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Influence of growing conditions on morphological and anatomical characteristics of pine needles in the northern taiga

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Abstract: The aim of the study was to determine the adaptive characteristics of pine needles associated with age and different growing conditions. The length of the needles decreases and its variability reduces with increasing dryness and poverty of the soil. In oppressed trees, the coefficient of variability of the length of the needles on the tree is 8%. The coefficient of variation in the length of needles approaching 20% will indicate the best conditions for the growth of a particular tree. Trends of the dependence of width and thickness of needles on growing conditions were not identified. The area of needles in pine forests with optimal water regime of soils (blueberry, cowberry type) varies in the range of 112–124 mm^2. In extreme growing conditions pine needles area is reduced by 27–33% and equals 76–86 mm^2. These ranges of values of the areas of needles are typical for plantings of the third and fourth classes of age. Changing the width and thickness of the needles is aimed at compensating for changes in the length of the needles in the direction of maintaining the optimal area for these conditions needles. In extreme conditions, the area of the assimilating tissue increases, and the area of the conducting tissue (stele) decreases. Correlation dependences of the area of the stele of needles with the cross-sectional area, with the area of conducting beams, with the number of resin canals and with the cover fabric are revealed.

Keywords: needles length; needles area; stele; mesophyll; resin canal; transfusion tissue

Pine stands perform an important environmental function and operational value. It is extremely important to take into account the possibilities of adaptation to changes in the growing conditions and to identify indicators of resistance to adverse environmental factors when carrying out forest management activities. Change in the conditions of growth of trees, first of all, affects the size of the assimilation apparatus. Many authors pointed out the indicator function of needles (Margaris, Mooney 1981; Korchagina 1986; Farjon, Styles 1997; Feklistov et al. 1997; Zaitsev, Kulagin 2006; López et al. 2008; Feklistov, Tyukavina 2014). Pine occupies a wide range of habitats (López et al. 2008), often grows in extreme conditions. 45% of the northern taiga pine forests of the Arkhangelsk region belong to excessively humid conditions of growth, 12% poor, arid, which is ultimately

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expressed is the formation of low site index stands (V–VI site index). The ability of pine to develop in extreme forest conditions, conditions of fierce competition and excessive moisture, determines their potential for survival (Egorova, Kulagin 2007). Adaptation to different environmental conditions occurs through changes in the proportions of needles (Apple et al. 2002; Grill et al. 2004; Luomala et al. 2005). Due to the fact that pine exhibits xeromorphic features (Farjon, Styles 1997), adaptation to changes in conditions will be manifested through the water supply tissue (Larcher 2003). The development of the assimilation apparatus causes radial growth (Nadutkin, Modyanov 1972; Shleynis, Ruguotis 1976), and, ultimately, affects the productivity of a stand (Bobkova 1990; Onuchin, Spitsyna 1995; Feklistov et al. 1997), as needles are the material basis of the most important physiological, energy and bioproduction processes in trees. The study of adaptation mechanisms based on the structural properties of pine needles will reveal the mechanisms of stability and productivity of pine.

The aim of the research is to study the influence of growing conditions on the morphological and anatomical characteristics of pine needles in the northern taiga.

MATERIAL AND METHODS

The object of the study was lichen, cowberry, blueberry, sphagnum pine forests and pine on swamp northern taiga subzone of the Arkhangelsk region, Russian Federation (Table 1). The type of forest was established according to the classification of Sukachev (1931). In the cowberry pine forest soil there are sand medium podzols developing on the moraine sand; in the blueberry pine forest soil there are thin sandy podzols developing on the moraine light loam (sample plots (SP) 5, 6); thin sandy podzols developing on the moraine light loam (SP 4); in the sphagnum pine forest there are peat soils. The study was carried out in 2017–2018. On the trial area, model trees from 5 to 10 pieces were chosen in proportion to the representation of trees in the forest stand according to the level of crown development and growing intensity. Needles of the first, second and third year were selected from the middle branch of the crown of the model tree. Needles were selected from the escape of the first and second order in two-fold repetition. As a result, 12 needles were selected from each tree. The length, width and thickness of the needles were measured by a calliper (Krasnyy instrumental'shchik, USSR). Cross sections were prepared from the middle part of the needles using a sledge microtome MS-2 (Tochmedpribor, Russia). The diameter and area of resin canals, the stele, conductive beams, the thickness of the endoderm, epidermis, hypodermis were measured using a microscope Axio Scope A1 (Zeiss, Germany) with A-Plant 10×/0.25 M27 lens, using Image-Pro Insight software (Version 8.0, 2011). Statistical processing of the results was carried out using the program STATISTICA (Version 10, 2011).

