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THE CHANGES IN REDOX STATUS OF ASCORBATE IN STEM TISSUE CELLS DURING SCOTS PINE GROWTH

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The contents of ascorbate (AsA) and dehydroascorbate (DHA) and their ratio, showing cellular redox state of AsA, were studied in the cells of the separate tissues at different levels of *Pinus sylvestris* L. stem during early- and latewood formation. Morphological status of the cells in the tissues and the content of soluble carbohydrates were also estimated. The cellular redox potential of AsA has been found to depend on the type of tissue, cell development degree, the level of stem and the type of forming wood. The content of AsA and AsA/DHA ratio in the cells of non-conducting phloem along the stem were higher than in mature xylem and less during earlywood than latewood formation. The cells of conducting phloem and forming xylem, as the principal tissues taking part in annual ring wood formation, differed in the content of acids in the course of early and late xylem formation. Along the stem, the content of AsA decreased in conducting phloem cells and increased in the cells of forming xylem during both early- and latewood formation. The AsA/DHA of conducting phloem during earlywood formation was greatest below the stem and diminished to the top of the tree, while in the course of latewood development it was similar at all levels. In forming xylem AsA/DHA increased to the top of tree during the early xylem formation and decreased in late xylem that indicates the differences in oxidation-reduction reactions into the cells of two type of forming wood. The data are discussed according to morphological development of cells and the content of carbohydrates.

Keywords: *Pinus sylvestris L., levels of stem, non-contacting phloem, conducting phloem, forming xylem, mature xylem, ascorbate/dehydroascorbate ratio.*

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INTRODUCTION

The growth and development of the plants are accompanied by the production of reactive oxygen species (ROS) such as superoxide oxygen anion radicals, hydrogen peroxide and hydroxyl radical in the course of normal development or as the response to abiotic and biotic factors (temperature, drought, wounding, pollution) (Smirnoff, 1993; Jimenez et al., 1998; Schopfer, 2001; Keles, Oncel, 2002; Foyer, Noctor, 2005, 2011; Sharma, Dubey, 2005; Asada, 2006; Suzuki, Mittler, 2006; Atkin, Macherel, 2009; Miller et al., 2010; Kärkönen, Kuchitsu, 2015). ROS are produced in such organelles as chloroplasts, peroxisomes, mitochondria during their functioning, the metabolic reactions in which are specific for each of the compartments (Jimenez et al., 1998; Kumar et al., 2003; Asada, 2006; Suzuki, Mittler, 2006; Atkin, Macherel, 2009; Miller et al., 2010; Noctor, Foyer, 2016). In addition to the intracellular compartments the cell walls (apoplast) and plasma membranes can be sources of ROS (Miller et al., 2010; Foyer, Noctor, 2011; Kärkönen, Kuchitsu, 2015).

The plants, as all aerobic organisms, control ROS-concentration by ROS-scavenging systems to ensue a stabilization of metabolism, sustainable growth and development. Among enzymatic and no enzymatic antioxidative pathways the important component of the active oxygen scavenging system is ascorbate–glutathione (AsA–GSH) cycle, involving the antioxidatant enzymes such as ascorbate peroxidase (APX), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR) and glutathione reductase (GR). In this cycle dehydroascorbate (DHA) fulfils important role being the mediator in oxidative events between AsA and GSH. The ascorbate-dehydroascorbate cycle, including GR along with ascorbate peroxidases, is involved in detoxification of drought-induced hydrogen peroxide (Kumar et al., 2003; Kärkönen, Fry, 2006) as well as active oxygen (Noctor, Foyer, 1998; De Gara et al., 2000). Being located into both apoplast and intracellular compartments and acting as scavenging agents or as co-factors of enzymes, AsA, DHA and GSH influence plant growth and development by modulating processes from mitosis and cell expansion or elongation to senescence and death (De Pinto, De Gara, 2004; Potters et al., 2004; Antonova, 2012). Due to that, ascorbate and glutathione are considered as molecules with a regulatory role participating in the redox signalling of the plant cells (Noctor, Foyer, 1998; Meyer, 2008; Szalai et al., 2009; Miller et al., 2010; Foyer, Noctor, 2011; Kärkönen, Kuchitsu, 2015) and as dynamic signaling compounds of metabolic interface between external effects and physiological responses (Foyer, Noctor, 2005, 2011). Although GSH and ascorbate fulfill similar essential antioxidant roles, they serve different functions in the control of cell division and cell growth and considered as ROS-independent signals (Foyer, Noctor, 2011).

