СИБИРСКИЙ ЛЕСНОЙ ЖУРНАЛ. 2016. № 6. С. 60–72

UDC 630*548(1-925.14/.16)+630*434:630*23

DYNAMICS OF FOREST ECOSYSTEMS REGENERATED ON BURNED AND HARVESTED AREAS IN MOUNTAIN REGIONS OF SIBERIA: CHARACTERISTICS OF BIOLOGICAL DIVERSITY, STRUCTURE AND PRODUCTIVITY

I. M. Danilin[1], I. A. Tselitan[2]

[1] *Federal Research Center Krasnoyarsk Scientific Center, Russian Academy of Sciences, Siberian Branch,*
Solitary Unit V. N. Sukachev Institute of Forest, Russian Academy of Sciences, Siberian Branch
Akademgorodok, 50/28, Krasnoyarsk, 660036 Russian Federation

[2] *Krasnoyarsk Institute of Economics – Branch of Saint-Petersburg Academic University*
Kirensky str., 70a, Krasnoyarsk, 660100, Russian Federation

E-mail: danilin@ksc.krasn.ru, igor57@akadem.ru

Received 01.02.2016

Complex estimation of forest ecosystems dynamics based on detailing characteristics of structure, growth and productivity of the stands and describing general geographical and biological management options for preserving their biodiversity and sustaining stability are discussed in the paper by describing examples of tree stands restored on burned and logged areas in mountain regions of Siberia. On vast areas in Siberia, characterized as sub-boreal, subarid and with a strongly continental climate, forests grow on seasonally frozen soils and in many cases are surrounded by vast steppe and forest-steppe areas and uplands. Developing criteria for sustainability of mountain forest ecosystems is necessary for forest resource management and conservation. It is therefore important to obtain complex biometric characteristics on forest stands and landscapes and to thoroughly study their structure, biological diversity and productivity. Morphometric methods, Weibull simulation and allometric equations were used to determine the dimensional hierarchies of coenopopulation individuals. Structure and productivity of the aboveground stand components were also studied.

Keywords: *forest ecosystems, structure, productivity, burned and harvested areas, restoration, biological diversity, mountain regions, Siberia.*

How to cite: *Danilin I. M., Tselitan I. A.* Dynamics of forest ecosystems regenerated on burned and harvested areas in mountain regions of Siberia: characteristics of biological diversity, structure and productivity // *Sibirskij Lesnoj Zurnal* (Siberian Journal of Forest Science). 2016. N. 6: 60–72 (in English with Russian abstract).

DOI: 10.15372/SJFS20160606

INTRODUCTION

Forest stands in the mountain regions of Siberia grow in the boreal zone, which is characterized by strongly continental climate and vast distribution of continuous permafrost which is the major limiting factor for growth of forest vegetation in this huge area. Forests in Siberia develop on seasonally frozen soils and are found predominantly in mountain regions. In many cases, they are surrounded by vast steppe and forest-steppe areas and uplands. The specific features of forest management in Siberia are: lengthy growing periods to final harvest age (about 100–120 years), the necessity for sustainable forest utilization, and the need to actively manage for regeneration of forest resources on burned, logged and insect-damaged areas.

The area of artificially restored forest lands in Central Siberia (ref. to Krasnoyarsk territory) totals more than 1 million ha at the present time, but only 50 % of them can be rated in good or satisfactory condition. About 10 % of all planted forests have

---

died due to forest fires, insect outbreaks caused by Siberian silkworm (*Dendrolimus sibiricus*) or gipsy moth (*Lymantria dispar*), industrial pollution, etc.

During the period 2000–2015, about 700 thousand ha of forest plantations were created in Central Siberia, and 160 thousand ha of those plantations were reclassified as lands covered by forests. In the last decade, plantations accounted for 18–20 % of the total reforested area. In 2010–2015, forest restoration work was carried out on about 70 thousand ha, and forest plantations were created on an additional 11 thousand ha (Varaksin, 2013; Varaksin, Vais, 2016).

STUDY AREAS, MATERIALS AND METHODS

Parameters of forest ecosystems regenerated on burned and commercially harvested areas in Central and Eastern Siberia (Krasnoyarsk Krai, Tuva and Buryatia Republics, Irkutsk Oblast and Zabaikalski Krai) were studied and analyzed (Fig. 1).

The area of non-regenerated burns, logged and dead stands totals nearly 15 million ha in Central and Eastern Siberia. This results in serious environmental and economic problems (Organizacsiya…, 2009; Evdokimenko, 2014; Sokolov, 2014; Sokolov et al., 2016) (Fig. 2–4).

Sixty nurseries (15 of them temporary) are available for growing tree seedlings in the area of this study. The total nursery area is 621 ha, including 375 ha in production. In 2010–2015, these nurseries produced 133.5 million seedlings of pine (*Pinus sylvestris*), Siberian pine (*P. sibirica*), larch (*Larix sibirica*) and fir (*Abies sibirica*) (Varaksin, 2013; Varaksin, Vais, 2016). The forested areas where plantations have recently been created, as well as naturally regenerated in Central Siberia are highly productive pine and larch stands that are commercially valuable and accessible by vehicles (Fig. 5–7).

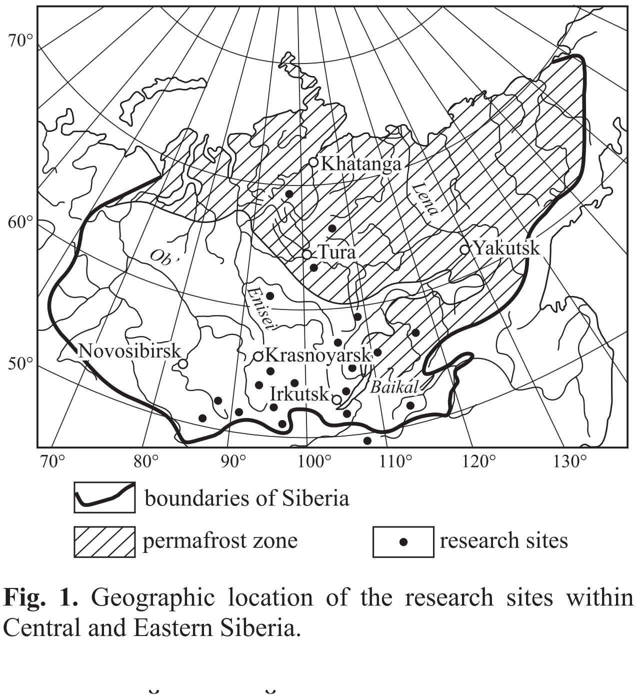

Fig. 1. Geographic location of the research sites within Central and Eastern Siberia.

