

Dynamics of *Pinus sylvestris* L. population structure and regeneration characteristics in coniferous broadleaf forests of the Middle Volga Region (Republic of Tatarstan, Russia)

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Abstract. *Pinus sylvestris* L. in the Middle Volga region is found in the boreal ecotone in areas of coniferous-broadleaved forests located on the southern border of the forest zone. The assessment of abundance and age structure c 2004-2023 reflects the fluctuating dynamics of the species on the territory of the Volzhsko-Kamsky Reserve, where anthropogenic factors are minimized and the effects of climatic and abiotic factors are revealed. In general, a positive number growth is noted for 20 years. According to the results of determination of abiotic conditions of sites of regeneration niches we found out that *P. sylvestris* regeneration is mainly carried out in conditions of open “windows” of canopy or on the top of windfall-soil microsites, very rarely in gaps with some shading by crowns. According to the results of the assessment of the undergrowth number dynamics in 2022-2023, drying of seedlings and juvenile individuals from May to October was noted, where the percentage of surviving *P. sylvestris* in 2022 was 86%, in 2023 – 34%. The relationship between the number of pregenerative individuals of *P. sylvestris* and climatic factors from 2004 to 2022 was determined, a positive dependence on the average temperature of the period May-September (0.69) and December-April (0.62) of the current year was revealed. Negative dependence of the undergrowth number with the sum of precipitation of May-September of the current year (-0.8) and, on the contrary, positive dependence with the sum of precipitation of the previous year (0.68) was noted.

1 Introduction

Actual tasks of forest phytocenology, rational use and monitoring of forest ecosystems in the context of climate change should be based on the functional-structural assessment of forest-forming tree populations. Coniferous-broadleaved forests, where *Pinus sylvestris* L. and *Picea fennica* (Regel) Kom. are the habitat-formers in the Republic of Tatarstan (RT), are located on the southern border of their area, therefore, along with constant anthropogenic pressure, they are affected by climatic factors. Periodically occurring in temperate continental climate dry and hot summer seasons (2009-2010; 2016; 2018; 2023),

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windfalls (2007), as well as infestation of forest areas by bark beetle and bark beetle (2011-2013) often lead to desiccation or reduction of *P. sylvestris* and *P. fennica* viability.

According to the Forest Plan of the Republic of Tatarstan (RT) (2018), the distribution of forest area by tree species groups is as follows: coniferous - 27.1%, hard-wooded broadleaved - 12.3%, soft-wooded broadleaved - 60.6%. The area of coniferous plantations on the territory of RT decreased by 0.2%, which is due to the drying of coniferous forests as a result of the drought of 2010 and the subsequent infestation of trees by parasites.

Purpose of the study: to assess the dynamics of abundance and population structure of *P. sylvestris* in formations of coniferous-broadleaved forests of the Raifa section of the Volzhsko-Kamsky State Natural Biosphere Reserve and to identify the influence of climatic and abiotic factors on the dynamics of *P. sylvestris* regeneration. The research was conducted from 2004 to 2023.

2 Materials and methods

The Raifa section of the Volga-Kama Reserve is located within the Raifa lowland, which is based on the lowered and eroded section of the fourth supra-floodplain terrace of the Volga River, resulting in a special microclimate. The small territory of Raifa combines all the main formations of three forest zones – southern taiga, coniferous-broad-leaved and broad-leaved forests. The study sites are located in the valley of the Serbulak River, on sandy loam soils. The objects of study are coniferous-broadleaved forests and populations of forest-forming trees *P. sylvestris* and *P. fennica*. It was found that *P. sylvestris* and *P. fennica*, which are close in transpiration intensity, differ: pine is 2 times more economical in transpiring moisture than spruce, which has a dense and large crown. Moisture requirements of pine and spruce are almost the same, but they sharply differ from each other: pine, due to its deeply branched root system, is unpretentious to moisture, while spruce is dependent, due to shallow rooting.