Two types of xylem, early and late, differed in the tracheid diameter and the cell wall thickness is a basic feature of coniferes wood. Although the development of two wood types in annual ring occurs by one process: cell production by cambium, growth of primary cell walls (expansion growth) and maturation, including secondary cell wall and lignification, their morphological parameters as well as the number of cells in the annual rings depend on the conditions of the formation and development of the cells (Antonova, Stasova, 1993, 1997). Physiological and biochemical events in the cells, leading to morphological differences, resulted from the changes in cell metabolism under influence of environmental factors. One of decisive factors affecting cell development transition from early to late type is internal water stress (Zahner et al., 1964; Nonami, Boyer, 1990*a*, *b*). The changes along the chain of metabolic reactions due to low water potential evoke the cells produced by the cambium to be further developed as late tracheids. Low water potential (internal water stress) in developing xylem can arise because of the lack of rainfall (external stress), the exhaustion of water stores in soil and increased solar radiation (Antonova, 1999), strengthening of evapotranspiration at high air temperature (Gregg et al., 1988) that reduces the internal water stores in stem tissues, or because of flooding of root system («physiological drought»). Physiological drought provoked by oxygen deficiency in soil decreases water absorption (Lyr et al., 1967).

From physical characteristics of water state in a plant (turgor, osmotic and water potential) the water potential gradient is the first reaction to the appearance of the water stress (Nonami, Boyer, 1990*a*). In tree stem water potential, a gradient appears between mature xylem and growing cells (Nonami, Boyer, 1990*a*) or between the roots and the crown due to transpiration (Schulze et al., 1985; Kaibijainen, Sazonova, 1993). Water potential in radial direction increases to phloem side (Boyer, 1988), while water potential of cells themselves decreases in the phloem (Cosgrove, 1986). Weakening of cell walls provokes the diminishing of cell water potential and the water from apoplast begins to go into cells causing the tension of apoplastic solutions that in turn initiates the inflow of water (Cosgrove, 1986). The changes of water potential can also occur because of the adhesion of water in cell wall during structural component deposition (Nobel, 1970). The variations in water potential under the influence of external factors and as a result of metabolic processes both into the cells and the structural changes in cell wall (weakening of wall, deposition new components and lignin as well), can be considered as the main trigger factor in the changes of plant metabolism. The apoplast is the first compartment, which reacts to a fluctuation of water potential. The apoplast, being transport system for water, anions and substances, acts as a mediator between cell wall and intracellular space of cell itself determining the state of internal medium in cytosol (Miller et al., 2010). The changes in water regime of the tissues along the radial and vertical directions of the stem, influencing cambium activity and differentiation of its xylem derivatives, lead to differences in the number of cells and morphological parameters of the tracheids at different levels of stem in larch *Larix sibirica* Ldb. and in other coniferes trees (Kramer, Kozlowski, 1979; Zimmermann, 1983; Antono-

va, 1999). The variation of water potential in the cells of plant tissues provokes the changes in cell growth rate and cell wall structure (Wodzicki, 1971; Cosgrove, 1986, 1997; Antonova, 1999), modulating availability of assimilates and growth-stimulate substances (Ahmad et al., 2010) and antioxidant defense (Duan et al., 2007).

The study of the redox-potential along the radial row of the tracheids showed the significant variations in the content of AsA, DHA and their proportion during annual wood ring formation in Scots pine *Pinus sylvestris* L. and in larch *Larix sibirica* Ldb. (Antonova, 2012). The changes in the AsA pool at cell developmental stages and its accessibility to be oxidized resulted in the activity of cambium, in cell expansion growth and lignification that in turn leaded to the differences in the number of early and late tracheids in annual wood layer as well as in their radial diameters and cell wall thickness and in the rate of lignification in two types of wood (Antonova, 2012; Antonova et al., 2014). The ratio AsA/DHA decreased from the start to the end of lignification and maturation of the early tracheids and, in contrast, increased during the late tracheid maturation, indicating the differences in the level of redox-processes in the cells of these tissues (Antonova et al., 2014).