During the past 50 years, these stands were subjected to intensive cutting. Commercial final clear cuts by heavy-duty harvesters and chain saws are a regular practice here. Heavy skidders usually drag harvested timber to landings, which results in considerable disturbance to ground cover and soil erosion. Parent uncut stands, harvested areas and plantations all suffer from frequent fires (Tcsvetkov, 2005; Organizacsiya…, 2009; Sokolov et al., 2016).

Forest regeneration work is not carried out in areas of winter logging, which are as a rule inaccessible in springtime, and on burned areas because of the lack of special engineering equipment for their development and for preparation of the sites for planting. On winter cuts, enough coniferous understory is usually kept for subsequent forest stand renewal. Since 1982, management practices to encourage natural forest restoration have been carried out on 1678 thousand ha, including 629 thousand ha in the last 10 years.

Studying growth dynamics, stand structure and biomass accumulation of such stands is important to understand and predict forest development both in terms of forest management improvement and environmental impact to forest ecosystems (Sokolov et al., 1998, 2003; Danilin, 2009*a*, *b*).

The stand structure, dynamics of organic matter and biodiversity serve as indices for stability of forest ecosystems. Studying stand structure and growth makes it possible to define permissible limits of management practices for affecting ecosystems and determining their effect on the environment. Permanent sample plots were established using conventional forest inventory and biometric techniques (Danilin, 1995, 2009*a*, *b*; Buzykin et al., 2002; Usoltsev, 2007). All trees on the sample plots were measured and mapped to establish their size-dependent position in the phytocenosis and to determine structure of the aboveground biomass and diversity of forest vegetation.

RESULTS AND DISCUSSION

The basic characteristics of the research sample plots are described in the Table 1. The forest cover of the experimental forest sites included stands of even-aged pine as well as both pure and mixed

Fig. 2.

Fig. 3.

Fig. 4.

Fig. 5.

Fig. 6.

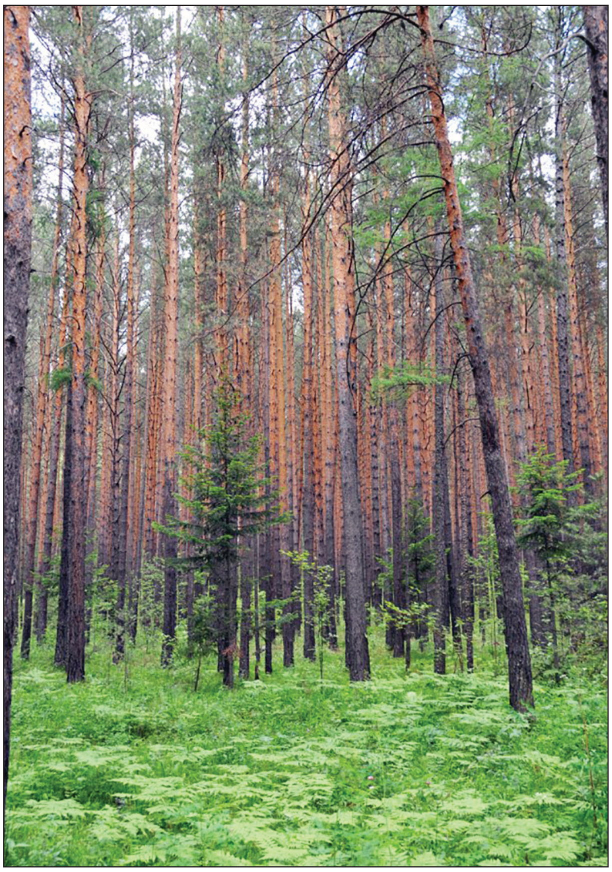

Fig. 7.

stands of larch and birch-aspen belonging to different forest types and natural formation patterns/series. Pure young pine stands occurred mostly on river terraces belong to the pine-bearberry-lichen (*Pinus sylvestris – Arctostaphylos uva-ursi – Cladina sylvatica*) and pine-red bilberry-green moss (*P. sylvestris – Vaccinium vitis idaea – Pleurozium schreberi*) forest community types. The tree density in these stands varied from 1.6 to 94.6 thousand trees per ha. Tree mortality was moderate.

Mixed pine, aspen and aspen-birch stands were common on flat interfluves with loamy soils. These belong to the pine-aspen-birch-red bilberry-herbaceous (*Pinus sylvestris – Populus tremula – Betula pendula – Vaccinium vitis idaea – Calamagrostis arundinacea – Carex macroura – Pulsatilla patens – Trifolium lupinaster – Bupleurum aureum – Geranium sylvaticum*) forest community type, and the density of these stands varied from 6.4 to 11.2 thousand trees per ha.

The study was also conducted where larch stands occur in a range of altitudinal belts. These sites are located approximately at 51–56° N, 95–115° E. All these areas are dominated by larch (*Larix sibirica* and *L. gmelinii*) stands with herbaceous ground cover. These stands are usually found in the lower portions of mountain slopes in Eastern Siberia (Evenkia, Irkutsk and Zabaykal'skiy krai). These are highly productive stands, commercially valuable, and accessible by vehicles. Over the last 30 years, these stands were subjected to intensive cutting. Commercial final cuts are practiced here. The harvested wood is usually dragged by tractors leading to considerable disturbance of ground cover and soils. After cutting, logging residue is placed into piles that are evenly distributed over the cut area and left untreated. In unlogged stands, understory numbers vary from 2400 to 5000 young larch per ha. Their quality and distribution depend on their age, basal area, and the area occupied by the parent stand. In logged areas, surviving understory averages, as a rule, from 400 to 600 trees per ha. Both parent larch stands and cut areas suffer from frequent fires that enhance natural regeneration.

In small clear-cuts (up to 5 ha), natural regeneration is usually abundant. Larch seeds germinate annually, and their resistance to environmental stresses is relatively high. In the first 5–6 years after cutting, the number of seedlings usually exceeds 50 thousand per ha, providing favorable conditions for regeneration of the harvested area. By the time the canopy of the young generation closes (in about 15 years), the herbaceous cover and litter layer characteristic of the previous stands are completely regenerated.

In this study, the structural relationships between biomass fractions changed with increasing average stand age and density. In dense stands, tree crowns were best developed. Consequently, the total crown biomass of dense, young stands was greater than in older stands with lower tree density. This may be due to the fact that trees at early development stages are able to make maximum use of their assimilation apparatus and branching systems, competing with equal success for light, nutrients, and water.

Empirical curves of the tree distribution series were noticeably steep, right-side-asymmetric and stretched (lengthened out). Parameter variation coefficients ranged from 43.4 to 73.9 %. This wide parameter variation can be attributed to distinct differences in tree height at the initial stages of the forest phytocoenosis development and also the root and crown competition for nutrients, sunlight and water. For all morphometric parameters, distribution appeared to be synchronous (autocorrelation). Adequate and effective smoothing of the empirical

---

Fig. 2. Fir (*Abies sibirica* Ledeb.) forest killed by catastrophic crown fire on the Manskii forest district of Krasnoyarsk krai in 2006 (total area burned was more than 50 000 ha).