The area of needles was calculated (Bazilevich et al. 1978) by Eq. 1:

Table 1. Key characteristics: Values (means) of the sampled stands

Sample plot	Forest type	Stand composition	Mean		Age (yr)	Stand density (No. of stems per hectare)
			DBH (cm)	height (m)		
1	pine on swamp	10P	4.6	4.5	62	–
2	pine on swamp	10P	2.8	3.4	40	–
3	sphagnum pine forest	10P+B	6.3	4.2	44	4,258
4	blueberry pine forest	9P1B	14.2	12	70	1,432
5	blueberry pine forest	9P1B	16.5	16.3	70	1,113
6	blueberry pine forest	8P2B	10	12	48	3,510
7	cowberry pine forest	10P	13	15	65	2,338
8	cowberry pine forest	10P	8	10	42	5,420
9	lichen pine forest	10P	10.3	11.2	68	3,025
10	lichen pine forest	10P	6	7.3	42	7,881

P – pine-tree, B – birch-tree

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$$S = 5.14\,L\left(\frac{a+\frac{b}{2}}{2}\right) \tag{1}$$

where:
S – area of needles (mm²),
L – length of needles (mm),
a – thickness of needles (mm),
b – width of needles (mm).

The paper presents averaged data on the first, second and third year of growth.

RESULTS AND DISCUSSION

The extreme values of the lengths of the needles are observed in the pine trees growing in extremely opposite in the productivity of plantations. The minimum values of the lengths of needles are observed in pine in the swamp – up to 15 mm (average 27.5 mm). The maximum values of the lengths of needles are found in blueberry pine – up to 76 mm (average 44 mm). Under these conditions, it is noted a high level of variability of a given characteristic 21–30% on a scale of Mamayev (1973). In cowberry pine, there is an average level of variability in the length of the needles, and in lichen pine, there is a low level of variability of the needles. The length of the needles decreases and the level of variability decreases with increasing dryness and poverty of the soil. The availability and sufficiency of mineral nutrition for pine increase the size of the assimilation apparatus (Will 2005). Soil-hydrological conditions of growth of trees affect the absolute size of most of their features (Lebedev 2014).

The maximum values of the length of the needles are typical for pine growing in blueberry pine, characterised by high average heights and diameters (46 mm) (Table 2). The reduction in the length of needles in blueberry pine, in which the average height of the stand is less by 26%, and the average diameter by 14% compared to more productive blueberry pine is 21%, the difference is significant (t = 4.6, P = 0.999). In this case, the coefficient of variability of the length of the needles is also reduced from 27 to 13%. With the deterioration of forest conditions, there is a decrease in the length of the needles and the coefficient of variability of this feature at the level of the tree and at the level of planting. Therefore, in extreme conditions, trees cannot realise their life potential, which leads to the alignment of trees in the same age pure planting.

In stands, there is a differentiation of trees. More developed trees bear needles of large sizes. Thus, in a more productive blueberry pine (SP 5) in trees with a highly developed crown and the best growth, the length of the needles is 57.3 ± 4.3 mm, and in trees depressed, weakened in growth with underdeveloped crown – 35.7 ± 1.0 mm. The difference is significant (t = 4.9). In the blueberry pine tree of lower productivity (SP 4) with a similar stand density in trees with a highly developed crown and the best growth, the length of the needles is 42.9 ± 1.3 mm, and in trees of the oppressed, weakened in growth with an underdeveloped crown – 32.9 ± 1.1 mm. The difference is significant (t = 5.8). Oppressed trees in blueberry pine forests of different

Table 2. Characteristics of the assimilation apparatus (needles) of pines

Forest type	Mean length (mm)	Mean width (mm)	Mean thickness (mm)	Mean area (mm²)
Age of the forest stand from 40 to 50 years				
Pine on swamp	26.6 ± 0.7	1.40 ± 0.03	0.50 ± 0.01	82.0 ± 2.4
Sphagnum pine forest	28.0 ± 0.6	1.40 ± 0.03	0.50 ± 0.02	86.0 ± 2.2
Blueberry pine forest	42.0 ± 0.9	1.10 ± 0.02	0.50 ± 0.01	113.0 ± 2.8
Cowberry pine forest	35.0 ± 0.8	1.30 ± 0.03	0.60 ± 0.02	112.0 ± 3.0
Lichen pine forest	27.0 ± 0.6	1.20 ± 0.02	0.50 ± 0.02	76.0 ± 2.1
Age of the forest stand from 60 to 70 years				
Pine on swamp	28.2 ± 0.8	1.30 ± 0.02	0.53 ± 0.01	86.1 ± 2.7
Blueberry pine forest	36.3 ± 0.8	1.40 ± 0.03	0.60 ± 0.01	121.0 ± 3.8
Blueberry pine forest	46.0 ± 1.9	1.30 ± 0.03	0.38 ± 0.01	124.0 ± 4.8
Cowberry pine forest	42.8 ± 1.3	1.20 ± 0.02	0.39 ± 0.02	112.0 ± 4.6
Lichen pine forest	33.0 ± 0.7	1.23 ± 0.03	0.39 ± 0.02	84.9 ± 2.5