The differences in the morphological parameters of tracheids in pine along both radial rows and the stem, caused by the changes in the cambium activity, the conditions for growth and development of cells due to the variations in the water potential are, obviously, resulted from the differences in pathways of ROS production in the organelles and the activities of enzymes in scavenging system. AsA, DHA and their ratio can be the indicators of steady development of the tissues at separate levels of tree stem.

The purpose of this work was to compare the changes in ascorbic and dehydroascorbic acids (and their ratio) in the tissues with different development degree at separate levels of pine stem in the periods of earlywood and latewood formation.

MATERIALS AND METHODS

Plant material. The tissues with different degree of development were sampled at separate stem levels of 30-year-old pine *Pinus sylvestris* L. trees in the periods of earlywood and latewood formation. Since during annual ring formation the stages of growth and development of early and late tracheids can overlap each with other in time (Antonova, Stasova, 2015) the tissues were sampled in late June and early August. In climatic conditions of Middle Siberia this corresponded to the periods of formation either earlywood or latewood. The height of trees (two in each time sampling) was in late June 14 m and in early August – 11 m.

Non-conducting phloem (ncPh), conducting phloem (cPh), developing xylem (dXyl) and mature xylem (mXyl) were scraping off layer by layer from stem segments located at three levels of the tree: 1.3, 6.8 and 12.3 m of the stem levels in late June and 1.3, 4.3, 7.3 m of the stem levels in early August. Each of the scraps was controlled by anatomical and histochemical tests. Simultaneously the tissue samples have been taken to assess the content of moisture.

The xylem cells with different developmental stages along radial row tracheids from the same trees were used to determine the redox-potentials of cells (Antonova et al., 2009).

To estimate of morphological status of the tissues and the development degree of the cells the cross-cut-sections, sampling at the same levels, were stained with cresyl-violet (Antonova, Shebeko, 1981). To test the beginning of lignification the staining with phloroglucinol-hydrochloric acid was employed. The number of cells in different tissues was calculated.

Biochemical tests. The tissues sampled were immediately fixed with ethanol at the final concentration not exceeding 80 %, weighed, and kept in a refrigerator until analyses. Sample weight was estimated, taking into account 96 % ethanol used for fixation. After grinding with mortar and pestle in liquid nitrogen the tissue samples were processed 80 % of ethanol at room temperature. The extracts were evaporated at 40 °C and dry residues were treated with water and chloroform by turns. Water extracts were combined and divided into two parts. The each of them was used to assess the content of carbohydrates (Dubois et al., 1956) and AsA, DHA (Antonova et al., 2009). To estimate of AsA and DHA the water solution was acidified by HCl to pH 2.0–2.5, phenols were extracted away with ethyl ether and AsA and DHA were determined in water solution with 2, 4-dinitrophenylhydrazine (Roe, Oesterling, 1944). This technique was adapted for parallel determination of both acids in the conifer tissues (Antonova et al., 2005, 2009). The solutions, contained 1 to 20 mg AsA (DHA) in 1.5 ml of 5 % metaphosphoric acid, were used for the calibration curves. DHA has been obtained by (Roe, Oesterling, 1944).

RESULTS AND DISCUSSION

Morphological state of tissue development at separate levels of pine tree stem is presented in the table (Table).

The mature (non-conducting) phloem contained the layers of early and late sieve cells as well as parenchyma cells (Table). From the sieve cells of non-conducting phloem the last cells, formed in the end of the previous season, are capable to transport of assimilates at the beginning of current year only. On the contrary, parenchyma cells can be considered as participants in a growth and development of forming xylem cells due to the presence of the starch and fatty acids, which can be used in metabolism of xylem cells and in synthesis of their structural components. For example, we observed the decrease in starch granules in parenchyma ray cells of different annual phloem layers (Antonova, Stasova, 2006) as the result of starch hydrolysis in the period when the photosynthesis was suppressed due to high temperature and additional substrates were required to synthesize structural compounds and / or support of a viability of cells.