Fig. 3. Scotch pine (*Pinus sylvestris* L.) commercial clear cut harvested in 2015 on the Ust'-Ilimsk forest district of Irkutsk oblast.

Fig. 4. Larch (*Larix sibirica* Ledeb.) forest severely damaged by gypsy moth (*Lymantria dispar*) near Tchagytai lake in Baikhaak forest district of the Tuva Republic.

Fig. 5. Burned area replanted by pine (*Pinus sylvestris*) seedlings on the Manskii forest district of Krasnoyarsk krai.

Fig. 6. 10-year-old successional birch (*Betula platyphylla*) and aspen (*Populus tremula*) forest naturally regenerated after catastrophic crown fire in a mature fir (*Abies sibirica*) and spruce (*Picea obovata*) stand on the Manskii forest district of Krasnoyarsk krai.

Fig. 7. 70-year-old pine (*Pinus sylvestris*) plantation on Karaul'noe forest district of Krasnoyarsk krai, created on a former logging area.

Table 1. Structure and aboveground phytomass of forest tree stands

Sample plot* number	Geographic location of sample plot	Species composition, percentage of timber stock, %	Dominant ground plant species	Tree stand species	Average					Above-ground phytomass	Annual phytomass increment
					Stand age, years	$D_{1.3}$**, cm	Height, m	Density, thousand trees per ha	Growing stock, m^3 per ha	ton per ha 100 % dry matter	
1	61° N 93° E	100 Pine	Bearberry lichen	Pine	12	1.1	1.2	94.6	23.1	10.90	0.90
2	58° N 104° E	100 Pine	Red bilberry green moss	Pine	15	2.4	2.6	6.8	7.6	5.00	0.30
3	59° N 97° E	62.8 Pine 33.8 Aspen 3.4 Birch	Herbaceous	Pine Aspen Birch	15 15 15	3.6 3.2 2.8	5.5 6.2 5.7	3.8 2.3 1.0	13.0 7.0 0.7	6.30 3.40 0.90	0.40 0.20 0.06
4	59° N 97° E	61.1 Pine 23.9 Aspen 15.0 Birch	Herbaceous	Pine Aspen Birch	28 30 25	6.5 4.7 6.9	8.4 8.8 11.2	4.8 3.3 0.8	69.0 27.0 17.0	42.30 16.50 10.20	1.50 0.60 0.40
5	57° N 99° E	80.4 Pine 19.6 Birch	Herbaceous	Pine Birch	36 30	5.3 8.2	6.2 9.0	10.4 0.8	86.0 21.0	40.40 13.50	1.10 0.50
6	56° N 105° E	100 Pine	Red bilberry green moss	Pine	36	5.8	8.8	10.3	126.0	69.80	1.90
7	57° N 98° E	95.8 Aspen 2.6 Pine 1.6 Birch	Herbaceous	Aspen Pine Birch	15 15 15	4.4 5.3 2.8	8.5 6.0 5.0	4.7 3.2 0.2	30.0 0.8 0.5	13.80 0.39 0.27	0.90 0.03 0.02
8	55° N 95° E	77.3 Aspen 20.4 Birch 2.3 Pine	Herbaceous	Aspen Birch Pine	15 15 15	3.6 5.0 2.3	6.9 7.6 2.9	8.1 1.1 0.8	34.0 9.0 1.0	19.90 5.40 0.27	1.30 0.40 0.02
9	52° N 95° E	100 Larch	Herbaceous	Larch	16	1.6	3.8	54.5	39.0	33.90	2.10
10	56° N 111° E	100 Larch	Herbaceous	Larch	28	5.9	7.9	5.2	74.0	55.20	2.00
11	49° N 109° E	100 Larch	Herbaceous	Larch	30	7.5	9.5	9.1	212.0	117.90	3.90
12	51° N 110° E	100 Larch	Herbaceous	Larch	37	18.4	15.4	1.2	305.0	163.70	4.40
13	52° N 114° E	100 Larch	Herbaceous	Larch	70	18.9	18.1	1.5	397.0	189.10	2.70
14	64° N 103° E	100 Larch	Red bilberry green moss	Larch	30	3.5	6.7	5.2	20	11.60	0.40
15	50° N 109° E	93.2 Birch 6.8 Aspen	Herbaceous	Birch Aspen	60 70	13.6 22.6	14.0 14.7	1.6 0.04	159.9 11.6	123.20 6.10	2.10 0.10

* Sample plot size was 1000 m^2 (20 × 50 m); ** $D_{1.3}$ – diameter at breast height (1.3 m above tree base).

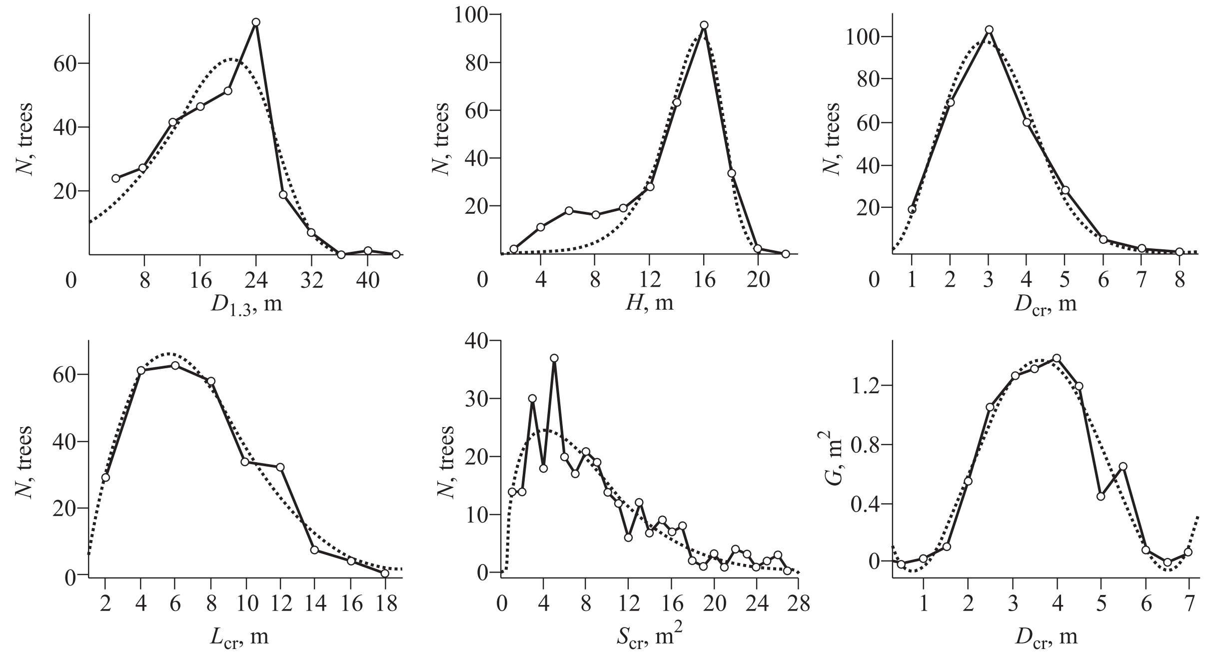

Fig. 8. Empirical (solid line) and Weibull (dotted line) distribution of larch trees by steps of morphometric indexes of the stems and crowns: N – number of trees; $D_{1.3}$ – stem diameter at breast height (1.3 m above tree base); H – tree height; D_{cr} – crown diameter; L_{cr} – crown length; S_{cr} – crown area; G – stem cross section area 1.3 m above tree base ($G = f D_{cr}$).