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productivity have similar values of the lengths of needles. The difference is not significant (t = 1.8). Therefore, the length of pine needles is influenced not only by soil conditions, but also by intraspecific competition, which is expressed not only in the struggle for mineral nutrition and water but also for light. Shortening the length of needles in response to stress is a widespread adaptation reaction of pine (Cregg 1994; Richardson, Rundel 1998; Dangasuk, Panetsos 2004; Wahid et al. 2006). In blueberry pine with higher productivity (SP 5), the difference in the length of the needles between the trees belonging to the extreme categories in the degree of crown development and growth rate reaches 49%, and in blueberry pine with lower productivity (SP 4), the difference is 30%. The coefficient of variation of length of needles of the trees with a strongly developed crown and the best growth in more productive forest blueberry is 20 ± 2.3%; in less productive pine forest blueberry – 10 ± 1.6%; the trees of the oppressed, weakened growth with poorly developed crown in both cases 8 ± 0.8%. Consequently, in oppressed trees, the coefficient of variability of the length of the needles on the tree is 8%. The coefficient of variation in the length of needles approaching 20% will indicate the best conditions for the growth of a particular tree.

The differentiation of trees on the degree of crown development and intensity of growth is less expressed at pine on a bog, in sphagnum and lichen pine forest aged from 60 to 70 years. The coefficient of endogenous (on a tree) variability of the length of needles makes from 11 to 15%.

Thus, the reduction of endogenous variability of the length of needles to 11–15% indicates unfavourable soil conditions, and the reduction to 8% and below indicates an unfavourable radiation regime.

The decrease in endogenous variability of needles, when the length of the needles becomes relatively stable over time, indicates a decrease in the response of trees to favourable climatic factors in extreme conditions.

Thus, the length of the needles as well as their population and endogenous variability in the period are the indicators of favourable conditions of growth of trees.

With a decrease in the age of the stand, there is a tendency to reduce the length of the needles. With the difference in the age of the forest stand of 22 years in blueberry pine and pine in the swamp, the length of the needles changed by 8%; the difference is not significant. In cowberry and lichen pine forests, with a decrease in age by 23 and 26 years, respectively, the length of the needles decreased by 18%, the difference is significant (t = 5.0–6.6).

Conditions of blueberry pine can be taken as the optimal conditions of growth from the analysed conditions, as in these conditions there is the greatest length of needles in the age group from 40 to 50 years, and in the age group from 60 to 70 years. According to Viktorov and Remezova (1988), the depth of groundwater is more than 10 m in the lichen pine forest, the depth is 3–5 m in the cowberry pine forest, the depth is up to 2 m in the blueberry pine forest, the depth is 0–0.2 m in the sphagnum pine. As with the increase and decrease in the level of groundwater is a reduction in the length of the needles. The difference in the length of needles in the blueberry pine and pine in the swamp is an average of 38%, in the shrub-sphagnum pine by 33%. The growing conditions of blueberry and cowberry pine are close. Differences in the length of needles in the age group from 40 to 50 years are 17%, in the age group from 60 to 70 years, the difference is reduced to 7%. The length of needles in lichen pine is 36% less compared to blueberry pine in the age group from 40 to 50 years; the difference is reduced to 28% in the age group from 60 to 70 years. The width of the needles in different types of forest varies from 1.1 to 1.4 mm; the thickness of the needles varies from 0.38 to 0.60 mm. The level of variability of the width of the needles is low; the thickness of the needles varies from low to high. Trends in the dependence of the width and thickness of the needles from the growing conditions were not identified.

The area of needles in pine forests with optimal water regime of soils (blueberry, cowberry) varies in the range of 112–124 mm^2. The difference between the average values of the square of the pine forest blueberry and cranberry is not significant (t = 0.5–1.8). In extreme growing conditions, the area of pine needles is reduced by 27–33%. The difference between the average area of pine needles in the swamp and lichen pine is not significant (t = 0.3–1.9). Consequently, the change in the width and thickness of the needles is aimed at compensating for changes in the length of the needles. In optimal conditions of the water regime of soils, the pine needles area is characterised by a range of 110–130 mm^2; in extreme conditions, the area is characterised by a range of 70–90 mm^2.

