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Anatomical structure and localisation of lignin in needles and shoots of Scots pine (*Pinus sylvestris* L.) growing in a habitat with varying environmental characteristics

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Abstract. We investigated the influence of a habitat with varying environmental characteristics on the anatomical structure and localisation of lignin in needles and shoots of Scots pine (*Pinus sylvestris* L.). A dune in South-West Estonia was chosen as the study area because it has extreme environmental characteristics: primitive sandy soil, deficiency of water, heavy winds and high light exposure. Analysis showed that the needles of all age and the current-year shoots of pines growing on the foot of the dune had the largest average cross section, mesophyll and parenchyma areas. The degree of the lignification of needles at the foot, on the slope and on the top of the dune differed distinctly. Intensive lignification of the cellular walls of the xylem was observed in needles and shoots of the pines, growing at the foot, but not in the trees growing on the top of the dune. Analysis showed that the anatomical structure and localisation of lignin, both in needles and in shoots, depend on their age, the trees location (foot, slope or top of the dune) and soil mineral composition.

Key words: *Pinus sylvestris*, environmental characteristics, anatomical structure, needle, shoot, lignification.

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Introduction

Natural habitat conditions are often stressful or unfavourable for the development and growth of pants. According to Zajtsev (1983), optimal growth conditions for plants are those that cause a minimum set of changes in the morphological structure and physiological functions in a plant. Stressful conditions, on the contrary, alter the normal physiological and biochemical processes, causing changes in the morphology and anatomy of plants. Natural stressful or unfavourable conditions embrace deficiency or excesses of water or several nutrients, low or high temperatures, extremes of irradiance (Rhodes & Nadolska-Orczyk, 1999).

On low dunes of South-West Estonia natural stressful factors are clearly expressed, especially on the tops of dunes. Dunes covered with pine forest are typical of coastal areas, which form a unique ecological system. The forests on South-West Estonian dunes are *Cladina*, *Calluna*, *Viccinium vitis-idaea* and *V. myrtillus* site type (Mandre, 2003). On the tops of dunes nutrients are washed away from the upper layer of the

soil. Continuous winds and high irradiance dry up the upper layer of the substrate diminishing the availability of nutrients even more. Scots pine is a very flexible species successfully adapted to various habitat conditions. It can grow in different climatic zones and soil conditions, both on sand and in bogs (Valk, 2005). The pines growing in various environmental conditions have differences in crown geometry, shoot architecture and the morphology of needles and shoots (Niinemets *et al.*, 2001; 2002a,b; Niinemets & Lukjanova, 2003). Numerous physiological and biochemical mechanisms are involved in the process of adaptation of plants to stressful and adverse conditions. The first response to stress occurs in cells. In process of development the cell walls of the plant go through several transformations, including chemical and physical changes. Lignification is of great importance. The accumulation of lignin into cell walls results in structural rigidity and durability of plant tissue and, therefore, is especially important in evergreen leaves that persist for many years (Polle *et al.*, 1994). The content of lignin in mature needles of Norway spruce is about 5% to 10% of dry matter (Miksche & Yasuda, 1977).

Intensive lignification of cell walls begins after the cell growth is stopped (Esau, 1965; Polle *et al.*, 1997), while the thickness of the cell wall is increasing and the cell lumen is decreasing. Lignification lowers the plasticity of the cell walls and fixes their form. In many cases cells loose their protoplast after the end of secondary thickening, but the cells continue functioning, fulfilling mainly support and transfusion functions. Environmental factors also affect the lignification process in trees; for example, by causing the synthesis of 'stress lignin' in response to adverse conditions (Ziegler, 1997; Mandre, 2002).