The phloem of the current year consisted of mature sieve cells, formed in the season, and conducing sieve cells. The number of both type of cells increased along the stem (Table). In late June the phloem layers in both ncPh and cPh increased to the top of the stem due to the production of new cells. In early August mature sieve cells increased at all levels of the stem whereas the number of conducting cells was practically the same. Total number of phloem cells was more at high level of the tree. This corresponded to increase in intensity of assimilative apparatus of tree to this period after the completion of its formation. Phloem cells, taking part in assimilate transport in both vertical and in radial directions, must have a steady state of redox-potential to coordinate multiple events in the time and the space and to promote not only phloem tissue functioning itself but also growth and development of xylem tissue.

Current year xylem layer consisted of three zones, including cambium, cell growth expansion, cell wall thickening as well as mature cells of earlywood and latewood (Table). In dXyl the cell growth zone in the period of earlywood formation (in late

Characteristics of the tissues at separate of *Pinus sylvestris* L. stem

Tissues in stem	Characteristics of tissue, the number of cells	June, 29			August, 11		
		Levels of stem, m					
		1.3	6.8	12.3	1.3	4.3	7.3
Phloem parenchyma, %		23.7 ± 2.6	15.0 ± 2.4	14.4 ± 2.3	16.2 ± 2.4	17.2 ± 1.3	13.8 ± 2.4
Phloem cells of previous year	Early Late	5.4 ± 0.8 3.4 ± 0.8	5.0 ± 0.7 4.8 ± 0.8	5.5 ± 1.0 3.8 ± 1.3	4.6 ± 0.6 6.4 ± 1.1	6.5 ± 1.0 7.0 ± 1.4	6.8 ± 1.5 14.0 ± 2.8
	Early, %	61.36	51.02	59.14	41.82	48.15	32.53
	Late, %	38.64	48.98	40.86	58.18	51.85	67.47
Phloem cells of current year	Non-conducting	4.6 ± 0.6	5.2 ± 1.1	5.2 ± 0.5	10.0 ± 1.0	11.2 ± 1.0	13.7 ± 1.5
	Conducting	2.2 ± 0.8	2.8 ± 0.8	4.0 ± 0.2	2.2 ± 0.8	2.4 ± 2.1	3.0 ± 0.8
Xylem cells of current year	Cambium	6.0 ± 0.1	5.4 ± 0.9	6.4 ± 0.6	7.6 ± 0.6	5.0 ± 0.7	6.4 ± 0.6
	expansion zone (G)	3.0 ± 0.1	3.2 ± 0.5	3.4 ± 0.6	3.4 ± 0.6	2.6 ± 0.6	2.6 ± 0.6
	Zone of wall thickening*: D1	2.0 ± 0.1	1.8 ± 0.5	1.6 ± 0.6	1.8 ± 0.5	1.4 ± 0.6	1.8 ± 0.5
	D2	8.4 ± 0.9	6.2 ± 0.5	4.6 ± 0.6	26.2 ± 2.3	22.8 ± 3.1	19.0 ± 1.2
	Mature cells: late				8.6 ± 1.8	2.8 ± 2.6	3.0 ± 1.9
	early	7.4 ± 0.6	1.6 ± 1.5	20.8 ± 1.1	26.6 ± 1.7	51.8 ± 2.1	> 45
Xylem cells of previous year	Late	4.4 ± 0.9	8.2 ± 1.1	15.0 ± 2.6	34.0 ± 1.4	35.4 ± 2.4	n. d.
	Early	8.0 ± 1.4	7.8 ± 1.3	50.6 ± 3.6	> 25	59.0 ± 2.7	n. d.
	Late cells, %	33.96	50.55	22.86	57.63	37.5	
	Early cells, %	66.04	49.44	77.13	42.37	62.5	

Note: * D1 – xylem cells at the first stage of wall thickening zone before lignifications; D2 – lignifying xylem cells in wall thickening zone; n. d. – no datum.

