

# The Function of Siberian Fir In The Formation Of Forest Phytocoenoses In The Floodplain Landscapes of North-Eastern European Russia

Natalya Gerling (✉ [Gerling1@rambler.ru](mailto:Gerling1@rambler.ru))

Institute of Biology of Komi Science Centre of the Ural Branch of the Russian Academy of Sciences  
<https://orcid.org/0000-0001-5224-8452>

Sergey Tarasov

Institute of Biology of Komi Science Centre of the Ural Branch of the Russian Academy of Sciences

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## Research

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THE FUNCTION OF SIBERIAN FIR IN THE FORMATION OF FOREST  
PHYTOCOENOSSES IN THE FLOODPLAIN LANDSCAPES OF NORTH-EASTERN  
EUROPEAN RUSSIA

Tarasov S. I., Gerling N.V.

Institute of Biology of Komi Science Centre of the Ural Branch of the Russian Academy of  
Sciences (IB FRC Komi SC UB RAS)

Russia, Komi Republic, Syktyvkar, 167982, 28 Kommunisticheskaya st.

tarasov@ib.komisc.ru, [gerling@ib.komisc.ru](mailto:gerling@ib.komisc.ru)

Gerling Natalya [gerling@ib.komisc.ru](mailto:gerling@ib.komisc.ru) (+79042343600)

### **Background**

The peculiarity of Siberian fir (*Abies sibirica* Ledeb.) growth in the territory of the North-East of the European part of Russia is that its habitats are confined to certain types of landscapes, namely floodplains of streams and rivers, slopes, and watersheds. In the structure of plant communities formed in such areas, fir is generally the predominant species. The purpose of this study is to find out causes why fir tree have been successful in colonizing specific types of landscapes.

The study was conducted in the Komi Republic, Russia. The objects of the study were chosen two forest phytocoenoses with fir dominance, one of which grows on a slope and the other — on a floodplain terrace. A comparative analysis of the complex of factors determining the growth and development of these forest communities was made.

### **Results**

Orographic conditions have been recognized as the main factor determining the species structure of phytocoenoses in the considered landscape types. The relief features of the areas where the forest stands under consideration are located contribute to the development of periodic water flows that have a significant impact on the species structure formation. Comparison of morphological and phenological features of the main forest-forming species of the Komi Republic has shown that the fir has a number of advantages contributing to its success under the conditions of a specific hydrological regime.

### **Conclusions**

The formation of spatial patterns with Siberian fir dominating on slopes and floodplains is a consequence of fir adaptability to the influence of periodic water flow due to the relief features.

Keywords: Siberian fir, slope, floodplain landscapes, forest formation, water flow, seeds

## Background

Siberian fir (*Abies sibirica* Ledeb.) is one of the forest-forming species of the dark coniferous taiga of central northern Eurasia. In most of its habitat it grows in a flatland landscape south of the permafrost distribution boundary, occupying the most fertile forest soils (Krylov et al., 1986). In mountainous landscapes fir often rises up to the upper boundary of the forest (1200-2000 m above sea level), forming a significant part of the dark coniferous mountain taiga of the Sayan, Kuznetsky Alatau, Mountain Shoria, North-Eastern and Western Altai, and Salair (Krylov et al., 1986; Belikovich, 2017).

In the north-east of the European part of Russia (Komi Republic), the siberian fir has similar habitats. In the plain part of the southern taiga and the southern part of the middle taiga of the Komi Republic, fir forests are found in all valleys of the Vychegda, Luza and Letka river basins. Another focus of fir forests is the slopes and foothills of the Ural Mountain Range, where they are also quite widespread in river valleys and, especially, in the upper part of the forest belt (Judin, 1954). The northernmost stands with fir can be found in the Subpolar Urals and in the upper reaches of the rivers Manyá and Naroda (Mamaev, 1983). In upper reaches of the Pechora river it is widely spread and grows on drained slopes, along valleys of rivers and streams (Sambuk, 1930; Smirnova et al., 2007).

The peculiarity of fir growth is its confinement to the riverside zones, stream floodplains, slopes and watersheds (Terekhov, Paramonov, 2008). Distinctive feature of such local landscapes is saturation of soil organogenic horizon with nutrients and organic matters (Chapin et al, 2011). Phytocoenoses boundaries, if they are in similar climatic conditions, usually associated with differences in a substrate and soil characteristics (Van Der Maarel, 1976). The physical matrix of soil serves as a source of water and nutrients for plants and is a physical support system in which terrestrial vegetation has taken root. For these reasons, soil physical and chemical properties strongly influence all aspects of ecosystem functioning (Chapin et al., 2011). The observed spatial pattern of fir distribution is traditionally associated with soil fertility and humidity and the amount of moisture in the air (Mamaev, 1983; Krylov et al., 1986; Belova, Bazhina, 2007; Zhelezova et al., 2008).

However, species-response model considering quality of soil organogenic horizon as main structure-forming factor of environment does not explain reasons of fir dominance in sites

with high soil fertility. Other forest-forming species, as a rule, have wider tolerance limits to edaphic conditions.

The purpose of this study is to reveal the reasons behind the characteristic spatial distribution of fir habitat and fir dominance in forest ecosystems of floodplain and slope sites. The task was carried out in two stages. At the first stage, the key factor influencing the formation of species structure of phytocoenoses under specific growth conditions was determined. The second stage considered the features of the main forest-forming woody species of the Komi Republic, namely: spruce (*Picea abies* (L.) H. Karst.), pine (*Pinus sylvestris* L.), fir (*Abies sibirica* Ledeb.), birch (*Betula pendula* Roth.), aspen (*Populus tremula* L.), allowing them to adapt to the action of this factor.

## METHODS

In line with the objective of the study, two permanent sample plots (PSPs) were established. The first (PSP-2), of size 0.2 ha, in the basin of the Vym river (Kniazhpogostskii district, Komi Republic, (62° 15'54" N, 50° 38'58" E)), located on the slope of the indigenous river bank, and the second (PSP-5), of size 0.25 ha, in the basin of the Luza river (Priluzskii District, Komi Republic, (60° 28'33" N, 49° 39'16" E)), located on a floodplain terrace. Sample plots had been established according to standard technique (OST 56-69-83, 1983) in 2017–2018. Descriptions of forest types of plots were based on (Judin, 1954). Wood stock was determined by the tables (Lesotaksacionnyj spravochnik ..., 1986). Geobotanical descriptions of ground cover were performed using standard methods (Polevaja geobotanika, 1964).