Investigation of structural parameters helps to understand and interpret the influence of environmental conditions on the trees (Rhodes & Nadolska-Orczyk, 1999; Mandre, 2003). Today micro structural research is very important because the first responses to stress occur at the cell level (Sutinen, 1998; Butorina & Mozgalina, 2004; Luomala *et al.*, 2005). Research of the physiological and biochemical processes occurring in the cells and tissues of the needles can significantly supplement the knowledge of the mechanisms and processes responsible for the tree tolerance to stress conditions.

The aim of this investigation was to study of the anatomical structure and lignin accumulation in the needles and shoots of Scots pine under adverse conditions with different environmental characteristics.

Material and Methods

Study area and plant material

The plant material was collected on the dune of Tõotusemägi in South-West Estonia in September 2004 and 2005. The investigation transect begins at the western foot, proceeds to the top and descends to the eastern foot of the dune. The length of the transect is 300 metres, but the relief varies and significant differences occur in the chemical composition of the soil, light exposure, water supply and other indicators (Mandre, 2003).

Five sample plots (Figure 1) were selected on the dune slopes, foot and top. The needles and shoots were collected from 30–50-year old (n = 15) Scots pines. The pine trees selected had similar morphological parameters (height 10–20 m, diameter at breast height 17–20 cm) and architecture of the crown.

For morphological, anatomical and chemical analyses needles of the current, first

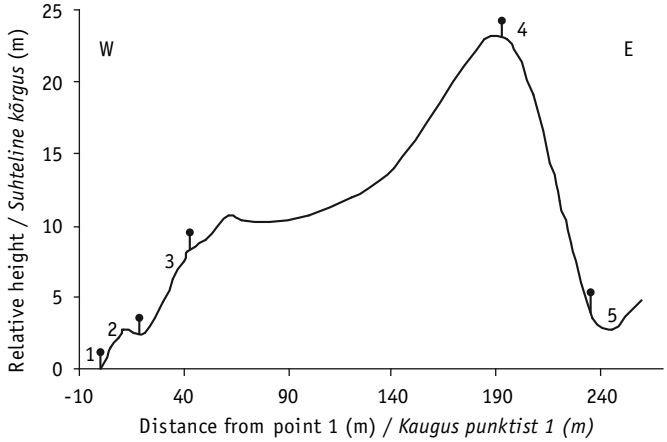


Figure 1. Sample plots on the W–E transect on the dune of Tõotusemägi in South-West Estonia. 1 – the foot of the western slope; 2, 3 – the western slope; 4 – top; 5 – the foot of the eastern slope.

Joonis 1. Vaatluspunktide asukoht lääne–idasuunalisel transektil Edela-Eestis Tõotusemäe luitel. 1 – läänepoole luitejalam; 2, 3 – luite läänenõlv; 4 – luitehari; 5 – idapoolne luitejalam.

and second year (n = 15) and current-year shoots (n = 12) from the middle of the crowns of the trees from each sampling plot were collected.

The concentration of chemical elements in the upper soil layer (30 cm) of all investigation plots of the transect, in the needles and shoots were determined in the Laboratory of Agrochemistry of the Estonian Agricultural Research Centre (Tables 1, 2).

Anatomy of needles and shoots

For anatomical and histochemical analyses cross-sections of needles and shoots were made. The needles and shoots were pre-fixed with 3% glutaraldehyde in 0.1 mol L^{-1} phosphate buffer, pH = 7.3, and fixed in 1% solution of OsO_4 by a widely known technique (Bozzola & Russell, 1992; Ruzin, 1999). Then tissues were dehydrated with ethanol and xylol (Fluka, USA) and embedded in paraffin. The cross-sections of needles (10–15 µm) and shoots (15–20 µm) were made with a microtome (Leitz, Germany) and mounted on glass.

For lignin visualisation, paraffin was removed and the slices were stained with 5% safranin O and Fast Green FCF (Fluka, USA). The lignified cell walls stained red and the others green. The cross-sections were viewed in the bright field at ×100 and ×400 magnification with the help of Micros MC400A (Austria) microscope and photographed with a Nikon Coolpix 5400 camera (Nikon, Tokyo, Japan).

