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Influence of the Biological and Chemical Structure of Spruce Wood on Xylophage Infestation

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Abstract

The process of forest death covers the entire boreal zone of the Northern Hemisphere. Due to the deterioration of the sanitary condition of forest areas, harmful organisms are becoming more active, where the most dangerous pest is *Ips typographus*. The aim of the work was to study the chemical structure of spruce wood in samples of various living conditions in the zones of active reproduction of bark beetles.The research studies the biochemical composition of *Píceao bovata* wood within the places of *Ips typographus* development (bythe example of the Udmurt Republic). The research was carried out within the European part of the Russian Federation, the Udmurt Republic region. The republic area is 42 thousand km2. A total of 15 sample plots were laid out and more than 8,000 trees were analyzed. It was revealed that in the subtaiga zone, the processes of death of spruce stands are observed.

Keywords: Biochemical composition, Ips typographus, subtaiga zone, deterioration of the sanitary condition.

1. INTRODUCTIONAND OBJECTIVES

Since the beginning of the 21st century, humanity has faced a period of active changes in climate factors, which led to the weakening of forest stands. Due to the imperfection of the conducting system and physiological and biochemical parameters, gymnosperms that dominate the boreal zone began to suffer to a large extent. Spruce stands having a lateral root system and most affected by the instability of precipitation are considered a particular case. The weakening of the plant defense mechanisms contributes to the distribution of pathogenic organisms (Leontovyc et al., 2006; Černý et al., 2016; Caudullo et al., 2016). Undoubtedly, these processes are associated with human activities and the globalization of the world economy (Magney et al., 2019; Movchan et al., 2021a,b).

Despite the huge variety of pathogenic organisms that consider spruce as an object for the attack, xylophagous from the bark beetle group have a special place. Weakened trees are most commonly inhabited by the *Polygraphus polygraphus*, *Ips typographus and Pityogenes chalcographus* species. Only the eight-toothed engraver beetle received special attention as the most dangerous bark beetle in Eurasia. The danger of this pest is related to its high fecundity (106–162 eggs/female) and gluttony (Dippel et al., 1997; Weslien & Regnander, 1992).

Due to the wide ecological amplitude and extensive food supply, the eight-toothed engraver beetle, under the conditions of climate warming, began to actively spread to the north of the European continent and generate outbreaks of mass reproduction in its natural habitat (Maslov, 2010). One of the most aggressive symbiotic relationships is formed between *Ips typographus* and *Ophiostoma polonicum* Siemaszko (Furniss et al., 1990)

Outbreaks of mass bark beetles lead to significant economic and environmental losses (Viiri & Lieutier, 2004; Faccoli et al., 2008; Nikulin et al., 2021; Elveny et al., 2021). For example, in North-Eastern France, damage from eight-toothed engraver beetles reached more than 100,000 m3 of damaged wood per year (Viiri&Lieutier, 2004). Outbreaks of mass reproduction have also been recorded in the Southern Alps of Italy, where annual monitoring of damage caused by *I. typographus* is recorded (Faccoli & Stergulc, 2008).

Large losses in the forest economy are also observed in the North of Europe (Sweden). According to official data, losses from the eight-toothed engraver beetle distribution exceeded losses from forest fires (Starn, 2019).The globalization led to an increase in the number of cases of bark beetle interception in United States seaports. As a result, bark beetle species such as *Ips typographus* and *Ips sexdentatus* were found (Zink et al., 2019).

In Central Russia, the last major reproduction outbreak of the eight-toothed engraver beetle began in 2010 as a result of a drought that affected the entire European part of Russia. In 2011 and 2012, the scale of the bark beetle population became threatening. As a result, some places began to deplete the food supply, which led to migration behavior and even the transition to another food species – pine (*Pinus silvestris*) (Maslov, 2014). In Central Europe, the mass death of common pine from bark beetles is a relatively new phenomenon for forest users and officials (Kunert, 2020).

Despite the obvious correlation interactions between spruce and the eight-toothed engraver beetle, the physiological component of the affected plant has not been fully studied. In this regard, the work objective was to study the chemical structure of spruce wood in samples of different life states in the areas of active reproduction of bark beetles.

2. MATERIALS AND METHODS

2.1. Study area

The research was conducted in the territory of the Udmurt Republic; the area of the Republic 42.06 thousand km^2. Udmurtia is located in the European part of the Russian Federation. The territory of Udmurtia is located within two landscape zones: the taiga (boreal) and sub-taiga (boreal-sub-boreal) zones. Udmurtia is a forest region, where the forest area is 46.2% of the republic area, the dominant plantations are spruce forests stands for 35.2% of all forest area (Geography of Udmurtia, 2009; Forest plan of the Udmurt Republic, 2018; Geography of Udmurtia, 2009; Forest Plan of the UR, 2018) (Figure 1).