Climate characteristics of the regions where the PSPs are located are given according to (<https://climatecharts.net>). The main climatic characteristics affecting the development of plants - temperatures and precipitation - are represented by climagrams (Fig. 1). Taylor's method (Miller, 1931) was used at construction of climagrams. On an axis ordinate the average monthly values of temperature for the period of 100 years and on an axis abscissa the average monthly quantity of precipitation for the period of 100 years were postponed. The necessary meteodata for the period from 1901 to 2001 were obtained from (<https://climatecharts.net>). The De Martonne seasonal aridity index (ISDM) was calculated according to (Moral et al., 2016).

Data on the average monthly water discharge of the Vym (observation period 1956 to 1988) and Luza (observation period 1955 to 1999) rivers are taken from (<http://www.r-arcticnet.sr.unh.edu/>).

Classification of soils in the regions where the PSPs are located is given according to (Dobrovol'skaya et al., 2010). The assessment of soil fertility is based on the edifice requirements of ground cover plant species of the studied fir forests, which according to the Landol'ta ecological scales (<http://www.impb.ru>).

Comparative characteristics of the ecological space of forest-forming species are given on the basis of the range ecological scales of D.N. Tsyganov (<http://www.impb.ru>).

Phenological characteristics (time and duration of seed dispersal) and morphological characteristics (size and weight of seeds,  $m$ ) of the tree species under consideration are given on the basis of literature data. Most of the data on seed morphology are given as species-specific averages, while some data are region-specific. In most literature sources, seed sizes are presented as length,  $L$ , and width,  $W$ , thickness,  $T$ , is given rarely, sometimes only one size is given. Seed sizes and weights of a particular species, given in each source, were averaged, and the average values were combined into samples. Sample mean  $\bar{L}$ ,  $\bar{W}$ ,  $\bar{T}$ ,  $\bar{m}$  were considered as species averages. The equivalent diameter used for comparison of species as a generalized characteristic of seed size was estimated as a geometric mean (Syvitski, 2007), for seeds whose sizes are represented by length and width, according to the expression:

$$d = \sqrt{\bar{L}\bar{W}}. \quad (1)$$

For seeds whose sizes are represented by length, width and thickness, according to the expression:

$$d = \sqrt[3]{\bar{L}\bar{W}\bar{T}}. \quad (2)$$

## Results

**Degree of species dominance.** The study has identified characteristic features of natural forest formation in the landscapes under consideration.

Abietetum oxalidoso-herbosum fir forest (PSP-2) is located on a slope formed as a result of erosion of the bank of the Vym river. The stand is mixed in composition; multiple-aged, stratification is not expressed. Fir is the most represented woody species. Two generations of fir trees are distinguished in the age structure: age class III and V. The number of viable understorey, forming clumps in the windows, is dominated by fir. The origin of the understorey is a seedling. Regeneration of other species is not expressed. The underwood is poorly developed and represented by *Rubus idaeus* L., *Juniperus communis* L., *Rosa acicularis* Lindl., *Lonicera pallasii* Ledeb. Projective coating of grass-shrub layer is 70%. The dominant species composition: *Oxalis acetosella* L., *Fragaria vesca* L., *Dryopteris carthusiana* (Vill.) H.P.Fuchs, *Luzula pilosa* (L.) Willd. The moss-lichen layer has a projective coating of about 80% and is formed by species of the g. *Hylocomium* and *Hypnum*'s mosses.

Abietetum rara herbosum fir forest (PSP-5) is located on the flood plain of the left bank of the Luza river. The stand is mixed in composition, multiple-aged. Trees in the stand are not differentiated by height. Prevailing woody species into the stand is fir, which develops

intensively. Two generations of fir trees are distinguished in the age structure: age class V and VIII. A viable fir understorey, of seed origin, is abundant, confined to windows and glades, under the crowns strongly oppressed. Regeneration of other woody species in the stand is almost absent, the number of their understorey, compared with fir is insignificant. The underwood is poorly developed, represented by *Rubus idaeus* L., *Sorbus aucuparia* L., *Lonicera xylosteum* L., *Viburnum opulus* L. Grass-shrub layer has a tessellation structure with dead cover inclusions formed by needles and leaves. Projective coating of this layer is 40%. The species composition is dominated by *Pyrola rotundifolia* L., *Rubus arcticus* L., *Dryopteris carthusiana* Vill., *Solidago virgaurea* L.. The moss-lichen layer with a 40% projection coating is represented by green mosses.

The main characteristics of stands are given in Table 1. Based on the obtained data it is possible to assert, that Siberian fir is the dominant species in the investigated forest stands: the forest yield of fir at PSP-2 is 58 %, at PSP-5 is 47 %. Taking into account the higher productivity of deciduous species in relation to conifers in the same conditions it is better to determine the degree of dominance of the species based on number. Evaluation of the degree of species dominance as a ratio of the number of individuals of this species to the total number of all individuals shows that the degree of dominance of fir is 72% at PSP-2, at PSP-5 is 77%.

Table 1.

Taxation characteristics of stands of investigated fir forests

	Species	Age class	Thickness of stand, ha <sup>-1</sup>	Forest yield, m <sup>3</sup> ha <sup>-1</sup>	Thickness of understorey, ha <sup>-1</sup>
PSP-2	Fir	III	810	279.1	8975
	Spruce	V	265	154.6	1085
	Pine	III	50	48.0	-
	Total of		1125	481.7	
PSP-5	Fir	V	1084	162.6	2332
	Birh	X	148	130.1	-
	Pine	II	120	26.8	32
	Spruce	IV	56	24.5	144
	Total of		1408	344.0	

**Climatic conditions.** According to Köppen's classification, the climate type of the PSPs regions corresponds to Dfc, which is equivalent to a moderately cold climate with uniform humidification and cold summers. Climate identification on the basis of long-term weather data shows that the observed forest stands grow in different climatic conditions: abietetum oxalidoso-herbosum fir forest (PSP-2) is located in Vychegodskiy climatic region, abietetum rara herbosum

fir forest (PSP-5) is located in Priluzkiy climatic region, which causes differences in a number of climatic parameters (Atlas ..., 1997). Comparison of climagrams of the study regions shows that the differences are not significant (Fig. 1): climagrams can be found at one place of the coordinate plane, their shape and area are almost the same, which indicates the coincidence of temperature and precipitation dynamics, both during the vegetation period and throughout the year.