Anatomical peculiarities of needles of different age were analysed. For this purpose the total area, the areas of tissues, and needle width and thickness were measured on the cross-sections in millimetres. On cross-sections of shoots the total area, its width and thickness, and the areas of tissues (also in millimetres) were measured.

MapInfo Professional for Windows 4.0 (MapInfo Corp. Inc., Troy, NY) were used to measure the tissue area from the images. The tissues of needles were separated from epidermis, mesophyll, xylem, phloem and sclerenchyma. The tissues of shoots

Table 1. Concentration of mineral elements in the soil on the W–E transect on the dune of Tõotusemägi in South-West Estonia.

Tabel 1. Mineraalelementide sisaldus mullas lääne–idasuunalisel transektil Tõotusemäe luitel Edela-Eestis.

Sample plot *Vaatluspunkt**	N, %	K	Ca	Mg	P, mg kg–1	pH
		mg 100 g–1				
1	1.95	8.0	83.5	20.6	13	3.8
2	0.26	5.0	37.0	13.6	4	4.4
3	0.10	1.5	20.0	5.5	2	4.3
4	0.05	0.1	87.5	1.1	17	5.5
5	0.11	4.5	28.0	15.6	12	4.0

*The locations of sample plots see in Figure 1 / *Vaatluspunktide asukohta vt. joonisel 1*

Table 2. Concentration of mineral elements (%) in the needles and shoots of Scots pines growing on the dune of Tõotusemägi.

Tabel 2. Mineraalelementide sisaldus (%) okastes ja võrsetes Tõotusemäe luitel kasvavatel mändidel.

Sample plot *Vaatluspunkt**	Needles / *Okkad*					Shoots / *Võrsed*				
	N	K	Ca	Mg	P	N	K	Ca	Mg	P
1	1.51	0.48	0.32	0.122	0.137	0.96	0.24	0.37	0.094	0.102
2	1.56	0.46	0.38	0.117	0.160	1.32	0.30	0.38	0.095	0.138
3	1.24	0.48	0.66	0.096	0.131	1.11	0.32	0.51	0.100	0.139
4	1.16	0.45	0.27	0.116	0.138	0.83	0.30	0.32	0.084	0.109
5	1.23	0.60	0.39	0.129	0.141	1.08	0.36	0.47	0.094	0.125

* The locations of sample plots see in Figure 1 / *Vaatluspunktide asukohta vt. joonisel 1*

Table 3. Mean anatomical parameters of Scots pine needles cross-section on the dune of Tõotusemägi (±SD, n = 15).

Tabel 3. Okka ristlõike keskmised anatoomilised parameetrid Tõotusemäe luite mändidel (±SD, n = 15).

Parameter *Parameeter*	Age of needles / *Okaste vanus*		
	Current year needles *Jooksva aasta okkad*	1-y-old *1-a.*	2-y-old *2-a.*
Width *Laius*, mm	1.20±0.12	1.13±0.19	1.25±0.16
Thickness *Paksus*, mm	0.53±0.08	0.49±0.09	0.54±0.05
Total cross-section area *Ristlõike üldpindala*, mm^2	319.50±36.9	294.98±30.1	244.59±24.1
Mesophyll area *Mesofülli pindala*, mm^2	185.31±20.1	166.03±17.2	144.53±14.0
Epidermis area *Epidermise pindala*, mm^2	25.86±1.8	23.48±1.1	20.83±3.2
Vascular bundles area *Juhtkimpude pindala*, mm^2	3.65±0.9	5.12±0.8	3.02±0.5
Xylem area *Ksüleemi pindala*, mm^2	2.45±0.6	3.17±0.8	1.73±0.1

Table 4. Mean anatomical parameters of Scots pine current-year shoots cross-section on the dune of Tõotusemägi (±SD, *n* = 12).