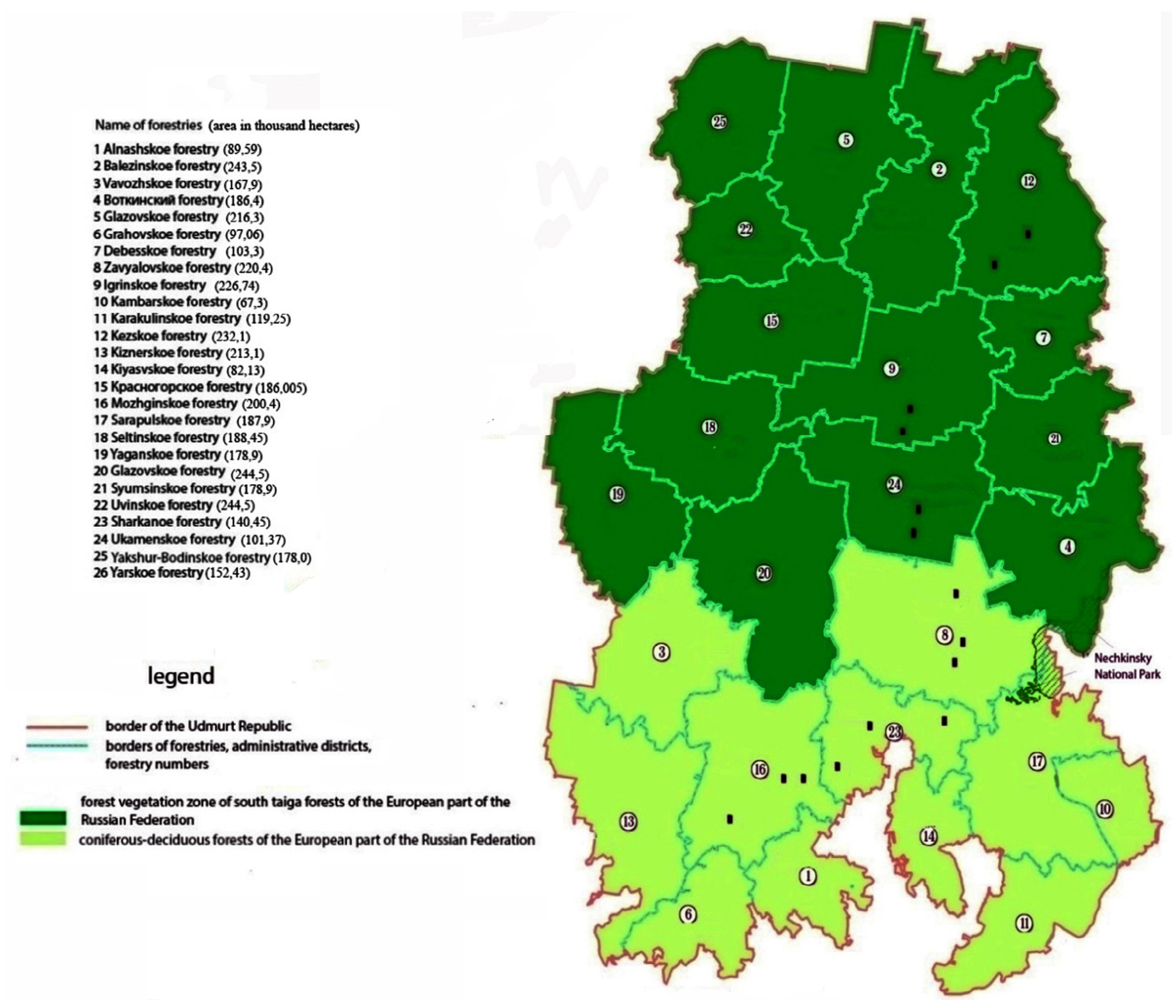

Figure 1. Schematic map of the location of sample plots in the territory of the Udmurt Republic.

One of the most aggressive bark beetles of Udmurtia is *Ips typographus* L (Figure 2).

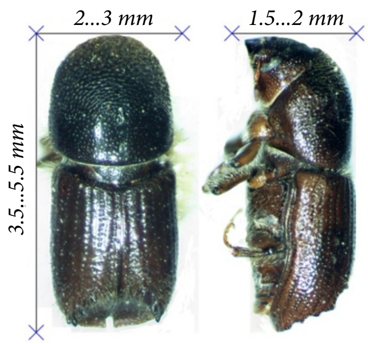

Figure 2. Ips typographus characteristics.