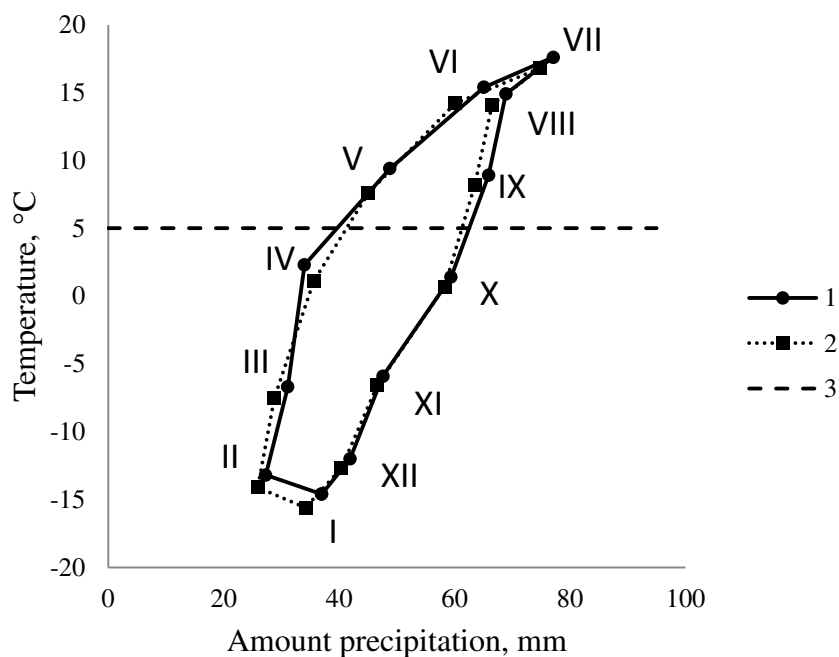


Fig. 1. Climagrams of the PSPs regions: 1 - Priluzskiy administrative district; 2 - Knyazhpogostskiy administrative district; 3 - vegetation threshold +5 °C; I, ..., XII - months.

However, the average annual temperature in the PSP-5 region is 1.5 °C and in the PSP-2 region is 0.1 °C. Effect of increasing average annual temperature is to a shift in climate patterns relative to one another along the ordinate axis and points a longer vegetation season and more heat availability in the PSP-5 region. This is a natural manifestation of the uneven distribution of solar radiation on the Earth's surface and leads to an increase in the vegetation season in the PSP-5 region by an average of 10 days (Atlas ..., 1997). The absolute maximum temperature in the PSP-5 region is 37.9 °C, in the PSP-2 region is 35.7 °C and the absolute minimum temperature is 47.3 °C (48.1 °C), respectively. The displacement of climagrams along the abscissa axis indicates greater precipitation in the PSP-5 region (mainly during the vegetation season), with an average annual precipitation of 604.2 mm for PSP-5 region and 573.3 mm for PSP-2 region. However, ISDM is practically the same: 45.2 for PSP-2 region and 44.8 for PSP-5 region.

**Edaphic conditions.** Soil fertility is an important factor in forest formation.

The territory of Priluzskiy administrative district is a part of Sysolo-Vychegodskaja province in Luzo-Sysolskii district of typical podzolic and swampy podzolic soils (Dobrovol'skaya et al., 2010). Fertile alluvial sod-gley soils were formed in flood plains of rivers and streams of Priluzskiy district. The territory of the Kniazhpogostskogo administrative district is a part of the Sysolo- Vychegodskoi province in the Vym-Vychegodskom district of typical podzolic, peat-podzolic-gleyic illuvial-humus soils (Dobrovol'skaya et al., 2010). Taking into account the relief features of the areas under consideration, the characteristics of their root-containing layer at the terrain level will be determined by the soil properties of the adjacent areas from which sediments are washed away.

The fertile soil layer in the area where PSP-2 is located represents sediments washed away and washed away by melt and rainwater from adjacent terraced areas because of deluvial process. At the site where PSP -5 is located, the fertile layer is formed by alluvial deposits, the composition of which is determined by the composition of soils and parent rocks of the catchment of the Luza River.

Some characteristics of the root-containing layer of soils formed because of wash-off can be estimated using the indicators characterizing the plants' exactness to the soil conditions. The presence of eutrophic plants in the ground cover of the plantations under consideration (Table 2) indicates the soil fertility of the root-containing layer at both PSPs. Based on the values of soil parameters necessary for normal existence of these plants, soils of the experimental sites can be characterized as medium dry, neutral in acidity ( $4.5 \div 7.5$  pH), in terms of nitrogen supply varying from medium to medium wealth, rich in humus, fine sand, well aerated (particle diameter  $0.002 \div 0.05$  mm).

Table 2. Exactingness of plants of the ground cover of forestations to soil conditions\*

	Species	Soil parameter				
		Moisture	Reaction	Nutrient	Humus	Dispersion
PSP-2	<i>Fragaria vesca</i> L.	3	3	3	3	4
	<i>Oxalis acetosella</i> L.	3	3	3	4	4
	<i>Trifolium europaeum</i> L.	4	2	2	5	4
PSP-5	<i>Pyrola rotundifolia</i> L.	3	3	2	5	4
	<i>Dryopteris carthusiana</i> (Vill.) H.P. Fuchs	3	2	2	5	5
	<i>Glechoma hederacea</i> L.	3	3	3	3	4

\* - according to Landolfa ecological scale (Baza dannyykh... <http://www.impb.ru>).