Dendrochronological analysis of *P. sylvestris*, conducted in the reserve Q. 25 in the blueberry-mossy pine forest with spruce, showed that the age of some trees dated 1790-1800. In green-moss pine forests with spruce in the Reserve Q. 52/42 according to the dendrochronological analysis in 2012, the age of some large specimens of pines dated 1817-1830, about 170-180 years – mature and old generative individuals. Dendrochronological analysis of the age structure of *P. fennica* population showed that the first generation of generative individuals is represented by trees dated 1817-1830 (old generative individuals), the second generation is 1863-1869 and the third generation is 1894-1898 (mature generative individuals), the fourth generation is 1967-1972 (young generative individuals).

To assess the influence of various factors on the population dynamics of *P. sylvestris*, 50x50 m forest plots were mapped. The material of the Tree Population Database collected by Fardeeva M.B., Islamova G.R. (2004-2012), supplemented by Ibragimova A.F., Abutalipov A.M. (2014-2018) and Fardeeva M.B., Islamova G.R., Tokarev S.A. (2022-2023) was used. During the study 3 phytocenoses were described: pine forest with spruce lingonberry-huckleberry-green-moss (sample area (SA) 8, N55.893056, E48.754722), spruce forest with pine huckleberry-lingonberry-mossy (SA 9, N55.893583, E48.755167) and pine forest with lingonberry-reed (artificial planting of pine in 1950) (SA 10, N55.896570, E48.738470). Phytocenoses were described according to generally accepted geobotanical methods, the stand formula, crown closure, general composition of tree species, their number and age structure were determined.

Within the established areas 13 plots of active reforestation (regeneration niches) were identified, where abiotic conditions were determined: illumination in lx, air temperature in °C, air humidity in %. Numbers of seedlings, juvenile and immature individuals were

evaluated in May and October (2016-2017 and 2022-2023) to assess the nature of growth patterns over the growing season. Based on the dynamics of precipitation sum and average temperatures (year, May-September, December-April) from 2004 to 2022, the correlation of tree growth with weather conditions was determined.

3 Results

Based on the distribution of tree species by ecosystem layers, according to the method of O.V. Smirnova (1990), it is possible to determine the age structure of populations. Along with conifers, deciduous trees were also noted: *Betula pendula* – singly in the stand layer, *Tilia cordata* – mainly in the undergrowth layer, singly in the stand. The first stand layer (A) included trees 20-28 m height (A1) – mature and old generative *P. sylvestris* and *P. fennica*, 10-18 m (A2) – their young generative individuals. The undergrowth and understory layer (B) included trees 4-8 m – virginial individuals (B1), immature (im2) and young virginial from 1 to 3 m included in the layer (B2) – predominantly *P. fennica*. The grass and moss layer (C) included immature (im1) plants 0.4-0.7m (C1), and seedlings and juvenile individuals 0.05-0.3m (C2) of conifers. Accordingly, if trees are found in all layers, we can speak about a complete (with all ontogenetic groups) tree population structure.

An important aspect in the fluctuations of *P. sylvestris* abundance is climatic factors, especially the catastrophic drought of 2010. The trees weakened after the drought were affected by bark beetle in 2011-2013, so some trees fell out of the stand, mainly *P. fennica*. Figure 1 shows the dynamics of abundance and age structure of *P. sylvestris* in the studied phytocenoses.