2.2. Sample selection

To estimate the taxation parameters and the state of spruce stands, the sample plots (hereinafter – SPs) with a size of 100×100 m were laid. The selection of places for SPs was made by studying fundamental materials (forest management materials). The total number of SPs was 15, including 9 – in the sub-taiga (in the zone of spruce mass drying) zone and 6 – in the taiga zone, in stands with a predominance of spruce, in the most productive types of forest – wood sorrel spruce forest.

To determine the main quantitative and qualitative indicators of stands, the enumerative method of taxation was used. In the process of enumerative assessment of the forest stand, the diameter of each tree and the sanitary states were measured. According to the results of the field study stage, 6009 trees were measured. The tree state was determined by external morphological signs under the scale of tree state categories recommended by the Decree of the Government of Russia No. 2047 (On the Approval of the Sanitary Safety Rules in Forests, Decree of the Government of the Russian Federation of December 9, 2020 No. 2047): 1 – healthy (no signs of weakening); 2 – weakened; 3 – severely weakened; 4 – drying; 5 – recently dead trees; 6 – long-dead trees. Then the weighted average score of the stand sanitary state was determined by the Equation 1.

$$\mathrm{Kaver} = (\mathrm{P1} \times \mathrm{K1} + \mathrm{P2} \times \mathrm{K2} + \cdots \mathrm{Pn} \times \mathrm{Kn})/100 \quad (1)$$

where Kaver – the weighted average score of the sanitary state of the species; Pi – proportion of spruce timber resources in each category of state, %; Ki – index of the tree state category (1 – healthy, 2 – weakened, 3 – severely weakened, 4 – dying trees, 5 – recently and long-dead trees).

Based on the resulting weighted average category of the sanitary state, forest stands are distributed under the scale for determining the forest stand sanitary state presented below: 1-1.5 – forest stands without signs of weakening; 1.51-2.5 – weakened forest stands; 2.51-3.5 – strongly weakened forest stands; 3.51-4.5 – drying forest stands; more than 4.5 – dead forest stands.

The diameter of the trees was determined using a diameter gauge, the age – by counting the annual rings on the cores selected using the age drill Haglof 350 mm (Sweden), the height – using the hypsometer Forestry Pro Nikon (China). The taxation parameters of the stands (average diameter, average height, average age, basal area, composition, and yield class) were determined by recalculation methods. The average diameter was determined as the arithmetic mean index of all individuals, by tree species. Forest stand height (H) was determined as an arithmetic means of the height of 10 trees with a trunk diameter at breast height - DBH, equal to the average forest stand diameter. The forest stand age (A) was found by counting tree rings on wood samples taken by an auger from five plants with a stem diameter equal to the average diameter in the forest stand.

The planting density (ΣG) was calculated as the sum of the cross-sectional areas of the trunk at a DBH using the Equation $G = PR^2$, where P = 3.14 (const), R is the radius of the tree trunk. The stand structure was conducted by counting the proportion of the timber resources for each tree species located in the tree layer. The timber resource was determined by the Equation M = ΣGHF (Ushakov, 1997).

The trees were divided into three groups according to their life state: 1) good, 2) satisfactory, 3) unsatisfactory. To study the biochemical characteristics of spruce wood, three samples were selected in each group.

2.3. Data collection

Wood samples were taken from plants of various life states in the autumn period (October 2018–2020) at a height of 0.3 m from the base of the tree.The extractive substances were extracted according to their chemical nature by sequential extraction with various solvents (Fedorova et al., 2016; Fedorova et al., 2019). To determine the water-soluble materials and tannins in wood samples (≈ 1 g), the moisture in the air-dry and absolutely dry state was preliminarily determined; then the weighed samples were sieved through a sieve with 3 mm mesh size, placed in 250 mL heat-resistant flasks, poured with heated to boiling distilled water (100mL) and boiled at reflux for 1 hour.

A programmable heating mantle EKROS PE-4100 (Russia) was used as a heating device.To determine the tannins, the obtained extract was cooled to room temperature and filtered through a paper filter.

The first 50 mL of the filtrate were discarded, a 2 mL aliquot was taken from the remaining filtrate, and 48 mL of distilled water was added to it. The optical density of the resulting solution was measured with anEKROS PE-5400UF spectrophotometer at 277 nm; distilled water was used as a reference solution (Technical Association of the Pulp and Paper Industry - TAPPI, 1988; Obolenskaya et al., 1991; Antoine et al., 2004). The tannin level (Xt) in the wood sample was calculated by the Equation 2:

$$Xt(\%)=(D \cdot 100 \cdot 50 \cdot 100)/(m \cdot 2{\cdot}508{\cdot}(100-W)) \quad (2)$$

where D – solution optical density;m – weight of the wood sample, g;W – moisture of wood sample,%.

After treatment with distilled water, the wood sample was dried to constant weight in a loss-on-drying oven at a temperature of 103 ± 2 °C; then its weight was determined in bone-dry humidity by analytical balance (0.001 g). The mass of recovered water-soluble compounds was determined by the mass variation method based on the mass difference before and after treatment (Obolenskaya et al., 1991).