**Orographic conditions.** Relief is an important factor in the formation of any forest ecosystems, although it is not included in its composition. Reliefs of the studied forest stands vary significantly.



The abietetum oxalidoso-herbosum fir forest (PSP-2) is located on the slope formed as a result of erosion of the terraced bank of the Vym river. It is oriented from north to south and occupies the entire width of the slope, which is approximately 20 m. The slope of the western exposure with active erosion processes has an incline from 45 to 60 °. The plot is intersected by three shallow hollows formed by temporary watercourses. The water flow on the site is intermittent and is mainly caused by snow melting in spring and precipitation in autumn. A large catchment area ensures the accumulation of large amounts of melt water and rainfall.

The abietetum rara herbosum fir forest (PSP-5) is located in the flood plain of the left bank of the Luza River. It occupies an elevated central part of the flood plain area. A feature of the hydrological regime of this area is periodic (1-2 times a year) flooding. The height of the water rise, which can be determined from the traces left by the flood on the trunks of trees, is 60÷70 cm.

## **Discussion**

**Analysis.** Analysis and comparison of soil-climatic conditions of the forest ecosystems under consideration shows if not complete identity of soil and climate, then at least the proximity of their main parameters. This provides an opportunity to assess the degree of influence of these factors on the formation of species structure of phytocoenoses, comparing ecological spaces (niches) of the forest-forming species under consideration. Fig. 2 presents the result of comparison in a graphical form, which shows that almost all considered parameters of soil and climate conditions the range of fir tolerance in comparison with other species of woody plants is the narrowest, and, accordingly, the ecological space of fir is part of the ecological spaces of other species. Consequently, if the living conditions of the fir are changed, the fir will be primarily affected by stress. Thus, there are no grounds to consider climatic and edaphic factors favorable for fir and limiting the development of other woody plant species in the local landscapes under consideration.

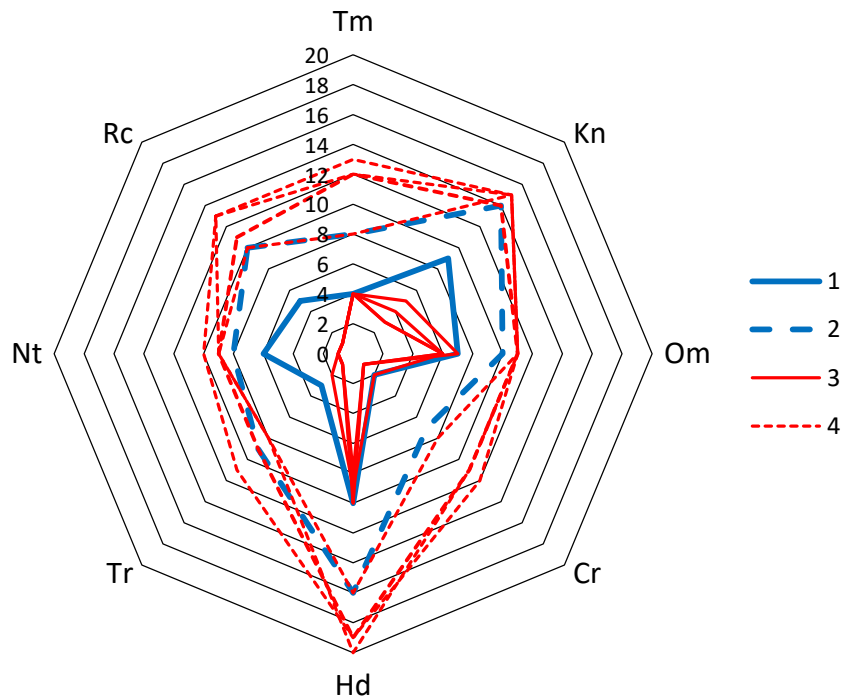


Fig. 2. Comparative characteristics of the ecological space of the woody species under consideration. 1 – lower boundary of fir ecological space; 2 – upper boundary of fir ecological space; 3 – lower boundaries of ecological space of other species; 4 – upper boundaries of ecological space of other species. Tsyganov's ecological scales: Tm – thermoclimatic, Kn – continental climate, Om – ombroclimatic aridity-humidity, Cr – cryoclimatic, Hd – soil moisture, Tr – salt regime of soils, Nt – riches of soils with nitrogen, Rc – acidity soil.

The orography of compared biogeocenoses differs significantly and, at first glance, cannot claim to be a general factor determining the species structure of the forest ecosystems under consideration. However, the relief effect on plant growth and development is indirect. Despite the marked difference in reliefs, both biogeocenoses have a specific hydrological regime, namely the presence of periodic water flow.

The influence of hydrogeomorphic conditions on the structure and number of populations cover the banks along rivers and streams has been noted by many researchers (McBride, Strahan, 1984; Bradley, Smith, 1986; Vansplunder et al., 1995; Scott et al. 1996; Cunnings at all., 2015). The species structure of plant communities in river floodplains is determined by two main processes: seed propagation and germination, which are regulated by time and speed of water flow, the morphology of the underlying surface or channel, and the peculiarities of vegetation phenology (Warren et al., 2001; Merritt, Wohl, 2002).

Since climatic and soil conditions do not favour any tree species in the circumstances under consideration, the topography can be identified as the main factor that forms the species composition of plant communities on slopes and floodplains of rivers and streams.

The relief determines the progressive movement of water towards the slope, thus forming a water flow. In turn, water flow generates water erosion, the extent of which is determined by the force and law of its movement, and is manifested by the destruction, movement and deposition of soil and rock particles (Morgan, 2005; Rodrigues et al., 2012). The influence of water flow on vegetation is carried out through the transformation of environmental gradients and disturbance of normal plant physiological functions (Warren et al., 2001; Baptist, 2005; Korzhenevskij, Kvitnitskaja, 2011; Prach, Walker, 2020). The negative impact of water flow on vegetation is especially critical in the initial stage of life cycle - the seed stage. Seeds of plants caught on the surface of slopes and floodplain terraces, as well as soil particles, are exposed to the water flow. Depending on the strength of the water flow, they can be washed off the soil surface or covered with a layer of sediment. Thus, when colonizing free areas, such as newly formed slopes and floodplain terraces, the ability of the seed to anchor itself on the soil surface and germinate is of paramount importance.