Tabel 4. Jooksva aasta võrse ristlõike keskmised anatoomilised parameetrid Tõotusemäe luite mändidel (±SD, n = 12).

Sample plot *Vaatluspunkt**	Xylem area *Ksüleemi pindala*, mm^2	Vascular bundle area *Juhtkimbu pindala*, mm^2	Parenchyma area *Parenhüümi pindala*, mm^2	Epidermis area *Epidermise pindala*, mm^2	Total shoot cross-section area *Võrse ristlõike üldpindala*, mm^2
1	297.77±7.42	435.85±16.99	1453.43±48.22	489.89±20.68	2430.63±63.72
2	160.89±9.35	209.57±5.63	409.72±12.60	230.94±11.75	878.50±7.30
3	112.90±6.95	174.46±9.04	483.43±28.86	308.07±22.65	994.42±15.56
4	760.37±52.3	962.71±60.85	1452.43±96.60	627.16±20.92	3087.72±157.70
5	383.70±38.48	590.21±54.28	2096.43±107.61	488.41±37.63	3238.65±181.55

* The locations of sample plots see in Figure 1 / *Vaatluspunktide asukohta vt. joonisel 1*

were separated from epidermis, parenchyma, xylem, phloem and cortex. Average values of anatomical characteristics were calculated for all these tissues. Tables 3 and 4 present the average values with standard error of the measured parameters. The stained cross-sections revealed the localisation of lignin. The degree of lignification was determined visually by the intensity of staining.

Results

Analysis of the histological preparations of needles of different age showed that the current-year needles had the largest average area of the total cross-section and mesophyll (Table 3).

Altogether the tissues accumulating lignin (xylem, epidermis and sclerenchyma) of current-year needles made up 13.2% of the average total area. For one-year-old and two-year-old needles these values were respectively 13.5% and 12.6%.

Visual analysis of the stained needle cross-sections showed that the xylem cellular walls, the stomata guard cells and the cuticles of the current-year needles were stained totally or partially. In one-year-old and two-year-old needles the cross-section colour intensified. In addition, in some needles the cellular walls of epidermis, endodermis and sclerenchyma were stained. This staining evidenced accumulation of lignin.

Average values of anatomical parameters of the needles and shoots depending on the location of the sample plot on the transect on Tõotusemägi are presented in Tables 4 and Figure 2. The needles and the current-year shoots collected from trees growing on the lower plot of the east slope (plot 5, Figure 1) had the largest total cross-section area (Table 4, Figure 2) among the sample plots. Histochemical reaction showed accumulation of lignin in the xylem cellular wall, external cellular walls of the epidermis and stomata guard cells of the needles and in the xylem cell walls and epidermis of the shoots. The needles and current-year shoots collected from trees on the western slope (plot 1, Figure 1) had neither minimal nor maximal average values of parameters (Table 4, Figure 2). Accumulation of lignin was marked in cellular walls of the xylem and epidermis both in the needles and in the shoots.

The needles and current-year shoots of trees in plot 2 on the western slope (Figure 1) had the lowest average total area of cross-sections. On the western slope (plot 3, Figure 1) lignification was observed in needles of all ages. On the cross-section