Resinous substances were extracted from the wood sample by treatment with ethyl alcohol and toluene mixture (1:2; volume:volume) at the boiling point of the solvent. For this, a wood sample in a paper sleeve was placed into a Soxhlet extractor (the extractor siphon volume was 250 mL) with a reflux condenser installed on it and was treated with a solvent three times. Then the wood sample was dried to constant weight in aloss-on-drying oven at a temperature of 103 ± 2 °C and weighed by the analytical balance (0.001 g) in bone-dry humidity. The content of resinous substances was determined by the mass variation method based on the mass difference before and after treatment (Obolenskaya et al., 1991).

After treatment with an alcohol-toluene (1:2) mixture, the wood sample was placed in a 250-mL heat-resistant flask; 10 mL of H_2SO_4 (72%) was added to it. Thus, the weighted sample was exposed to acid hydrolysis for 2.5 hours at a temperature of 24-25°C. Then, 100 mL of distilled water was added to the sample and the sample was boiled in the resulting solution for 1 hour at reflux at a temperature of 100°C. The resulting extract was filtered through a paper filter; the remaining acid-insoluble lignin was rinsed with distilled water until the sulfuric acid was completely removed and dried in the loss-on-drying oven at 103 ± 2 °Cto constant weight, and weighed by analytical balance (0.001 g) in bone-dry humidity. The acid-insoluble lignin, as well as the recovered polysaccharides, was determined by mass variation method based on the difference in masses before and after treatment (TAPPI, 1988; Obolenskaya et al., 1991; Shebani, 2008).

The wood of samples in unsatisfactory condition was studied for the degree of decomposition by mycodestructors by absorption of 1% sodium hydroxide (NaOH). In this regard, when selecting wood samples from trees of unsatisfactory life state, samples with a high degree of wood destruction and having internal voids in the trunk were selected. The solubility of sodium hydroxide in such wood samples ranged from 12.3% to 16.7% (TAPPI, 1993).

2.4. Data analysis

Statistical processing of the research results was performed using the Statistica 6.0 software package. Nine sample plots were embedded in each natural zone, within which, three *Piceaobovata* trees of good, satisfactory and unsatisfactory vital state were selected for chemical analyses. Thus, wood of 162 trees was studied for total content of extractive substances, content of water-soluble extractive substances, content of tannins, and content of resinous substances. Chemical analyses were carried out in three-fold repetition. The normality of data distribution was determined with3σ rule for normal distribution.The principal component analysis and the variance analysis (ANOVA) (LCD-test multiple comparison method) analysis were used.

3. RESULTS AND DISCUSSION

According to taxation parameters, the test plantations belong to highly productive, middle-aged spruce forests. Plantations in the subtaiga zone are characterized by a low tree density of the main stand, a large number of standing dead trees. The planting taxation parameters in the sample plots are presented in Table 1.

Low density was noted in sample plots laid out in the taiga zone; however, with movement to the north, the plantation density increased. By the number of drying and dead trees, plantations in the south of the republic are characterized as drying (except for the sample plot SP3 of the Mozhginsky forestry), while in the south the sanitary state of plantations is characterized as weakened.

A distinctive feature of sample plots in thesubtaiga zone from the taiga zone was that most of the dead trees had a trunk diameter more than the average diameter of the stand. In the north of the republic, dead trees had a trunk diameter less than the average diameter of the forest stand without traces of xylophagous activity. This indicates natural mortality during which less developed individuals died.

Table 1. The average forest taxation characteristics of trees in sample plots (SPs) (the Udmurt Republic, 2018–2020).