The seeds of all woody plants under consideration initially have the ability to float, although their buoyancy is not the same (Andersson et al., 2000). If the seeds of spruce, pine and fir sink in 7-15 days, the seeds of birch are able to float for 235 days (Andersson, et al., 2000; Sannikov, Sannikova, 2008). No data on the buoyancy of aspen seeds are given, but the seeds of *Salix sachalinensis* and *S. Integra* seeds, which have similar morphology, remain buoyant for no more than 15 days (Seiwa et al., 2008). In our opinion, this value can be used as an estimate of the buoyancy of aspen seeds. The buoyancy of seeds is largely due to their appendages, such as wings and hair. All wings are covered with a cuticle, which helps avoid moisture (Kozlowski, 1972), and therefore maintain buoyancy. The film wings of coniferous seeds, like the hairs of aspen seeds, form independently of the seed coat and are easily separated from the coat when wet (Kozlowski, 1972; Fedorov, 1978; Gordeeva et al., 1971). The winged growths of birch seeds are formed from the same tissue as the seed coat and contain air-bearing cavities (Takhtajan, 1991). Taking into account peculiarities of seed appendages formation, two scenarios of seed interaction with water flow are possible. The first is the transfer of seeds as any physical body with buoyancy, regardless of their morphology, and the second is the transfer of seeds that have lost their buoyancy. Seeds that have not lost their buoyancy will be washed away with almost any force of the water flow and have few chance hold on to the free territory. Of greatest interest is the impact of water erosion on seeds that have lost their ability to float.

Subaqueous hydrochory, which studies the movement of seeds that have lost their buoyancy, is now seen as an important seed dispersal (plant migration) mechanism. Such seeds are comparable in their physical properties to sediment particles and therefore the sediment

transport theory is also used to consider the movement of seeds that have lost their buoyancy (Markwith, Leigh, 2008).

The most important factors affecting sediment transport are size, shape, density and mechanical properties of particles. In order for a particle of sediment to move, the force exerted on it by water must be greater than all the forces opposing the movement. Simulating the movement of particles that are irregularly shaped and differ in size is not an easy task. Accurate description of the motion of such particles is impossible due to the complex nature of the phenomenon. It is common practice to perform experimental measurements to determine the parameters of motion.

A simple model that binds the velocity of the water flow at which the particle breaks off and begins to move, and its average diameter is offered in (Gordon et al., 2004). The expression has a form:

$$V_c = 0,155\sqrt{d}, \quad (3)$$

where  $V_c$  is the critical velocity (breakaway velocity),  $\text{ms}^{-1}$ ;  $d$  is the average particle diameter, mm.

From expression (Equation 3) it follows that the bigger the particle size, the bigger must be the water flow speed to start the particle movement. If this model is applied to describe the movement of a seed that has lost its buoyancy, the conclusion is obvious: seeds that are larger in size are more resistant to washing out and therefore have a better chance of settling on the soil surface.

The size of a particle is usually understood as its diameter, but with this parameter only spherically shaped particles can be clearly described. In the case where a particle is irregularly shaped, the concept of equivalent diameter is introduced. By calculating the average equivalent diameters (Equations 1, 2) characterizing the size of the seeds and comparing them, it is possible to establish the tree species whose seeds are most resistant to washing by water flow.

Soil particle sizes of organogenic horizon do not exceed seed sizes and move even at such water flow rates, at which seeds rest. Simultaneously with the process of sediment movement there is a process of sedimentation, which leads to the coverage of seeds, not washed away by water flow, by soil particles. Seed germination depends on the sowing depth (Pugnaire, Valladares, 2007; Fenner, Thompson, 2005) and therefore the thickness of the sediment layer may be critical for the seed. In (Bond, et al., 1999) an allometric expression is suggested linking the weight of the seed and the sowing depth, which allows us to evaluate the adaptability of the seed to sedimentation. The model has a form:

$$h = cm^{0,334}, \quad (4)$$

where  $h$  is the maximum depth of seed placement at which a seedling still appears, mm;  $m$  is the weight of the seed, mg;  $c$  is a constant equal to 27.3.

From expression (Equation 4) it follows that the greater the weight of the seed, the greater the soil layer through which it can germinate. That is, seeds with a large weight are more resistant to sedimentation and, therefore, are more likely to settle in local landscapes where sedimentation is common.

Morphometric characteristics of seeds of the considered woody species, obtained from the literature sources, are given in Table 4.

Table 4

Morphological parameters of seeds of the considered forest-forming species.

Species	Length, mm	Width, mm	Thickness, mm	Weight of 1000 pcs, g	The sample collection point	Information resource
Birch	1,2-2,4	0,8-1,3		0,19-0,21	Great Britain	Atkinson, 1992
	1,5-2	1			Generalized data	Vetchinnikova, 2004
	1,74-2,26	1,1-1,28		0,099-0,208	Ural (Southern, Middle, Northern)	Mahnev, 1987
	2,01-2,11	1,17-1,24			Generalized data	Kac, Kac, 1946
Aspen	0,8				North America	DeByle, Winokur, 1985
	1-2				North America	Landhäusser, 2019
	0,9-1,2	0,3-0,6	0,2-0,4	0,1	Estonia	Reim, 1930
				0,06-0,14	Finland	Lagerberg, 1922
				0,06-0,17	Norway	Fystro, 1962
				0,12	Generalized data	Smilga, 1986
Spruce	4-4,22	2,04-2,25	1,44-1,53	6,1-6,84	Poland	Kaliniewicz, 2016
	4			4,5-5	Generalized data	Kazimirov, 1983
	4	2-2,3		3,54-5,86	Ural	Mamaev, 1989
	4				Generalized data	Chepik, 1981
	1,75-3,1	1,15-1,95			Centre of European Russia	Kac, Kac, 1946
	4				Generalized data	Ouden, Boom, 1978
	4			4,86	Generalized data	Kapper, 1954
Pine	3-5	2-3		3,6-10,3	Centre of European Russia	Pchelin, 2007
				5,09-6,18	Southern Urals	Luganskaja, 2001
	3-4				Generalized data	Chepik, 1981
	3,15-4,5	1,25-1,7			Centre of European Russia	Kac, Kac, 1946
	3-5				Generalized data	Ouden, Boom, 1978
	3-5	2-3		3,62-5,2	Finland, Russia (Republic of Karelia, Arkhangelsk region)	Pravdin, 1964
Fir	5-7	3-5		5,01-10,5	Generalized data	Krylov et al., 1986
				4,75-10,35	Western Siberia	Nekrasova, Ryabinkov, 1978
	6-7				Generalized data	Chepik, 1981
	6-7				Generalized data	Ouden, Boom, 1978
	7-8	6-7		10,5	Generalized data	Kapper, 1954