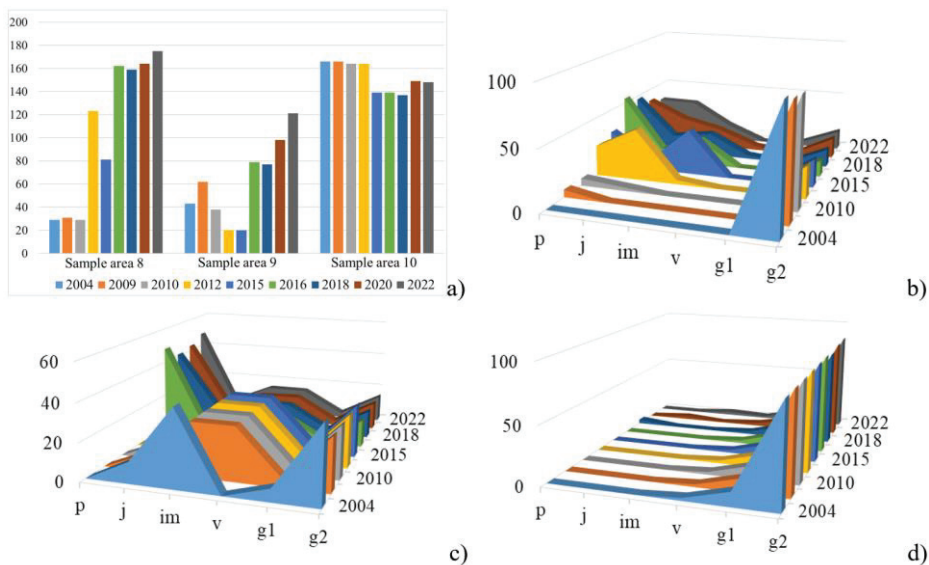


Fig. 1. Abundance dynamics of *P. sylvestris* (a) and age structure dynamics of *P. sylvestris* in different phytocenoses – sample area 8 (b), sample area 9 (c), sample area 10 (d).

The population dynamics of *P. sylvestris* for 2004-2022 shows an increase in the number of trees in natural spruce-pine communities: in SA 8 from 59 individuals (0.02 ind/m²) to 165 individuals (0.07 ind/m²), in SA 9 – from 37 (0.01 ind/m²) to 94 individuals (0.04 ind/m²) due to intensive development of undergrowth. On the contrary, in the conditions of artificial pine planting (SA 10) there was a decrease in the number of pine

trees during the same periods from 160 in 2004-2009 (0.065 ind/m²) to 143 in 2022 (0.05 ind/m²) individuals, which was caused by the loss of adult trees and disturbance of pine regeneration due to fragmentation of moss cover (5-20%) and growth of forest meadow grasses.

After the drought (2010), an increase in the number of *P. sylvestris* at the expense of undergrowth (p – seedlings; j – juvenile; im – immature individuals) is noted already from 2012 in the green-moss pine forest with spruce (SA 8), located in the depression to the sphagnum swamp. With the landscape elevation in the spruce-pine mossy forest (SA 9), the number of *P. sylvestris*, due to the loss of weakened trees, decreased until 2015, and in the artificial pine plantation (SA 10) – until 2018. Only since 2020, the number of *P. sylvestris* increases at all sites with positive increase of undergrowth up to 2023, which is reflected in the age spectra of *P. sylvestris* populations in natural forests (SA 8 and SA 9) and artificial planting (SA 10).

To assess the dependence of the dynamics of *Pinus sylvestris* undergrowth number with the dynamics of weather conditions, climatic factors of the current and previous year were used. Due to the fact that the number of adult trees (generative individuals) is relatively less affected by external factors, we estimated the relationship of the pregenerative groups number (p – seedlings, j – juvenile, im – immature and v – virgin individuals) with climatic characteristics (average temperature and precipitation amount) using Pearson's correlation coefficient (Table 1; Figure 2).

Table 1. Relationship of *P. sylvestris* number with climatic factors of the current and previous year.

Climatic factors	Current year number for period		
	Year	May-September	December-April
Precipitation amount, mm current year	0.58	-0.8	-0.3
Average temperature, °C current year	-0.23	0.69	0.62
Precipitation amount, mm previous year	-0.09	0.68	0.35
Average temperature, °C previous year	0.03	0.06	-0.15

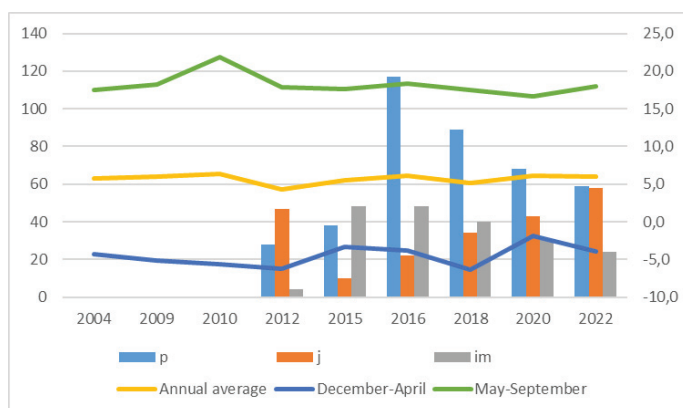


Fig. 2. Changes in *P. sylvestris* undergrowth (p, j, im) number and average temperature dynamics (2004-2022).