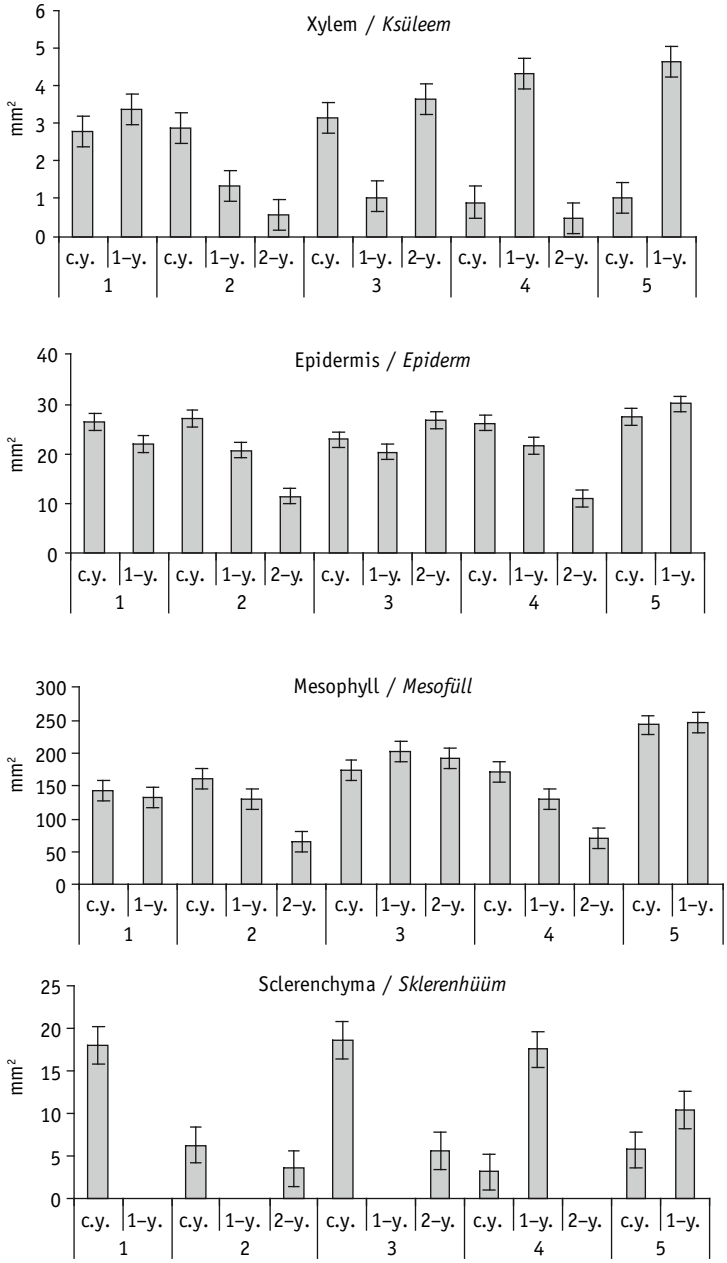


Figure 2. Distribution of tissue in Scots pine needles in different sample plots on the dune of Tõotusemägi (±SD, *n* = 15). c.y. – current year; 1-y. – 1-year-old; 2-y. – 2-year-old.

Joonis 2. Kudede jaotuvus männiokastes sõltuvalt okka vanusest ja kasvukohast Tõotusemäe luite transektil (±SD, n = 15). c.y – jooksva aasta okkad; 1-y. – 1-aastased; 2-y. – 2-aastased.

of the current-year needles the xylem and epidermis were stained partially but on the cross-section of one-year-old needles the colour of these tissues was more intensive. The xylem and the epidermis cells of two-year-old needles were totally stained. The colour reaction of lignin in the cross-sections of current-year shoots showed slightly stained cellular walls of the xylem and epidermis.

On the trees growing on the top of the dune (plot 4, Figure 1) the current-year needles had the smallest average area of xylem and of the whole vascular bundle (plot 4, Figure 2). The shoots, on the contrary, had the largest average area of the xylem and vascular bundle. Histochemical reaction revealed no obvious process of lignification either in the needles or in the shoots of these trees. On the cross-section of needles some xylem and cellular walls of epidermis and stomata guard cells were stained. Such a picture was observed on the preparations of needles of all investigated ages.