curves was provided by the Weibull distribution function of probability density with three basic parameters – b, c and θ: $f(x) = c/b \cdot [(x - \theta)/b]^{c-1} \cdot e -$ $- [(x - \theta)/b]^c$, $0 \le x < \infty$, $b > 0$, $c > 0$, $\theta > 0$, where, b – parameter of scale, c – parameter of form, θ – parameter of move (location), e – base for Eiler's natural logarithm (Statistica…, 2015) (Fig. 8, Table 2).

The Weibull distribution, as it has been shown earlier by a number of studies (Mason, 1968; Falls, 1970; Burkhart, 1971; Bailey, Dell, 1973; Svalov, 1982; Ganina, 1984; Kaplunov, 2001; Danilin, 2009*a*, *b*), makes it possible to obtain adequate, reliable approximations of the distribution of trees by stem thickness (DBH) as well as by the other morphometric parameters (tree height, crown length and crown diameter), adequately smoothing cenotic hierarchy of trees in the forest stand.

Morphometric parameters of the trees were found to be closely correlated (0.51 $R \le 0.98$; $P < 0.05$) (Table 3, 4).

Correlation between the sample tree morphometric and biomass parameters was also consistently high ($0.70 \le R \le 0.99$; $P < 0.05$) (Table 5, 6).

These correlations are normally in accordance with law of allometry (Enquist et al., 2002; West et al., 1999), valid for all tree species globally and proved by numerous studies throughout the world (Yandle, Wiant, 1981; Hagihara et al., 1993; Danilin, 1995, 2009*a*; Ter-Mikaelian, Korzukhin, 1997; Niklas et al., 2003; Kaitaniemi, 2004; Pilli et al., 2006; Usoltsev, 2007).

Correlation of the biomass fractions with stem diameter (DBH) was closer than with tree height and crown length. This is due to non-uniformity of the vertical tree layer structure and significant variation in tree heights. The maximum aboveground biomass of the larch overstory, the major stand component, was found to be 189 100 kg per ha (sample plot 13). Of the total biomass, 71 % is accounted for by stems, of which timber and bark make up 58 and 13 %, respectively. Nine percent of the total biomass is accounted for by the main (skeleton) tree branches (more than 1 cm in diameter at the base), 8 % by small branches (less than 1 cm in diameter at the base), 8 % by needles, and 3.8 % by dead branches.

Comparisons of the above mentioned data on the stem analysis of larch trees and their biomass structure (look Tables 1 and 6) with other studies in Siberia (Schulze et al., 1995; Shchepashchenko et al., 1998; Alexeyev et al., 2000; Shvidenko et al., 2000; Utkin et al., 2001; Fuchen et al., 2002; Usoltsev, 2007), have shown a high level of accordance, which indicates a possibility to use unified recursive approximations for aboveground biomass assessment in larch forest ecosystems of Northern Eurasia.

Table 2. Coefficients for Weibull smoothed distributions (y = weibull (x, b, c, t)$\cdot a$) of the larch (*Larix sibirica*) trees by morphometric indexes of stems and crowns at 95 % confidence level (valid for sample plot 12)

Parameter	Coefficient	Standard error	t-value	p-value	Confidence level	
					lower	upper
$D_{1.3}$ ($R^2 = 0.884$)						
b	741.717	22313.970	0.033	0.97	–52022.400	53505.860
c	99.990	2997.530	0.033	0.97	–6988.100	7188.030
t	–721.135	22314.910	–0.032	0.98	–53487.500	52045.240
a	1229.599	191.360	6.426	0.00	777.100	1682.100
H ($R^2 = 0.928$)						
b	200.645	3887.131	0.052	0.96	–8990.960	9392.249
c	99.980	1934.713	0.052	0.96	–4474.890	4674.850
t	–184.857	3887.223	–0.048	0.96	–9376.680	9006.964
a	497.152	50.049	9.933	0.00	378.810	615.500
D_{cr} ($R^2 = 0.988$)						
b	3.0312	0.360	8.420	0.00	2.032	4.031
c	2.597	0.389	6.673	0.00	1.517	3.678
t	0.393	0.376	1.045	0.36	–0.651	1.436
a	283.586	12.951	21.897	0.00	247.628	319.544
L_{cr} ($R^2 = 0.970$)						
b	7.183	0.845	8.498	0.00	5.011	9.356
c	1.849	0.309	5.980	0.00	1.054	2.644
t	0.900	0.934	0.964	0.38	–1.500	3.300
a	580.206	32.436	17.88	0.00	496.826	663.585
S_{cr} ($R^2 = 0.822$)						
b	8.299	0.764	10.858	0.00	6.7182	9.881
c	1.432	0.195	7.341	0.00	1.029	1.836
t	0.608	0.657	0.925	0.36	–0.752	1.968
a	278.405	21.225	13.117	0.00	234.497	322.313
$G = f\,\mathrm{D}_{\mathrm{cr}}$ ($\mathrm{G} = a + a_1 D_{\mathrm{cr}} + a_2 D_{\mathrm{cr}}^2 + a_3 D_{\mathrm{cr}}^3 + a_4 D_{\mathrm{cr}}^4$) ($R^2 = 0.945$)						
a	0.450	0.342	1.317	0.22	–0.323	1.223
a_1	–1.488	0.584	–2.550	0.03	–2.809	–0.168
a_2	1.297	0.302	4.299	0.00	0.615	1.980
a_3	–0.300	0.060	–5.042	0.00	–0.435	–0.165
a_4	0.021	0.004	5.222	0.00	0.012	0.030

Where: $D_{1.3}$ – stem diameter at breast height (1.3 m above tree base); H – tree height; D_{cr} – crown diameter; L_{cr} – crown length; S_{cr} – crown area; G – stem cross section area 1.3 m above tree base, and further the same in other tables.