The above data (Table 1) indicate a direct dependence of *P. sylvestris* pregenerative individuals on the average temperature during the vegetation period (0.69) and in winter (0.62), when pine seedlings are in a latent state. This is due to the ecological requirements of pine as the most light-demanding and rather drought-tolerant tree species. There is a

negative dependence of the number (especially seedlings) on the amount of precipitation in the current vegetation period (-0.8), which is due to the large projective cover of mosses that retain moisture and, with increasing precipitation, reduce soil aeration, but contribute to the germination of conifer seeds. To a greater extent, the number of *P. sylvestris* undergrowth and their renewal waves are positively affected by the sum of precipitation for the whole current year (0.58) and for the vegetation season of the previous year (0.68), which ensures further development of juvenile and immature individuals.

Despite the positive dynamics of undergrowth number in the long-term dynamics of 2004-2022 (Figure 2), we observed drying of seedlings, juvenile and immature individuals of *P. sylvestris* during the growing season (from May to September) both in 2022 and 2023. The percentage of surviving individuals of *P. sylvestris* in 2022 was 86%, and in 2023 only 34%. The decrease in the number of pre-generative individuals may be related to the climatic factors (early dry spring and hot dry summer), as well as activity of wild boars on the territory of the studied phytocenoses. To make sure of this, we conducted a correlation analysis of the relationship between the number of pregenerative individuals and weather conditions from May to September in 2022-2023 (Table 2).

Table 2. Climatic factors and *P. sylvestris* pregenerative individuals' number relationship (2022-2023 vegetation period).

Climatic factors	Sample area 8 2022	Sample area 9 2022	Sample area 8 2023	Sample area 9 2023
Average temperature, °C	-0.63	-0.66	0.16	0.1
Precipitation amount, mm	0.23	0.27	0.51	0.53

For the vegetation period of 2022, a negative correlation of the number of *P. sylvestris* pregenerative individuals with average monthly temperatures was recorded, and no correlation with the amount of precipitation was revealed. The decrease in the number of pregenerative individuals of *P. sylvestris* in 2023 is significant, which may be due to the spring frost (2.05-9.05.2023), and insufficient summer precipitation.

Table 3. Abiotic factors under the forest canopy and at canopy gaps affecting *P. sylvestris* and *P. fennica* regeneration (2022-2023 vegetation period).

SA	Moss projective cover	Location	Light intensity, lx	Temperature, °C	Humidity, %	<i>P. sylvestris</i>	<i>P. fennica</i>
8	70%	Canopy	5308 - 8000	17.9 - 30	20 - 28	<u>3p 7j 4im</u> 6j 5im	<u>65p 21j 2im</u> 3j 2im
		Gap	27667 - 37597	19.5 - 31	22 - 30	<u>77p 45j 16im</u> 30j 14im	<u>21p 56j 8j</u> 52j 7im
9	80%	Canopy	4184 - 4767	18.3 - 30	26 - 28	<u>5p</u> -	<u>7p 13j 5im</u> 3p 9j 14im
		Gap	25655 - 35000	19.4 - 30	22 - 24	<u>17p</u> -	<u>6p 1j 17im</u> 7j 17im
10	10%	Canopy	1008 - 1970	16.8 - 23	22 - 32	- 1j 2im	<u>5i 1im</u> 2im
		Gap	30433 - 52620	20 - 24	16 - 20	- -	<u>3p 1j 1im</u> 1im

Measurements of abiotic factors in the regeneration niches at the three SA were made to determine the most suitable conditions for *P. sylvestris* and *P. fennica* regeneration (Table 3). The table presents the sum of the pre-generative individuals of *P. sylvestris* and *P. fennica* across all identified regeneration niches. Measurements were taken in 2022 and 2023 at May 25 noon.

4 Discussion

Analyzing the age structure, it should be noted that in natural spruce-pine and pine-spruce mossy forests (SA 8 and 9) *P. sylvestris* populations have a tendency to form a complete population structure due to intensive development of undergrowth. On the contrary, in forest plantation the population of *P. sylvestris* is incomplete, adult and young generative individuals prevail (86% and 10%, respectively), and pine undergrowth is found sporadically.