Discussion

The investigation of the anatomical structure of the needles of pine growing in a habitat with variable environmental characteristics, including adverse conditions such as on tops of dunes, showed normal development and growth of needles. Analysis of the stained preparations of needles of all age showed that the process of lignification began already in cellular walls of the xylem of the needles of the current year, which accords with the literature data (Polle *et al.*, 1997; Lukjanova & Mandre, 2006). Then this process reaches the cells of epidermis and sclerenchyma. In the current-year needles the cellular walls of the xylem, the stomata guard cells and the cuticle were stained fully or partially. On the cross-section of the needles of the first and second year of development the colour of the stained tissues became more intensive. In some samples the cellular walls of the endodermis and sclerenchyma (the mechanical tissue with a supporting function) were stained as well.

Several researches into the morphological and physiological characteristics of needles (Niinemets *et al.*, 2001, 2002a, 2002b; Niinemets & Lukjanova, 2003) have revealed a strong dependence of the structure of the needles and shoots, the architecture of the shoot and crown geometry of the tree on the mineral composition of the soil. Needles from trees growing in nutrient-poor soil are thinner, narrower and with lower photosynthetic activity than needles from nutrient-rich sites. It is possible to connect those differences with the deficiency of phosphorus and nitrogen in the substrate. Besides, a low concentration of mineral elements in the soil combined with the light deficit results in changes in the morphology and architecture of shoots and the crown.

The study showed that the anatomical structure and the lignification process in both needles and shoots depend on the mineral composition of the soil on the dune. The pine needles from all plots of the transect showed a deficit of basic mineral elements (Table 1). According to Orlov and Koshel'kov (1971), the optimum concentration of nitrogen in the needles of pines should be within the range 1.6–2.4%, phosphorus 0.1–0.15% and potassium 0.45–0.9%. Based on our data, the most favourable conditions for growth are on the sample plot at the foot of the slope. The content of nutrients in the soil on this plot and the chemical elements in the needles in comparison with other needles from other sample plots of the transect were the closest to the optimum.

In the needles from the pines growing on the western (plot 1, Figure 1) and on the eastern (plot 5, Figure 1) foot of the slope an increase of the total and relative area of the tissues accumulating lignin was observed with age. Analysis of the stained cross-sec-

tions of needles showed that the lignification process began already in the current-year needles, and the colouring of the cellular walls of the one-year-old needles became more intensive. Comparative analysis of the preparations of the current-year needles and shoots revealed that the average area of the cross-section and the area of assimilative tissue were the greatest both in the needles and in the shoots of the pines from the lower plot of the east slope. Besides, these shoots had the largest pith area, where living cells capable of growth and division are located. Lignification was noted in some cells of the xylem, external cellular walls of the epidermis and stomata guard cells of the needles and also in cellular walls of the xylem and epidermis of the shoots.

Both the needles and the current-year shoots of the trees growing on the western slope (plot 2, Figure 1) had the smallest average total area of cross-sections and assimilative tissue area. Accumulation of lignin in the cellular walls of the xylem and epidermis indicated the beginning of lignification.

The most pronounced lignification among all investigated needles was noted in needles collected from pines on the western slope (plot 3, Figure 1). The stained slide of the current-year needles showed a small content of lignin in the xylem of the vascular bundle, sclerenchyma and epidermis cells wall. No difference in the localisation of lignin on the cross-sections of needles of the first and second year of development was observed, but slides of needles of the second year differed having an intensive colouring. On these samples slightly stained cellular walls of the endodermis were noted. The average total and relative areas of the xylem increased with the age of the needles. The same tendency was observed in the epidermis. Thus, as established at these samples by measurements and visually by the noticeable intensification of staining, in these needles the average total and relative areas of the tissues accumulating lignin increased with age and considerable lignification of the xylem and epidermis was observed. Comparative analysis of the cross-sections of needles and the current-year shoots revealed the following: the needles had the largest average area of the xylem and the shoots, on the contrary, the smallest average area of the xylem. The colour reaction of lignin showed slightly stained cellular walls of the xylem and epidermis in the current-year shoots.