Biomass increment is a more objective index for production processes and ecosystem stability than is total biomass. Over the past 5 years, current annual increment of diameter and height increased consistently with increasing tree size. The maximum average annual biomass increment was found to be 4.4 and 3.9 ton per ha (100 % dry matter) on sample plots 11 and 12 (look Table 1).

Forest fires and clear-cuts significantly impact the structure and diversity of plant groundcover, which is characterized by highly mosaic patterns and forms in communities of varying shapes, from round to stretched, with both straight and twisting contours.

After forest fires in the northern mountains, plant groundcover in naturally regenerated larch forests (look Table 1, sample plot 14) consists predominantly of low shrubs such as *Vaccinium uliginosum* L., *V. vitis-idaea* L., *Rubus arcticus* L., *Ledum palustre* L., *Arctous alpina* (L.) Nied., *Arctostaphylos uva-ursi* (L.) Spreng., *Empetrum nigrum* L., with green mosses *Hylocomium splendens* (Hedw.) Schimp. in B. S. G., *Pleurozium schreberi* (Brid.) Mitt., *Dicranum congestum* Brid. dominating the

Table 3. Correlation matrix (R) for relationship between tree morphometric indices at larch (*Larix sibirica*) tree stand (sample plot 12)

Index	$D_{1.3}$	H	D_{cr}	L_{cr}	S_{cr}
$D_{1.3}$	1.00	0.86	0.83	0.70	0.77
H	0.86	1.00	0.60	0.65	0.51
D_{cr}	0.83	0.60	1.00	0.72	0.98
L_{cr}	0.70	0.65	0.72	1.00	0.69
S_{cr}	0.77	0.51	0.98	0.69	1.00
Average statistical	17.46	13.34	3.07	6.96	8.37
Standard deviation	7.37	3.95	1.12	3.22	5.95
Number of observations	288	288	288	288	288

Table 4. The parameters of multiply regression equations between larch (*Larix sibirica*) trees' forest inventory and morphometric indices at 95 % confidence level (significance level $a < 0.05$) (sample plot 12)

Parameter	Coefficient	Standard error of the coefficient	t-value	p-value	Confidence level	
					lower	upper
$D_{1.3} = \exp(a + a_1 H + a_2 D_{cr})$ ($R^2 = 0.734$)						
a	1.3826	0.081	17.096	0.00	1.223	1.542
a_1	0.1079	0.005	21.381	0.00	0.098	0.118
a_2	–0.0141	0.008	–1.888	0.06	–0.029	0.001
$D_{1.3} = \exp(a + a_1 H + a_2 L_{cr})$ ($R^2 = 0.733$)						
a	1.3801	0.081	17.045	0.00	1.221	1.540
a_1	0.1076	0.005	21.332	0.00	0.098	0.118
a_2	–0.0051	0.003	–1.649	0.10	–0.011	0.001
$S_{cr} = \exp(a + a_1 D_{1.3} + a_2 H)$ ($R^2 = 0.675$)						
a	0.8289	0.091	9.102	0.00	0.650	1.008
a_1	0.0764	0.004	22.027	0.00	0.070	0.083
a_2	–0.0171	0.003	–5.849	0.00	–0.023	–0.011

lower layers, lichens represented by *Peltigera aphthosa* (L.) Willd., *Cladonia gracilis* (L.) Willd., *Cladina rangiferina* (L.) Nyl., and grasses *Carex globularis* L. and *Pyrola incarnata* (DC.) Freyn. The communities on this site were determined to be from 0.5 to 100 m^2 in area. When comparing structure of the groundcover with the distribution patterns of the tree overstory and understory, we were able to identify certain trends. The *V. uliginosum* + *Hylocomium splendens*, *Pleurozium schreberi* plant community that forms the background is distributed in well-sunlit openings. However, the larch overstory does not suppress the lower layers of the phytocoenosis because the crowns, even in tree biogroups, are naturally thinned. Nanorelief and the diversity of soil microconditions mainly control the community's shape, size and species composition. *V. uliginosum* + *Arctous erhytrocarpa* communities occupy level sites. The *V. uliginosum* + *V. vitis-idaea* community is found on raised nanorelief elements and in microsites of partially or completely decomposed downed wood dominated by humic and peat soil. Even where sun radiation is intense, the *V. uliginosum* + *V. vitis idaea* community is limited to vegetation-covered nanohillocks. *Ledum palustre* + *Hylocomium splendens*, *Ledum palustre*, *A. erhytrocarpa*, and *A. erhytrocarpa* + *Hylocomium splendens* communities occur mostly in small, wet microdepressions with humic podzols. Some communities, such as *V. uliginosum* + *V. vitis-idaea* + *Hylocomium splendens* + *Arctous sp.*, *V. uliginosum* + *Arctous* sp., and *V. uliginosum* + *Empetrum nigrum* + *Arctous* sp. with *Arctostaphylos uva-ursi,* are of limited extent.

The groundcover biomass totaled 5818 kg per ha (100 % dry weight) for sample plot 14. Of this, 87 % (5055 kg per ha) is accounted by low shrubs, which can be listed in order of decreasing biomass (kg per ha) as follows: 4179 *Vaccinium uliginosum*; 335 *V. vitis-idaea*; 299 *Rubus arcticus*; 169 *Ledum*

Table 5. Morphometric parameters and aboveground phytomass of the test larch (*Larix sibirica*) trees (sample plot 12)

Tree number	Age, years	$D_{1.3}$, cm	H, m	D_{cr}, m	L_{cr}, m	S_{cr}, m^2	Stem volume, m^3		Bark volume, m^3	Tree phytomass by fractions, kg absolutely dry matter									
												Stem			Crown				
							with bark	without bark		Tree total	Stem total	Wood	Bark	Alive part of crown total	Skeleton branches ∅ > 1 cm	Needled branches ∅ <1 cm	Current year shoots	Needle	Dead branches
114	44	31.0	17.8	5.8	13.8	26.4	0.6187	0.4747	0.1440	333.0	272.0	233.3	38.7	61.0	41.7	10.9	0.57	7.8	41.1
1	43	27.4	17.6	4.7	11.5	17.3	0.5084	0.3941	0.1143	271.5	228.9	195.7	33.2	42.6	28.1	7.7	0.56	6.2	24.5
318	39	23.5	17.3	3.6	9.1	10.2	0.3980	0.3135	0.0845	209.8	185.7	158.0	27.7	24.1	14.5	4.4	0.55	4.6	7.5
107	42	19.8	16.8	3.1	8.2	7.5	0.2884	0.2279	0.0605	145.7	128.5	107.8	20.7	17.2	9.6	3.8	0.35	3.4	6.4
87	43	15.9	16.2	2.4	7.2	4.5	0.1788	0.1423	0.0365	81.3	71.2	57.6	13.6	10.1	4.7	3.1	0.14	2.2	5.3
169	41	12.0	12.6	2.3	5.8	4.2	0.1024	0.0808	0.0216	46.8	40.8	32.7	8.1	6.0	2.8	1.8	0.09	1.3	3.3
103	40	8.1	9.0	2.0	4.3	3.1	0.0259	0.0192	0.0067	12.3	10.3	7.8	2.5	2.0	0.9	0.5	0.04	0.6	1.2
118	33	4.5	6.6	0.9	3.7	0.6	0.0158	0.0117	0.0041	4.6	3.1	2.4	0.7	1.5	0.7	0.3	0.03	0.5	0.1
246 dead	24	4.7	4.2	–	–	–	0.0056	0.0042	0.0014	2.4	2.0	1.6	0.4	–	–	–	–	–	0.4