The development of *P. sylvestris* seedlings, as a light-demanding species, is influenced by the presence of open “light” windows and gaps that appeared after the drought, as a result of the loss of young or weakened large *P. fennica*. Persistently high spring and summer temperatures (summer 2009, 2010; spring 2011, 2016 and 2023) may have also influenced. However, pine seedlings both renewed well and dried out rather quickly, or were dug up by wild boars. Development of tree undergrowth in the study plots was also observed on the fallen old trees – windfall-soil microsite, along or on fallen trunks (Figure 3). For example, at the very top of the windthrow-soil microsite (Figure 3, b), seedlings and juvenile *P. sylvestris* predominate, and along the slope surface and at the bottom of the windthrow-soil microsite, seedlings of *P. fennica* predominate.



Fig. 3. Light “window” (a) and windfall-soil microsite (b), in a pine forest with mossy spruce on sandy loam (SA 8).

In general, the revealed patterns of development of *P. sylvestris* undergrowth in certain areas, according to the theory of “forest growth cycle” or “gap theory” are observed in the gaps in the forest canopy – “windows”. In our study plots, the size of “windows” varied from 5 to 30 m². According to Marthews et al. (2008), window formation changes the structure of the plantation by creating an open space in the canopy that allows light of varying intensity to pass through, depending on the size of the break, shape and height of the trees surrounding the “window”. In general, the data on abiotic factors in the “windows” where juvenile *P. sylvestris* is more often observed correspond to the data collected in 2016 at the renewal sites in the phytocenoses under study. According to the comments, entering light influences microenvironmental factors such as soil moisture and nutrition, and tree regeneration processes. On the contrary, *P. fennica* is more frequently observed along gaps where partially the regeneration site is under the canopy of surrounding trees. According to normal development of seedlings and successful growth of forest-forming species of coniferous forests *P. sylvestris* and *P. fennica* require good illumination with soft shading. Exactly such conditions are created inside crown gaps or windfall-soil microsite, the combination of which can be called a regeneration niche within a forest ecosystem.

In the age structure of *P. sylvestris* and *P. fennica* populations in plots of natural spruce-pine mossy forests (SA 8 and SA 9), the proportion of pre-generative individuals increases.

In these communities, the greatest number of regeneration niches (11 from 13) confined to light windows was detected. Comparing phytocenoses SA 8 and SA 9, it is worth noting that in the first community the regeneration of pine and spruce is more active – 248 pregenerative individuals were found in 6 regeneration sites. In SA 9, 140 individuals were found in 5 regeneration plots. This is due to the favorable location of pine forests with spruce in the ecotone conditions, at the border of forest and sphagnum sylvina.

5 Conclusions

At the Raifa site of the Volzhsko-Kamsky Reserve in coniferous-broadleaved forests, small-scale fluctuations caused by abiotic, biotic and climatic factors have been observed in the dynamics of *P. sylvestris* number for almost 20 years. Positive growth of seedlings, juvenile and immature plants has been observed since 2012. According to the results of evaluation of growths for the vegetation period 2022-23, drying of seedlings during the summer was revealed, which is caused by climatic factors of the summer season and confirmed by correlation analysis.

The catastrophic drought (2010) and the subsequent irruption of bark beetles led to weakening, drying and loss of dominant positions of *P. fennica* in coniferous-broadleaved forests of the Reserve. Such exogenous spontaneous succession in coniferous-broadleaved forests led to restoration of *Pinus sylvestris* position and formation of its complete age structure in light green-moss pine forests in low relief areas and dry pine forests of reed-moss on elevated relief areas. This is also due to the character of sandy loam soils – poor water-holding capacity, poor mineral composition, which in valley complexes of large rivers contribute to the stability of *Pinus sylvestris*. *P. fennica* is much inferior to pine in sensitivity to the complex of similar environmental factors.

However, under conditions of artificial planting the renewal of *P. sylvestris* as well as *P. fennica* is reduced due to fragmentation and low projective cover of moss – 5-10% and overgrowth of *Calamagrostis epigeios* and forest-meadow grasses.

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