SamplePlot (SP) No.	Forestry	A_{aver}±m, years	H_{aver} ±m, m	$D_{aver.1.3}$±m, cm	ΣG, m²/ha M, m³	Crop health index	Composition Number of trees in the SP (% of drying and dead)
	Subtaigazone						
1	Zavyalovskoe	70 ± 2.3	21 ± 0.6	27.9 ± 0.4	10.7 107.0	3.48	9E1P+B) .260 47.7-
2	Zavyalovskoe	67 ± 3.8	23 ± 0.6	26.0 ± 0.3	11.1 119.9	3.20	9E1P) .324 38.3-
3	Zavyalovskoe,	60 ± 1.8	20 ± 0.8	26.9 ± 0.3	22.0 198.0	2.72	9E1P+Os) .464 25.6-
1	Yaganskoe	60 ± 1.7	18 ± 0.5	25.9 ± 0.8	6.0 52.8	3.14	10E+P) .252 50.8-
2	Yaganskoe	65 ± 1.6	22 ± 0.3	21.4 ± 0.4	2.95 30.7	3.73	10E) .155 56.1-
3	Yaganskoe	60 ± 1.1	18 ± 0.7	20.3 ± 0.2	7.0 61.6	3.71	10E) .155 57.4-
1	Mozhginskoe	60 ± 1.6	23 ± 0.6	25.7 ± 0.5	16.6 178.8	3.54	9E1P+Lp) .383 56.7-
2	Mozhginskoe	50 ± 1.1	20 ± 0.9	22.6 ± 0.3	15.2 145.7	3.10	9E1P) .408 50.2-
3	Mozhginskoe	60 ± 1.5	19 ± 0.5	19.1 ± 0.2	28.8 264.9	2.62	9E1C+B) .456 20.1-
	Taigazone						
1	Yakshur-Bodinskoe	77 ± 1.1	18 ± 0.4	22.2 ± 0.4	10.1 109.12	2.76	7E1P1B1Os) .312 27.9-
2	Yakshur-Bodinskoe	74 ± 1.6	23 ± 0.4	26.8 ± 0.1	17.7 191.2	3.09	9E1Os+P) .441 42.6-
1	Igrinskoe	69 ± 0.7	19 ± 0.9	22.9 ± 0.3	19.8 182.16	1.87	8E2P) .515 13.6-
2	Igrinskoe	70 ± 0.7	19 ± 0.9	23.9 ± 0.2	26.0 239.2	1.92	9E1P) .581 12.6-
1	Kezskoe	65 ± 0.7	22 ± 0.3	21.7 ± 0.3	19.8 222.4	2.42	9E1P) .575 8.7-
2	Kezskoe	76 ± 0.7	24 ± 0.5	22.1 ± 0.4	26.0 242.4	2.44	10E) .596 9.1-

Note: A_{aver}±m: age± standard deviation, H_{aver} ±m: height ± standard deviation, $D_{aver.1.3}$±m: diameter at breast height± standard deviation, ΣG, m²/ha: the basal area taking into account dead trees, M, m³: the stock of dead wood on the SP

Before the biochemical analysis of wood in unsatisfactory condition trees, the samples were checked for destruction by woodboring beetles (ambrosia beetles) by the fact that wood decaying fungus introduced by ambrosia beetles change the quantitative and qualitative state of the wood. The vital activity of these organisms leads to a change in the amount and composition of extractive substances (Kang et al., 2007; Ferraz, 2008; Ateş et al., 2016) and also leads to a change in the wood structural components (lignin, hemicellulose, and cellulose) (Nilsson, 2009).

To avoid the impact of this factor,trees with an unsatisfactory vital state with a high degree of wood destruction (old standing dead trees) and with internal voids in the trunk were rejected. The wood damage level by fungi was tested by boiling the test samples in a 1% sodium hydroxide (NaOH) solution. The sodium hydroxide solubility in wood samples of plants of unsatisfactory condition ranged from 12.3 to 16.7%, which corresponds to wood with minor damage (TAPPI, 1993).

A comparative study of the chemical structure of the wood was carried out using various methods of statistical analysis. As a result of data analysis by the method of principal components, two factors were identified. The first factor positively correlates with the total extractive substances, with the water-soluble group, and with tannins in the wood. The second factor positively correlates with polysaccharides in the wood. Also, according to the method of principal component results, there was a distribution of the tested objects by study areas: I –subtaiga zone, II – taiga zone (Figure 3).

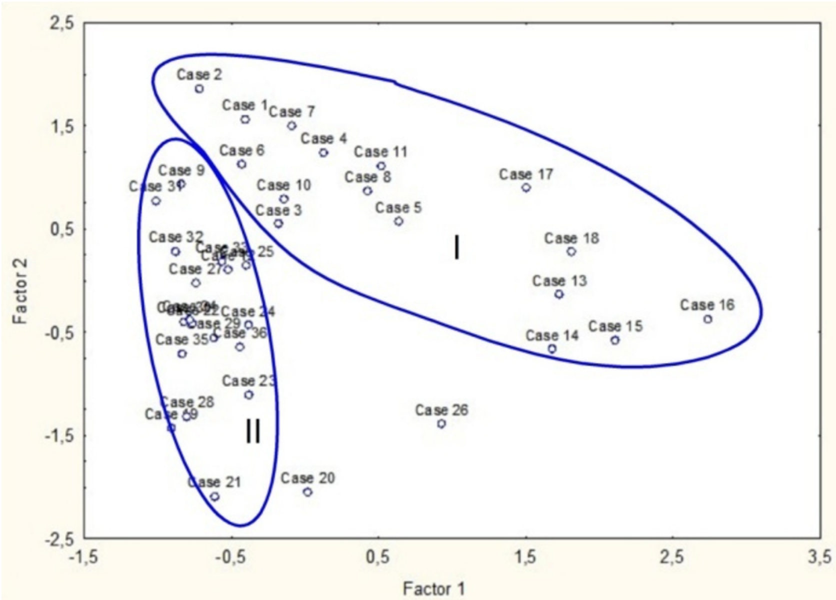

Figure 3. Distribution of the studied objects in the axes of the principal components (I – sub-taiga zone, II – taiga zone, Case 1…36 – studied objects).