Table 6. Correlation (R) between morphometric indices and phytomass fractions of the test larch (*Larix sibirica, L. gmelinii*) trees (sample plots 1–15)

Parameter	Age	$D_{1.3}$	H	D_{cr}	L_{cr}	S_{cr}	Stem volume with bark	Phytomass total	Stem	Wood	Bark	Crown	Branches		Current year shoots	Needle	Dead branches
													∅ > 1 cm	∅ < 1 cm			
Age	1.00	0.79	0.89	0.51	0.59	0.43	0.73	0.70	0.72	0.71	0.75	0.47	0.40	0.61	0.36	0.49	0.49
$D_{1.3}$	0.79	1.00	0.95	0.87	0.91	0.84	0.95	0.95	0.94	0.94	0.94	0.87	0.82	0.93	0.81	0.87	0.82
H	0.89	0.95	1.00	0.74	0.81	0.67	0.86	0.85	0.86	0.85	0.85	0.71	0.64	0.78	0.65	0.71	0.68
D_{cr}	0.51	0.87	0.74	1.00	0.98	0.96	0.78	0.81	0.78	0.78	0.76	0.90	0.85	0.89	0.89	0.94	0.80
L_{cr}	0.59	0.91	0.81	0.98	1.00	0.94	0.81	0.83	0.81	0.81	0.78	0.91	0.86	0.90	0.89	0.94	0.81
S_{cr}	0.43	0.84	0.67	0.96	0.94	1.00	0.79	0.83	0.79	0.80	0.75	0.96	0.94	0.91	0.91	0.96	0.89
Stem volume with bark	0.73	0.95	0.86	0.78	0.81	0.79	1.00	1.00	1.00	1.00	0.99	0.88	0.85	0.93	0.74	0.83	0.87
Phytomass total	0.70	0.95	0.85	0.81	0.83	0.83	1.00	1.00	1.00	1.00	0.98	0.91	0.88	0.94	0.78	0.85	0.89
Stem	0.72	0.94	0.86	0.78	0.81	0.79	1.00	1.00	1.00	1.00	0.98	0.88	0.85	0.92	0.74	0.82	0.87
Wood	0.71	0.94	0.85	0.78	0.81	0.80	1.00	1.00	1.00	1.00	0.98	0.89	0.86	0.92	0.74	0.82	0.88
Bark	0.75	0.94	0.85	0.76	0.78	0.75	0.99	0.98	0.98	0.98	1.00	0.85	0.79	0.93	0.73	0.82	0.81
Crown	0.47	0.87	0.71	0.90	0.91	0.96	0.88	0.91	0.88	0.89	0.85	1.00	0.99	0.96	0.90	0.95	0.94
Branches ∅ > 1 cm	0.40	0.82	0.64	0.85	0.86	0.94	0.85	0.88	0.85	0.86	0.79	0.99	1.00	0.90	0.86	0.89	0.96
Branches ∅ < 1 cm	0.61	0.93	0.78	0.89	0.90	0.91	0.93	0.94	0.92	0.92	0.93	0.96	0.90	1.00	0.87	0.95	0.87
Current year shoots	0.36	0.81	0.65	0.89	0.89	0.91	0.74	0.78	0.74	0.74	0.73	0.90	0.86	0.87	1.00	0.96	0.74
Needle	0.49	0.87	0.71	0.94	0.94	0.96	0.83	0.85	0.82	0.82	0.82	0.95	0.89	0.95	0.96	1.00	0.81
Dead branches	0.49	0.82	0.68	0.80	0.81	0.89	0.87	0.89	0.87	0.88	0.81	0.94	0.96	0.87	0.74	0.81	1.00

palustre; 38 *Arctous erythrocarpa*; 27 *Empetrum nigrum* and 8 *Arctostaphylos uva-ursi.* Eight percent (448 kg per ha) of the total groundcover biomass is made up of mosses, namely *Hylocomium splendens*, *Pleurozium schreberi and Dicranum congestum* accounting for 200, 137 and 111 kg per ha, respectively. Lichens make up 5 % (288 kg per ha) of the total ground plant biomass. These include *Peltigera aphthosa* (179 kg per ha), *Cladonia gracilis* (58 kg per ha) and *Cladina rangiferina* (51 kg per ha). The grass biomass proportion is relatively small and does not exceed 0.5 % (27 kg per ha), represented by *Carex globularis* and *Pyrola incarnata*, 24 and 3 kg per ha, respectively.

CONCLUSIONS

If the process of succession follows its natural course and the existing rate of biomass increment is maintained, these forests can be expected to regain their original state (i. e., a relatively stable climax forest ecosystem whose components are in balance with the environment) in about 100 years for the pure larch, pine and mixed stands, and about 50 years for birch and aspen phytocenosis. However, this time period would become much longer if disturbances such as fire, insect outbreaks or wind fall occurred. In this case, if phytocenosis is partly or completely destroyed, succession would take the form of replacement of coenopopulations: secondary aspen and birch stands on flat interfluves with loamy soils, or the native edificator tree species on river terraces with sands and loamy sands.

With no regeneration of birch, larch or pine due to poor silvicultural practices, seed-crop failures, droughts, forest fires or after logging, succession may take the course of forming meadow or steppe ecosystems. Such development is undesirable because it decreases forested area, reduces protective and environmental functions of the ecosystem and reduces tolerance to harmful environmental factors. Specific forest management activities such as thinning can considerably reduce the time necessary for a native phytocenosis to fully recover. From the biological viewpoint, thinning is useful because about 50 % of wood produced in an unthinned forest stand dies by the time it reaches maturity. Extraction of some dead and injured trees changes the insolation and temperature conditions, as well as those of humidity and soil moisture, and the decomposition rate of the forest floor organic layer increases. The conditions for tree growth and development improve, and trees drop their dead branches and accumulate wood that is free of knots. These factors facilitate higher productivity and consequently induce higher resistance to pests in the phytocenosis. Moreover, the increased yield of valuable conifer wood results in higher economic returns and decreases the conifer cultivation period.