The sample mean sizes equivalent to diameters calculated using equations (Equations 1, 2) and the mean seed weight are given in Table 5.

Table 5.

Average morphometric parameters of seeds, considered tree species

Species	Length, $\bar{L}$ , mm	Width, $\bar{W}$ , mm	Thickness, $\bar{T}$ , mm	Equivalent diameter, $d$ , mm	Weight, $\bar{m}$ , mg
Aspen	1,1	0,5	0,3	0,5	0,11
Birch	1,9	1,1	-	1,5	0,18
Spruce	3,9	1,9	1,5	2,2	5,03
Pine	3,9	2,2	-	2,9	5,31
Fir	6,6	5,3	-	5,9	9,52

The mean critical flow velocity,  $V_c$ , (Equation 3), at which seed movement begins, and the maximum soil layer depth,  $h$ , (Equation 4), at which seed germination still occurs, are given in Table 6.

Table 6.

Habitat parameters affecting the development of tree species at the seed stage.

Species	Habitat parameters	
Aspen	Critical velocity, $V_c$ , $m \cdot c^{-1}$	Maximum depth, $h$ , mm
Birch	0,8	13,0
Spruce	1,4	15,3
Pine	1,7	46,8
Fir	2,0	47,7
Species	2,8	57,9

Comparison of average equivalent diameters and masses of seeds of the considered rocks, as well as critical parameters of the habitat, shows that Siberian fir seeds are larger in size and have a larger mass than seeds of other compared species. This means that they are more resistant to being washed away from the soil surface and can also germinate through thicker sediments. This gives fir an advantage when settling landscapes that are subject to periodic water flow.

The effect of water flow is not constant and is periodic. Obviously, if the timing and duration of such phases of seasonal plant development as the onset of seed, mass seed dispersal and end of seed dispersal will be different from the timing and duration of spring and autumn floods, the plant will be less exposed to water flow or can completely avoid its influence. Such plant will have the advantage of colonizing landscapes that are characterised by periodic water flow. By comparing the dates of these phenological phases for different species and the dates of floods, species less affected by water flow can be identified.

Table 7 shows data on the duration and timing of the phenological phase of seed dispersal of major forest-forming species of the Komi Republic.

Table 7.

Average deadlines of seed dispersal of the main forest-forming species of the Komi Republic.

Species	Birch	Spruce	Aspen	Fir	Pine	Information resource
Seed departure time, month	VIII	II-III	V-VI	IX- X	IV-VI	Sinadskij, 1973; Sukachev, 1928; Krylov et al., 1986; Kapper, 1954; Fomina, 2016;

Comparison of the timing and duration of seed dispersal with the graphs of average monthly water flow in the Vym and Luza Rivers (Fig. 3), as well as average monthly precipitation in the sites where the investigated forest stands are located (Fig. 4), shows that the timing and duration of seed dispatches of such species as pine, spruce and aspen coincide with the timing of spring flooding, i.e., with the period of the highest water flow intensity on slopes and floodplain terraces. In this situation, the likelihood of seeds fixation is low. Fir and birch are in a more advantageous position, the seed dispersal of these species coincides with the beginning of the autumn flood due to seasonal increase in precipitation. The intensity of hydrological events during this period, in comparison with the spring flood, is lower, therefore, the probability of fir and birch seeds fixation is higher. Taking into account the higher resistance of fir seeds to water flow and the ability of birch seeds to remain buoyant for a long time, when settling free areas fir trees have an advantage not only in relation to spruce, pine and aspen, but also in relation to the birch.

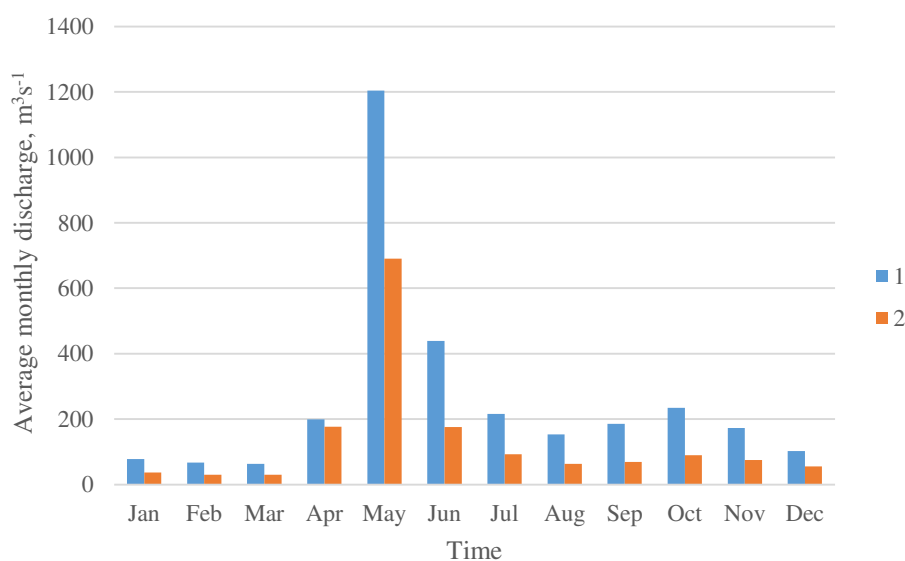


Fig. 3. Average monthly water flow: 1 –Vym River; 2 – Luza River.