For further interpretation of the data obtained, the authors used ANOVA according to a cross-hierarchical scheme, whereas the factors were the sampling point (forestry and sample plot) and the state of plants.The results of ANOVA for the extractives substance in spruce wood growing within the taiga zone (northern part of the republic) did not reveal significant differences in plants of different vital states. Within the subtaiga zone (southern part of the republic), the growth states (forestry and sample plot) and the factor interaction (forestry, sample plot, and plant state) significantly affect the total extractives substances (Table 2).

A graphic representation of the factor interaction based on the ANOVA results is shown in Figure 4. According to the study results, the variation of extractives substances is observed within a wide range. Depending on the forestry, the sample plot, and the plant state, the extractives substances vary from 5.82 to 27.67% of absolutely dry weight**.**

A special pattern is noted in the Mozhginskoye forestry. Regardless of the growing conditions and the vital state of trees, there are no statistically significant differences between plants. In the authors'opinion, this is due to the lack of individual reaction to stimuli. According to the on-site investigation results inthesample plotSP1, the authorsdid not record the presence of a spruce bark beetle, and the death of plants in these stands is associated with natural loss of growing forest. However, in the sample plot (SP2), the authorsidentified a focus of the xylophagous initial development. The dead individuals were 2 to 8 locally located plants with the trunk in which emergence holes of insects were observed.

Table 2. Results of variance analysis on the total content of extractives in Piceaobovata wood.

Factors	df Effect	MS Effect	df Error	MS Error	F	p-level
1*	2	307.51	54	13.66	22.51	0.05
2	2	438.50	54	13.66	32.10	0.05
3	2	8.70	54	13.66	0.64	0.05
12	4	184.41	54	13.66	13.50	0.05
13	4	23.52	54	13.66	1.72	0.05
23	4	41.82	54	13.66	3.06	0.05
123	8	33.19	54	13.66	2.43	0.05

Note: * 1 – forestry; 2 – sample plots, 3 – plant life state, df Effect - the number of degrees of freedom of the effect, MS Effect - the average square of the effect, df Error - the number of degrees of freedom of error, MS Error - Average error square

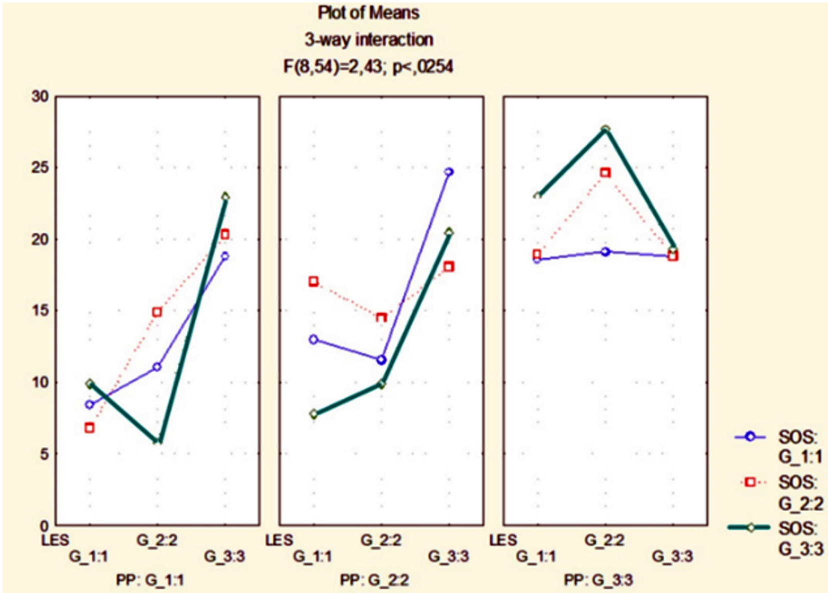

Figure 4. The total content of extractive substances in wood under the interaction of factors (PP G_1:1 – sample plot 1, PPG_2:2 – sample plot 2, PP G_3:3 – sample plot 3; LESG_1:1 – Zavyalovskoe forestry, LESG_2:2 – Yaganskoe forestry, LESG_3:3 – Mozhginskoe forestry; SOSG_1:1 – good state, SOSG_2:2 – satisfactory state, SOSG_3:3 – unsatisfactory state).

