of Science, who kindly corrected the part of the English text. This study is supported by Russian Foundation of Basic Research, grants No 13-04-01128 and No 14-04-01239 and by the Russian Government Megagrant Project No 14.B25.31.0031.

REFERENCES

- A checklist of the lichen flora of Russia* 2010, Nauka, Saint Petersburg (In Russian).
- Bulokhov, AD 1993 'Phytocoenology and floristics: analysis of the flora in syntaxonomical space', *Zhurnal obshchey biologii*, vol. 54, no. 2, pp. 201–209 (In Russian).
- Cherepanov, SK 1995, *Vascular plants of Russia and neighbouring countries*, Mir I Sem'ya, Saint Petersburg (In Russian).
- Climatic Atlas of USSR* 1960, vol. 1, Hydrometeoizdat, Moscow (In Russian).
- Gerasimov, IP (ed.) 1964, *The Middle Siberia*, Nauka, Moscow (In Russian).
- Ignatov, MS, Afonina, OM & Ignatova, EA 2006, 'Check-list of mosses of East Europe and North Asia', *Arctoa*, vol. 15, pp. 1–13.

- Korotkov, AI 1994 'Forest subdivision of Russia and Republics of former USSR' in VA Alekseev, RA Berdsy (ed.), *Carbon in the ecosystems of forests and bogs of Russia*, Institute of Forests, Krasnoyarsk, pp. 29–47 (In Russian).
- Krestov, P, Ermakov, N, Osipov, S & Nakamura, Y 2009 'Classification and Phytogeography of Larch Forests of Northeast Asia', *Folia Geobotanica et Phytotaxonomica*, vol. 44, no. 4, pp. 323–363.
- Malyshev, LI & Peshkova, GA 1984, *Characteristic Properties and Genesis of the Flora of Siberia (Prebaikalia and Tansbaikalia)*, Nauka, Novosibirsk (In Russian).
- Pykhalova, TD, Boikov, TG & Anenkhonov, OA 2007, *Flora of Ulan-Burgasy ridge (Eastern Cisbaikalia)*, Buryat Scientific Center Pub., Ulan-Ude. (In Russian).
- Serebryakov, IG 1962, *Plant ecological morphology: life forms of angiosperm and coniferous*, Moscow (In Russian).
- Sukachev, VN 1972, *General principles and program of forests type study: Selected works*, V1, Nauka Leningrad. (In Russian).
- Tolmachev, BA 1974, *Introduction in geography of plants*, Leningrad (In Russian).
- Vodopyanova, NS 1984, *Zonality of flora of Middle Siberian plateau*, Nauka, Novosibirsk (In Russian).
- Yurtsev, BA 1966, Hypoarctic botanical-geographical belt and origin of it flora, in *Komarovskie chteniya*, vol. 19, Nauka, Leningrad (In Russian).
- Yurtsev, BA 1968, *The Flora of the Suntar-Khayata Range. Some Issues of the History of High-Mountain Landscapes of North-Eastern Siberia*, Nauka, Leningrad (In Russian).
- Yurtsev, BA 1987 'Flora as fundamental conception of floristic: content of conception, study approach' in *Theoretical and Methodological Problems in Comparative Floristics*, Nauka, Leningrad. pp. 13–28 (In Russian).
- Zverev, AA 2007, *Information technologies in studies of vegetation: Tutorial*, TML Press, Tomsk (In Russian).
- Zyryanova, OA, Abaimov, AP, Daimaru, H & Matsuura Y 2009 'Floristic Diversity and its Geographical Background in Central Siberia' in A Osawa, OA Zyryanova, Y Matsuura, T Kajimoto, RW Wein (ed.), *Permafrost Ecosystems: Siberian Larch Forests*, Ecological Studies, vol. 209, pp. 17–39.