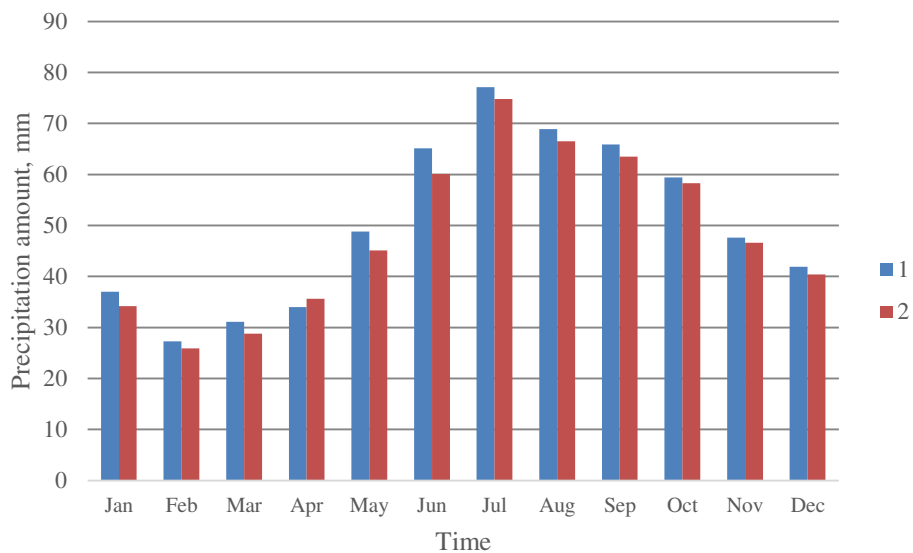


Fig. 4. Average monthly precipitation: 1 – Knyazhpogostskiy administrative district; 2 – Priluzskiy administrative district.

Summarizing the results, we can say that morphological features of Siberian fir seeds (seed size and weight) allow them to withstand the impact (washout from the soil surface and buried by sediments) of more intense water flows than seeds of other forest-forming woody species of the Komi Republic. In addition, the fir seed dispersal phase shift relative to the spring flood date allows it to avoid the most unfavorable period in terms of seed fixation and germination. Thus, with all other conditions being equal, the revealed features of the fir provide it with an advantage in the colonization of slope and riverside landscapes.

## Conclusion

By the example of two floodplain forest phytocoenoses of the boreal zone of the Komi Republic, in which the fir is the dominant species in the stand, it is shown, that at the similarity of climatic and edaphic parameters, the main factor determining the structure of plant communities is the relief, causing the presence of periodic water flow. Plant seeds, as well as soil particles, are included in the processes of transport and sedimentation caused by water flow, which is crucial for seed establishment and germination. The study showed that wood species adapted to the influence of water erosion have an advantage when colonizing free areas of slopes and floodplain terraces. Properties that lead to adaptation to the impact of water flow are large size and weight of seeds, low buoyancy of seeds, and asynchrony of the dispersal phase in relation to the most intensive phases of water flow. Fir, due to its morphological and phenological features, is better adapted to the negative effects of water erosion. Dispersal time,



size and weight of seeds are attributes of Siberian fir, providing it with better adaptation to specific forest conditions of slopes and floodplain terraces.

It should be noted that the adaptation of fir to the phases of water flow occurrence has a negative impact on the inhabitation of plain landscapes, where the effect of water erosion is negligible and the role of such factors as soil temperature and humidity increases. The reverse side of late fir seed dispersal is the shortening of the period of favourable germination, which reduces the competitiveness of fir.

Thus, the dominance of Siberian fir growing in the forest phytocoenoses of the riparian zone of rivers and streams is a consequence of a complex of morphological and phenological features of this coniferous species.

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# Figures

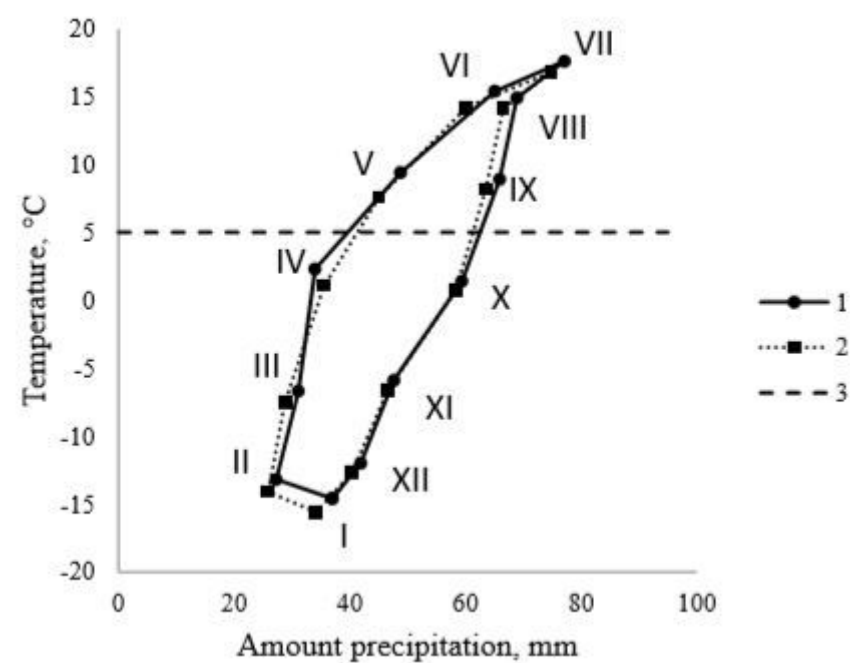


Figure 1

Climagrams of the PSPs regions: 1 - Priluzskiy administrative district; 2 - Knyazhpogostskiy administrative district; 3 - vegetation threshold +5 °C; I, ..., XII - months.