Determination of the extractives substance components associated with unfavorable factors makes it possible to understand the functioning of the immune mechanism ina plant organism. As a rule, the substances extracted by hot water are substances incorporated into the cell wall, while resin-like substances are formed in the intercellular space (Taylor et al., 2002).

The analysis of the content of resinous substances in wood revealed that site conditions (natural climatic zone) ($p<0.05$) were a significant factor. In plants growing in the north of the region of interest, the resinous substance level is an order of magnitude higher than in plants growing in the south of the republic. The vital state of plants does not affect the content of resinous substances in wood ($p>0.05$).

The study on water-soluble materials revealed that the growing conditions (forestry and sample plot) and the interaction of factors (state and growing conditions) had a significant effect on this group profile ($p<0.05$). The ANOVA results for the water-soluble extractives in the wood are identical with the ANOVA results for the total extractives substances. Thus, the change in the total extractives substances is associated with changes in the water-soluble group.

Water-soluble extractives are poly- and monosaccharides, pectins, gums, proteins, dyes, cyclic alcohols, and tannins. However, according to research articles, it is tannins that play an important protective role when exposed to negative factors (Schofield et al., 1998; Onuorah, 2001; Fuksman et al., 2005).

According to the research, a significant difference in tannins was revealed depending on the vital state (Figure 5). In plants of good and satisfactory state, tannins levels are significantly higher than in plants of unsatisfactory condition.

A significant difference in tannins in plants growing in different natural zones was revealed. In spruce trees growing in the subtaiga zone, the content of tannins is higher (3.47% to 6.43% of absolutely dry weight depending on the plant state) than in trees growing in the taiga zone (1.2% to 1.89% of absolutely dry weight depending on the plant state).

ANOVA did not reveal statistically significant differences in the content of learning and polysaccharides in the plant cell wall. The content of the structural components of the cell wall varies: lignin from 15.2% to 32.14%and polysaccharides from 47.15% to 66.25% of absolutely dry weight. Perhaps, this is because the profile of these components is more affected by species membership than by environmental factors (Vanholme et al., 2010).

The obtained test results for the wood extractives substances revealed that their total content was affected by the vital state of trees and site conditions. Under the influence of bark beetle, spruce has a quantitative increase in non-structural components of wood.

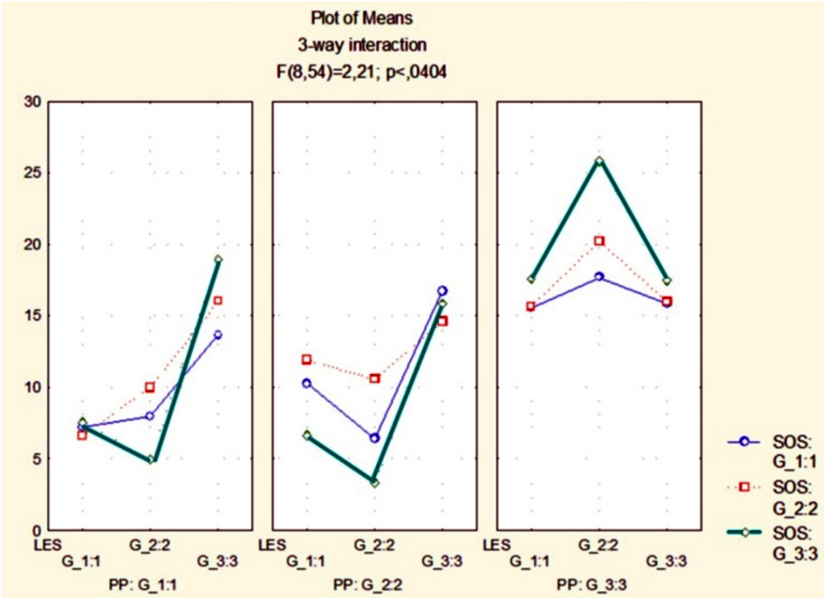

Figure 5. The content of a water-soluble group of extractive substances in wood under the interaction of factors (PP G_1:1 – sample plot 1, PPG_2:2 – sample plot 2, PP G_3:3 – sample plot 3; LESG_1:1 – Zavyalovskoe forestry, LESG_2:2 – Yaganskoe forestry, LESG_3:3 – Mozhginskoe forestry; SOSG_1:1 – good state, SOSG_2:2 – satisfactory state, SOSG_3:3 – unsatisfactory state).

This may be because the resin constituents such as α-pinene, β-pinene, and limonene act as attractants (Rudinsky et al., 1970; Schultz et al., 2000). Perhaps this is associated with a decrease in resinous substances and an increase in tannins. However, the authors'data is inconsistent with the data of Leufven and Birgersson (1987). The authors note that during the period of infection by the European spruce bark beetle, the content of tannins in the wood tissues surrounding the breeding chambers decreases. At the same time, according to the literature data, substances incorporate into the cell wall have more protective properties than substances from the intercellular space (Hillis, 1987; Kleist, 1999; Srinivasan, 1999). In support of this, the authors noted that the tannins level in wood was two times less in the north of the republic, where the spread of insects was not recorded, than in places of mass drying out (the southern region of the republic) (Figure 6).