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Table 3. The partial ratio of needles tissue on the cross-section of Scots pine (in the percentage of the cross-sectional area)

Forest type	Epidermis + hypodermis	Resin canals	Mesophyll	Central cylinder	Transfusion tissue
Pine on swamp	12.3 ± 0.2	10.6 ± 0.5	44.2 ± 1.6	32.9 ± 1.0	3.4 ± 0.2
Blueberry pine forest (III site index)	10.0 ± 0.4	14.6 ± 0.5	37.9 ± 2.3	38.5 ± 1.7	3.1 ± 0.2
Cowberry pine forest	9.4 ± 0.3	11.0 ± 0.6	42.6 ± 2.0	36.9 ± 1.6	2.9 ± 0.2
Lichen pine forest	10.5 ± 0.6	10.9 ± 0.9	45.5 ± 2.6	33.1 ± 1.3	2.5 ± 0.1

The anatomical characteristics of pine were considered in the pine forests of the age group from 60 to 70 years. The partial ratio of tissues on the cross-section of pine needles is relatively stable (Table 3). The largest volume is mesophyll (from 37 to 47%). About a third of the volume of needles occupies the stele (from 30 to 39%). The volume occupied by the covering tissues is 10–12%. This ratio of pine needles tissue corresponds to the literature data (López et al. 2008; Oskorbina et al. 2010).

The percentage of epithelial tissue in the cross section of the needles increased with the increase of excessive moisture. Under optimal water regime of soils of blueberry and cowberry pine forests and in arid conditions of lichen pine forests, this indicator does not differ significantly and is about 10%. The formation of a larger volume of cover tissues in pine needles growing in the swamp is associated with their free-standing and the formation of needles by light type (Lebedev 2014). At the best light intensity develop cover tissue (Kovalev, Antipova 1983), which protect the needles from adverse factors and regulate evaporation (Knyazeva 2012). The largest volume of resin passages is observed in optimal growing conditions (14.6%), with the deterioration of forest conditions, the volume of resin passages is reduced to 10%. The main volume of needles is mesophyll. Under extreme conditions, the percentage of mesophyll in the cross-section of needles increases by 8–10%, the percentage of area occupied by the stele is reduced by 5–8%. Thus, with the deterioration of growing conditions, there is a redistribution of the volume of assimilating and conducting tissue towards the assimilating tissue. Increase of the area of the stele and resin canals with better growing conditions is also mentioned by several authors (López et al. 2008; Tsandekova, Kolmogorova 2016). Changes in the stele occur primarily due to transfusion tissue. In extreme conditions, compared with optimal conditions, the volume of transfusion tissue is reduced by 5–8%. According to Gambles and Dengler (1982), Larcher (2003) and López et al. (2008), transfusion tissue is capable of storing water. Therefore, under optimal conditions of growth in the coniferous, the transfusion tissue is formed to make the water supply operation effective during the day to prevent the daily wilting of the plant. As soil moisture increases, the volume of conducting beams in the needles increases as well.

The dependence of the morphological and anatomical characteristics of needles of Scots pine in different growth conditions is not unique. In all considered conditions of growth with an increasing cross-sectional area of needles the area of the stele increases (r = 0.44–0.85). Moreover, the drier the forest conditions, the higher the relationship between these indicators. In the swamp, the tightness of the cross-sectional area of needles and the stele area is weak (r = 0.28). As the area of the stele increases, the area of conducting beams increases (r = 0.6–0.86). As the area of the stele increases, the number of resin strokes increases (r = 0.64–0.82). In extreme conditions of water regime of soils (swamp, lichen pine), the tissue cover thickens with increasing length of needles, reflecting xeromorphic characteristics of plants growing in conditions of physiological dryness. With an increase in the stele of pine needles in lichen, the tissue cover becomes thinner (r = 0.51), and in the swamp, on the contrary, thicken (r = 0.53).

CONCLUSIONS

The length of needles in different types of forest varies from 15 to 76 mm. With an increase in the dryness and the poverty of soil, the length of the needles decreases as well as the level of the variability. In oppressed trees, the coefficient of variability of the length of the needles on the tree is 8%. The coefficient of variation in the length of needles approaching 20% will indicate the best conditions for the growth of a particular tree.

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The width of pine needles in different forest types varies from 1.1 to 1.4 mm; thickness of pine needles varies from 0.38 to 0.60 mm. Trends in the dependence of the width and thickness of the needles on the growing conditions were not identified.

The area of needles in pine forests with optimal water regime of soils (blueberry, cowberry) varies in the range of 112–124 mm^2. In extreme growing conditions pine needles area is reduced by 27–33% and is 76–86 mm^2. Changing the width and thickness of the needles is aimed at compensating for changes in the length of the needles in the direction of maintaining the optimal for these conditions needles area.

In extreme conditions, the area of the assimilating tissue increases, and the area of the conducting (stele) decreases.

The correlation dependences of the area of the stele of needles on the cross-sectional area, the area of conducting beams and the area of the stele, the number of resin canals and the area of the stele, the area of the stele and the cover tissue are revealed.

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