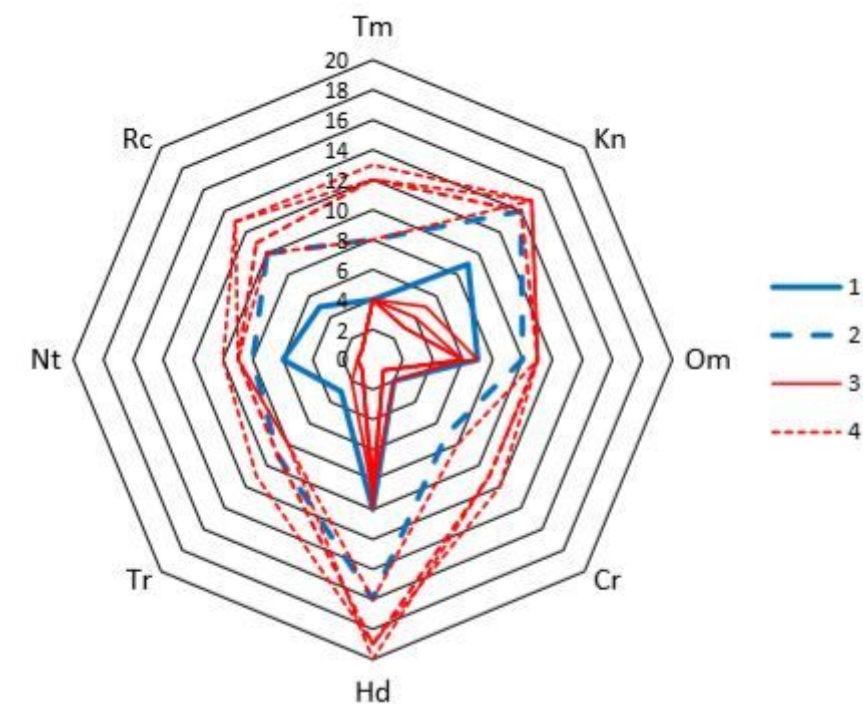
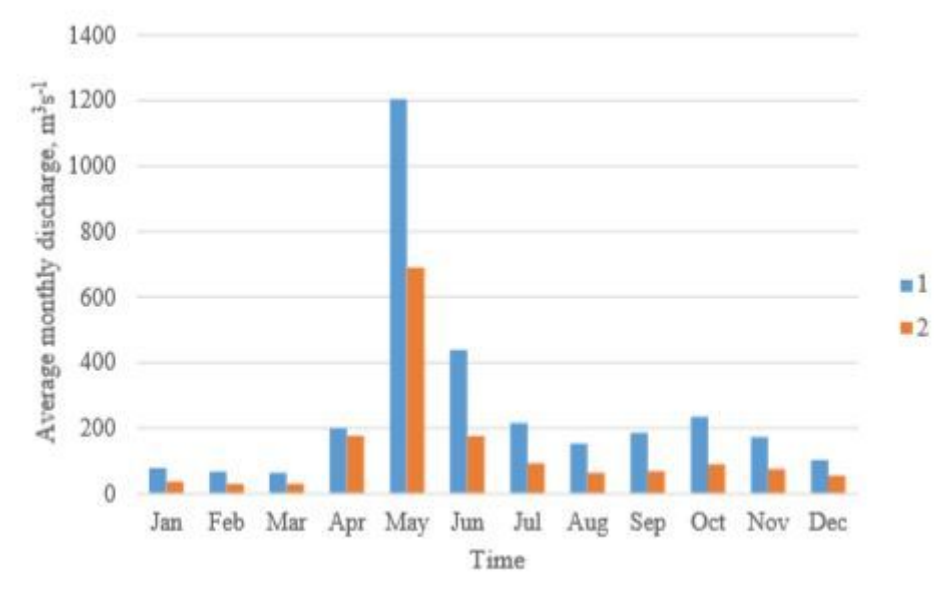
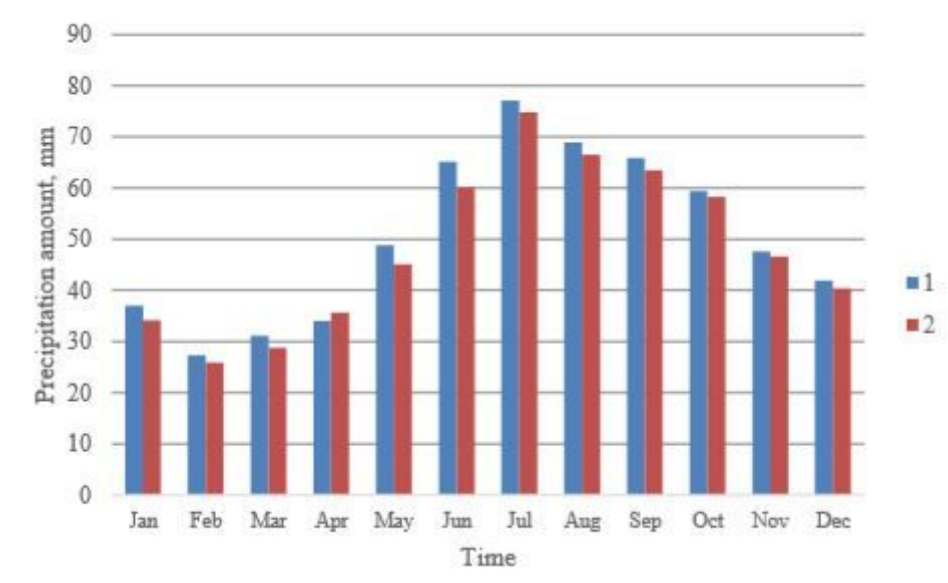


Figure 2

Comparative characteristics of the ecological space of the woody species under consideration. 1 – lower boundary of fir ecological space; 2 – upper boundary of fir ecological space; 3 – lower boundaries of ecological space of other species; 4 – upper boundaries of ecological space of other species. Tsyganov's ecological scales: Tm – thermoclimatic, Kn – continental climate, Om – ombroclimatic aridity-humidity, Cr – cryoclimatic, Hd – soil moisture, Tr – salt regime of soils, Nt – riches of soils with nitrogen, Rc – acidity soil.



**Figure 3**  
Average monthly water flow: 1 –Vym River; 2 – Luza River.



**Figure 4**  
Average monthly precipitation: 1 – Knyazhpogostskiy administrative district; 2 – Priluzskiy administrative district.