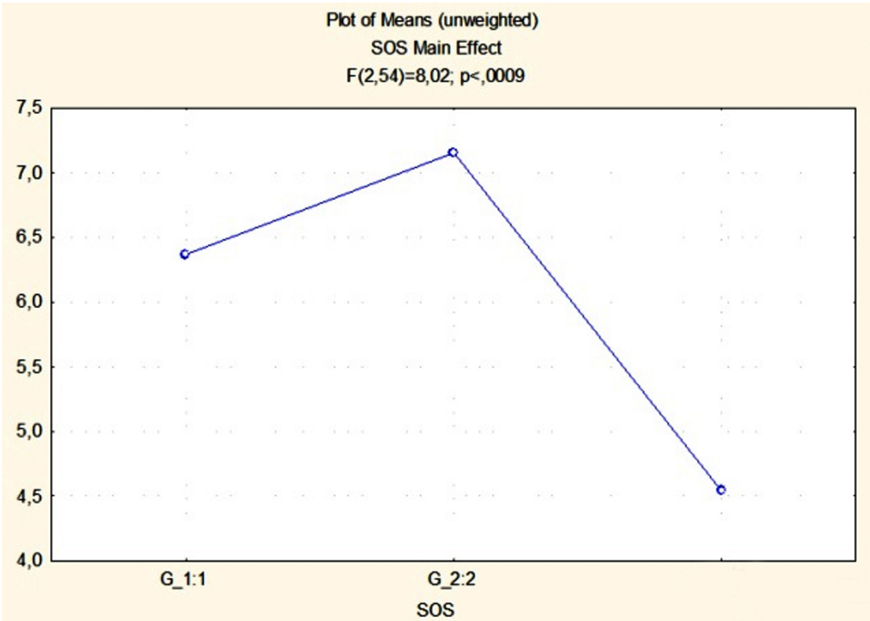

Figure 6. The tannins content in the wood of Piceaobovata depending on the life state (SOSG_1:1 – good state, SOSG_2:2 – satisfactory state, SOSG_3: 3 – unsatisfactory state).

Correlation analysis revealed the impact of the sanitary state of the forest stand on the content of tannins in the wood of spruce trees. With the deterioration of the sanitary condition, tannins in the wood increase. An increase in the coefficient of sanitary state (the higher the coefficient, the worse the sanitary state) is in direct positive relation with tannins in the wood ($r = 0.62$, $n = 54$, $P = 6.78E-07$). Thus, plants can change the chemical composition of wood extractive compounds under bark beetle infestation, where tannins are an important protective element. Bark beetles (ambrosia beetles) are inextricably linked with a complex of phytopathogenic fungi and, acting together on a tree, form a more effective attack system (Viiri&Lieutier, 2004; Lieutier et al., 2009). Taking this into account, it can be assumed that tannins suppress the vital activity of not only beetles but also pathogenic microorganisms.

ANOVA results revealed that the extractive substance level changes depending on the virtual state of plants. Moreover, the highest content of extractive substances was observed in suppressed plants. Trees of this group show signs of drying out and other pathologies of the trunk and crown; however, the increased content of extractive substances in the wood contributes to the functioning of the defense mechanism.

4. CONCLUSIONS

The research revealed that in the subtaiga part, spruce stands were actively drying out due to the waves of spruce bark beetle development.

The obtained test results for the wood extractive substances revealed that their total content was affected by the vital state of trees and site conditions. Under the impact of bark beetles, the polymer structural components of spruce wood (lignin and polysaccharides) do not change, however.

The content extractivesubstances and their composition directly depend on the sanitary state of the forest stand. Suppressed trees increase the level of extractive substances in the wood. A total increase in biologically active compounds in wood occurs by changing the balance between resinous substances and a water-soluble extractive substance group. An increase in the water-soluble group is associated with an increase in thetannins content. A direct correlation was determined between the deterioration of thesanitary state of forest stands and an increase in the content of tannins in the wood.

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AUTHORS' CONTRIBUTIONS

Konstantin Vedernikov: Conceptualization (Equal), Formal analysis (Equal), Funding acquisition (Equal), Project administration (Equal), Writing – original draft (Equal).

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Irina Leonidovna Bukharina: Resources (Equal), Software (Equal), Writing – review & editing (Equal).

Petr Anatolevich Kuzmin: Supervision (Equal), Validation (Equal), Visualization (Equal).

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