The needles collected from tree growing on the top (plot 4, Figure 1) of the dune were interesting because there the lignification process faded with age. The colour reaction did not show an intensive process of lignification in the current-year needles. Some portion of the cellular walls of the xylem, of the epidermis and of the stomata guard cells was stained. During the two first years of the needle growth a small accumulation of lignin was noticed, but then the process of lignification became undistinguishable. The intensity of the colouring of the xylem and epidermis of the two-year-old needles was comparable to the colouring of the preparations of the current-year needles, i.e. degradation of lignification occurred; however, the stained nucleus of the cells indicated to a correctly occurred histochemical reaction. The average total area of the cross-sections decreased in the one-year-old needles while the xylem total and relative area increased up to the maximum value, but on the slides of two-year-old needles these parameters suddenly decreased. The same pattern was seen with the epidermis.

The current-year needles of the trees growing on the top of the dune had the smallest average area of the xylem and vascular bundle. In shoots, on the contrary, the average area of the xylem and vascular bundle were the largest. Despite that, the histochemical reaction did not reveal any obvious process of lignification either in the needles or shoots of these trees.

The differences found in the anatomical structure and in the accumulation of lignin in the needles of pines growing on dunes with varying environmental characteristics prove the influence of the environment on the anatomy of the needles and define the ability of trees to adapt to various conditions. Besides, the obtained results show that the adaptability to environmental conditions begins with changes in the anatomical structure of needles, which in turn defines to some extent ability of the whole tree for adaptation.

Conclusions

This research revealed that on the foot of the slope of a dune, where the soil is relatively rich in nutrients, the water supply is good and no strong winds and no high light intensity occur, the needles and shoots are best developed. The concentrations of minerals, determined by the quality of the environmental conditions, are close to optimum. On the contrary, in the pines growing on the top of the dune with adverse conditions a deficit of mineral elements for effective growth was observed both in needles and in shoots. This deficit was confirmed by a slow lignification process in the needles and shoots of these trees. To sum up, this study showed that on the dunes of South-West Estonia the anatomical structure of pines as well as localisations and accumulation of lignin in the needles and shoots significantly depend on the specific place of growth of the tree on the dune and on mineral composition of the soil in that place.

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Hariliku männi (*Pinus sylvestris*) okaste ja võrsete anatoomiline ehitus ja lignifikatsioon ökoloogiliselt erinevates kasvutingimustes

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Kokkuvõte

Okaste ja võrsete anatoomilist ehitust ja lignifikatsiooni uuriti Tõotusemäe luite jalamil, nõlval ja harjal kasvavatel mändidel. Okaste ja võrsete ristlõigete analüüs näitas, et nende anatoomiline ehitus ja lignifikatsioon sõltuvad puude kasvukohast luitel ja substraadi mineraalsest koostisest. Luite jalamil kasvate mändide okkad ja võrsed olid suurema ristlõike üldpindalaga ja assimilatsioonikoe pindalaga, võrreldes nõlval ja harjal kasvate puude okaste/võrsetega. Luite harjal kasvavate mändide jooksva aasta okkad olid väiksema ksüleemi ja juhtkoe pindalaga, nende mändide jooksva aasta võrsetel aga vastupidi – juhtkimbu ja ksüleemi osa oli suurim.

Suuremal osal analüüsitud okastest ja võrsetest oli lignifitseerumisprotsess hästi jälgitav. Ligniini akumulatsioon algab okaste ja võrsete ksüleemi ja epidermi rakukestades. Vanemates okastes ligniini hulk suureneb, kuigi ligniini koguvate kudede pindala ei suurene – jooksva aasta okastes ksüleemi, epidermi ja sklerenhüümi osakaal oli 13,2%, esimese ja teise aasta okastes vastavalt 13,5% ja 12,6%. Luite harjal kasvavatel mändidel oli lignifitseerumisprotsess vähem intensiivne nii okastes kui ka võrsetes, võrreldes luite jalamil ja nõlval kasvavate mändidega.

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