Thinning, however, is a complex biotechnical measure that needs careful planning and implementation at each site. Before thinning, account should be taken of the biological characteristics of the stand, i.e. its composition, age, density and productivity, as well as site conditions, such as topography, soils, climate, the rate and character of anthropogenic disturbance, wildfire dynamics, etc.

In the event of phytocenosis succession controlled by man (anthropogenic succession) it is preferable for the forest ecosystem to regenerate through the native edificator species to form the original uneven-aged (of several generations) pine or larch coenopopulation with birch and aspen admixture (mosaic) which is more resistant to fire, ecologically stable and productive for longer economic usage. After logging or fire breakdown of forest ecosystem its place might also become occupied by an analogous but different ecosystem – a forest plantation.

Acknowledgments. *This work was funded by the Siberian Branch of the Russian Academy of Sciences. The authors highly appreciated Dr. Peyton W. Owston for his critical reading, scientific and language editing, suggestions and discussion on an earlier version of this manuscript. We also thank associate editors and three anonymous reviewers for their valuable comments that helped us to improve the quality of this article and clarify some of the important results with prior empirical and theoretical evidences.*

REFERENCES

Alexeyev V. A., Birdsey R. A., Stakanov V. D., Korotkov I. A. Carbon storage in the Asian boreal forests of Russia *In* E. S. Kasischke, B. J. Stocks (Eds.). Fire, climate change, and carbon cycling in the boreal forest. Ecol. Stud. Ser. New York: Springer-Verlag, 2000. P. 239–257.

Bailey R. L., Dell T. R. Quantifying diameter distributions with the Weibull distribution // For. Sci. 1973. V. 19. P. 97–104.

Burkhart H. E. Slash pine plantation yield estimates based on diameter distribution: an evaluation // For. Sci. 1971. V. 17. N. 4. P. 452–453.

Buzykin A. I., Pshenichnikova L. S., Sukhovol'skii V. G. Gustota i produktivnost' drevesnykh csenozov (density and productivity of woody cenoses).

Novosibirsk: Nauka, 2002. 152 p. (in Russian with English title, summary and contents).

Danilin I. M. Structure and biomass of larch stands regenerating naturally after clear-cut logging // Water, Air and Soil Pollut. 1995. V. 82. N. 1–2. P. 125–131.

Danilin I. M. Structural and functional organization of a larch phytocenosis in a postfire progressive succession in the north of Central Siberia // Contemp. Probl. Ecol. 2009*a*. V. 2. N. 1. P. 55–65.

Danilin I. M. Struktura poslepozarnykh bereznyakov na yuznom predele rasprostraneniya (The structure of post-fire birch forests at their southern range) // Lesovedenie (Rus. J. For. Sci.). 2009*b*. N. 3. P. 20–31 (in Russian with English abstract).

Enquist B. J. Universal scaling in tree and vascular plant allometry: toward a general quantitative theory linking plant form and function from cells to ecosystems // Tree Physiol. 2002. V. 22. N. 15. P. 1045–1064.

Evdokimenko M. D. Pirogennye transformacsii baikalskih lesov. Retrospektiva i sovremennost' (Pyrogenic transformations of the Baikal lake forests. Retrospective and contemporary issues) // Sibirskij Lesnoj Zurnal (Sib. J. For. Sci.). 2014. N. 3. P. 64–75 (in Russian with English abstract).

Falls L. W. Estimation of parameters in compound Weibull distributions // Technometrics. 1970. V. 12. P. 399–407.

Fuchen S., Laiye Q., Wenjie W., Yojiro M., Takayoshi K., Kaichiro S. Aboveground biomass and productivity of *Larix gmelinii* forests in Northeast China // Euras. J. For. Res. 2002. N. 5. P. 23–32.

Ganina N. V. Raspredelenie derev'ev po diametru s pomosch'yu funkscii Veibulla (Tree diameter distribution with the Weibull function) // Lesovedenie (Rus. J. For. Sci.). 1984. N. 2. P. 26–32 (in Russian with English abstract).

Hagihara A., Yokota T., Ogawa K. Allometric relations in hinoki (*Chamaecyparis obtusa* (Sieb. et Zucc.) Endl.) trees // Bull. Nagoya Univ. Forestry. 1993. N. 12. P. 11–29.

Kaitaniemi P. Testing allometric scaling laws // J. Theor. Biol. 2004. V. 228. P. 149–153.

Kaplunov V. Ya. Sopryazennost' raspredelenii derev'ev po poperechniku kron i diametru stvolov (Association of tree distribution by crown cross section and stem diameter) // Lesovedenie (Rus. J. For. Sci.). 2001. N. 3. P. 63–69 (in Russian with English abstract).

Organizacsiya ustoichivogo lesopolzovaniya v Krasnoyarskom krae (Management of sustainable forestry in Krasnoyarsk krai) / I. V. Semechkin (Ed.). Novosibirsk: Rus. Acad. Sci., Sib. Br. Publ. House, 2009. 361 p. (in Russian with English title, summary and contents).

Mason T. J. Maximum likelihood estimation in a mixture of two Weibull distributions. MSc. Thesis, Univ. Georgia, USA, 1968. 135 p.

Niklas K. J., Midgley J. J., Enquist B. J. A general model for mass-growth-density relations across tree-dominated communities // Evolut. Ecol. Res. 2003. N. **3.** P. 459–468.

Pilli R., Anfodillo T., Carrer M. Towards a functional and simplified allometry for estimating forest biomass // For. Ecol. Manag. 2006. V. 237. N. 1–3. P. 583–593.

Shchepashchenko D., Shvidenko A., Nilsson S. Phytomass (live biomass) and carbon of Siberian forests // Biomass and Bioenergy. 1998. V. 14. N. 1. P. 21–31.

Schulze E. D., Schulze W., Kelliher F. M., Vygodskaya N. N., Ziegler W., Kobak I., Koch H., Arneth A., Kusnetsova W. A., Sogatchev A., Issajev A., Bauer G., Hollinger D. Y. Aboveground biomass and nitrogen nutrition in a chronosequence of pristine Dahurian *Larix* stands in eastern Siberia // Can. J. For. Res. 1995. V. 25. N. 6. P. 943–960.

Shvidenko A. Z., Nilsson S., Stolbovoi V. S., Gluck M., Shchepashchenko D. G., Rozhkov V. A. Aggregated estimation of basic parameters of biological production and carbon budget of Russian terrestrial ecosystems. 1. Stocks of plant organic mass // Rus. J. Ecol. 2000. V. 31. Iss. 6. P. 371–378.

Sokolov V. A. Osnovy organizacsii ustoichivogo lesopolzovaniya (Fundamentals for sustainable forest use) // Sibirskij Lesnoj Zurnal (Sib. J. For. Sci.). 2014. N. 1. P. 14–24 (in Russian with English abstract).

Sokolov V. A., Danilin I. M., Semetchkin I. V., Farber S. K., Bel'kov V. V., Burenina T. A., Vtyurina O. P., Onuchin A. A., Raspopin K. I., Sokolova N. V., Shishikin A. S. Siberian expectations: An overview of regional forest policy and sustainable forest management. Portland, OR: World Forest Institute, 2003. 67 p.

Sokolov V. A., Danilin I. M., Farber S. K., Benderskii Yu. G., Buzykin A. I., Varaksin G. S., Vladyshevskii D. V., Vtyurina O. P., Efremov S. P., Zabelin A. I., Ziganshin R. A., Ivanov V. V., Koropachinskii Yu. I., Mikhalev Yu. A., Onuchin A. A., Pleshikov F. I., Polyakov V. I., Pfannenshtil' I. V., Raspopin K. I., Semetchkin I. V., Sokolova N. V., Soldatov V. V., Furyaev V. V., Shishikin A. S. Problemy ustoichivogo lesopolzovaniya (Problems of sustainable forestry). Krasnoyarsk: Rus. Acad. Sci., Sib. Br. Publ. House, 1998. 225 p. (in Russian with English title, summary and contents).

Sokolov V. A., Vtyurina O. P., Sokolova N. V. O razrabotke strategii razvitiya lesnogo kompleksa

Krasnoyarskogo kraya na period do 2030 goda (On elaboration of strategy for developing forest complex of Krasnoyarsk Krai until 2030) // Sibirskij Lesnoj Zurnal (Sib. J. For. Sci.). 2016. N. 4. P. 39–48 (in Russian with English abstract).

Statistica Advanced (Multivariate Exploratory Techniques). 2015. www.statsoft.com.

Svalov S. N. Ob otsenke prigodnosti raspredeleniya Veibulla dlya opisaniya stroeniya drevostoev (About evaluating fitness of the Weibull distribution for tree stand structure description) // Voprosy lesovyraschivaniya i ratsionalnogo lesopolzovaniya. Nauchnye trudy Moskovskogo lesotekhnicheskogo instituta (Problems of growing forests and rational forest use. Proc. Moscow Inst. For. Technol.). 1982. Iss. 139. P. 172–174 (in Russian).

Tcsvetkov P. A. Pirogennye svoistva listvenniscy Gmelina v severnoi taige Srednei Sibiri (Pyrogenic features of *Larix gmelinii* in northern taiga of Central Siberia). DSc. Thesis. Krasnoyarsk: V. N. Sukachev Inst. Forest, Rus. Acad. Sci., Sib. Br., 2005. 35 p. (in Russian).

Ter-Mikaelian M. T., Korzukhin M. D. Biomass equations for sixty-five North American tree species // For. Ecol. Manag. 1997. V. 97. P. 1–24.

Usoltsev V. A. Biologicheskaya produktivnost' lesov Severnoi Evrazii: Metody, baza dannykh i ee prilozeniya (Biological productivity of Northern Eurasia's forests. Methods, datasets, applications). Yekaterinburg: Rus. Acad. Sci., Ural Br., 2007. 637 p. (in Russian with English title, summary and contents).

Utkin A. I., Zamolodchikov D. G., Chestnykh O. V., Korovin G. N., Zukert N. V. Lesa Rossii kak rezervuar organicheskogo ugleroda biosfery (Forests of Russia as a reservoir-storage of organic carbon in the biosphere) // Lesovedenie (Rus. J. For. Sci.). 2001. N. 5. P. 8–23 (in Russian with English summary).

Varaksin G. S. Lesnye kultury v ravninnoi podzone yuznoi taigi Sibiri (Forest crops in the plain subzone of southern taiga in Siberia). Kranoyarsk: Krasnoyask State Agr. Univ. Publ. House, 2013. 251 p. (in Russian).

Varaksin G. S., Vais A. A. Tendenscii v sostoyanii polezaschitnykh lesnykh polos yuznoi Sibiri (The tendencies in the condition of field-protecting shelter belts in southern Siberia) // Sibirskij Lesnoj Zurnal (Sib. J. For. Sci.). 2016. N. 4. P. 86–97 (in Russian with English abstract).

West G. B., Brown J. H., Enquist B. J. A general model for the structure and allometry of plant vascular systems // Nature. 1999. V. 400. N. 6745. P. 664–667.

Yandle D. O., Wiant H. V. Estimation of plant biomass based on the allometric equation // Can. J. For. Res. 1981. N. 11. P. 833–834.

УДК 630*548(1-925.14/.16)+630*434:630*23

ДИНАМИКА ЛЕСНЫХ ЭКОСИСТЕМ, ФОРМИРУЮЩИХСЯ НА ГАРЯХ И ВЫРУБКАХ В ГОРНЫХ РАЙОНАХ СИБИРИ: ОСОБЕННОСТИ БИОЛОГИЧЕСКОГО РАЗНООБРАЗИЯ, СТРУКТУРЫ И ПРОДУКТИВНОСТИ

И. М. Данилин, И. А. Целитан

[1] *Институт леса им. В. Н. Сукачева СО РАН – Обособленное подразделение ФИЦ КНЦ СО РАН*
660036, Красноярск, Академгородок, 50/28

[2] *Красноярский институт экономики –*
филиал Санкт-Петербургского академического университета
660100, Красноярск, ул. Киренского, 70а

E-mail: danilin@ksc.krasn.ru, igor57@akadem.ru

Поступила в редакцию 01.02.2016 г.

Рассматриваются вопросы комплексной оценки и динамики лесных экосистем на основе детализации местных особенностей структуры, роста и продуктивности, раскрытия общих закономерностей географического и биологического разнообразия и поддержания устойчивости на примере насаждений, формирующихся на гарях и вырубках в горных районах Сибири. В этом обширном регионе с характерным суббореальным, субаридным резко континентальным климатом леса произрастают на сезонно-мерзлых почвах, во многих случаях в степных, лесостепных и высокогорных ландшафтах. Разработка критериев устойчивости горных лесных экосистем необходима для обеспечения рационального использования и сохранения лесных ресурсов. Основой для этого служат комплексные биометрические характеристики лесных насаждений и ландшафтов, детальное изучение их структуры, биологического разнообразия и продуктивности. В статье анализируются и обсуждаются морфологические параметры деревьев, строение, рост, фитомасса и биологическая продуктивность древостоев, накопление отмершей органики восстановительных послепожарных и послерубочных сукцессий, установленные с использованием морфометрических методов, распределения Вейбулла и аллометрических функций.

Ключевые слова: *лесные экосистемы, гари и вырубки, восстановление, биологическое разнообразие, структура, продуктивность, горные районы, Сибирь.*