June) increased with the height of the stem while in early August it was rather small at both the middle and the top of tree as tracheid growth practically was completed. The wall thickening zone before lignification (D1) was always very narrow and the number of cells within the zone didn't change with height. In the course of both earlywood and latewood formation the number of tracheids in D2 zone decreased with the height. As the result the wall thickness of tracheids was declined to the top of tree. Xylem cell wall thickness has been shown to depend on the time of the development in secondary wall thickening zone (Antonova, Stasova, 2015), that in turn is determined by the number of cells in that zone (Antonova, 1999). Mature xylem of current year in the end of June contained only early tracheids and their number increased to the top of the stem as well as in early August. The number of latewood tracheids was more at the bottom of the tree and their maturation was continued in that time yet. Basic production of ROS in dXyl tissues can be assumed to form during cell growth in expansion zone and, especially, in the course of biomass deposition within cell walls and lignification (D2). All processes were ensured by carbohydrates supplied from the phloem and further along radial row that also required the specific expenditures for the transport.

Carbohydrates. The changes in the content of soluble carbohydrates due to which goes multiple events of metabolism and accumulation of biomass in wood annual ring are presented in Fig. 1.

In late June ncPh contained smaller amount of soluble carbohydrates compared with the early August when the part of carbohydrates can be accumulated as storage substances. The conducting phloem, as transport system, contained the large amount of carbohydrates at all levels of stem. During earlywood formation the content of carbohydrates didn't practically change with the height of the stem and was always more than that in the period of latewood formation (early August). In early August the amount of carbohydrates was largest in the cells at bottom level of the tree, probably, due to the higher demand to assimilates for the development of latewood tracheids, the wall thickness of which are always more than earlywood tracheids. Such distribution of carbohydrates is stimulated also by lowering of water potential to that direction (Sazonova et al., 2011).

The content of carbohydrates in dXyl cells at separate levels of the tree in late June changed in dependence on xylem development degree. In late June at the low level of the stem the number of cells in forming xylem, including cambium, was more (19.4) than at the middle and the top of tree (16.6 and 16.0 correspondingly) and the amount of carbohydrates was also more. In early August the forming latewood cells contained smaller amount of carbohydrates at low stem level compared with the late June, indicating their active utilization in synthesis. At the middle and the top of tree, the changes were not observed. This can point to the existence of some homeostasis in a demand and a using of substrates in biochemical and energetic processes what is in agreement with the number of developing xylem cells at those levels. The mature xylem cells along the stem contained practically similar amount of carbohydrates located in ray parenchyma.

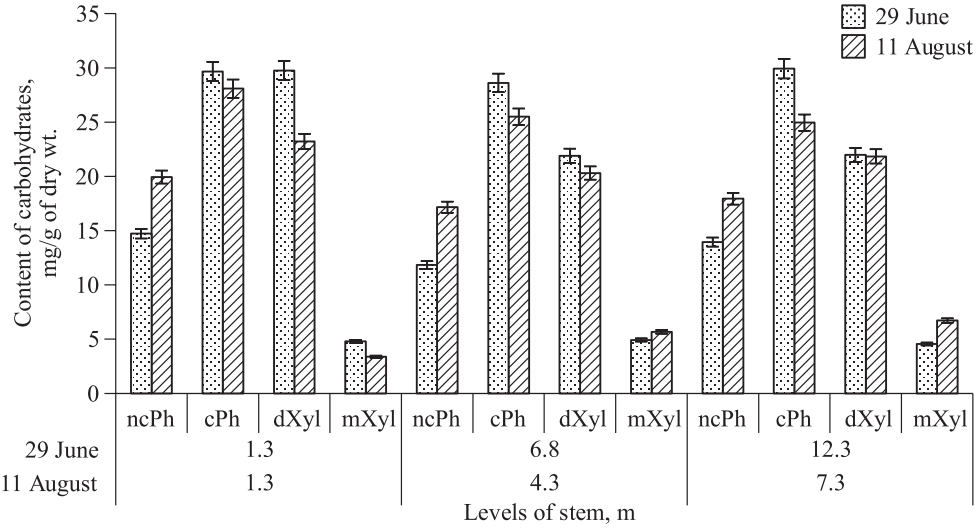

Fig. 1. The content of carbohydrates in the cells of non-conducting phloem, conducting phloem, developing xylem and mature xylem at different levels of Scots pine stem during the formation of earlywood and latewood in the season.

Soluble sugars through various metabolic reactions directly link with the production rates of ROS and with anti-oxidative processes. The variations in sugar levels have been likely connected with the changes of ROS production and with modification the expression of genes involved in the response to abiotic stress (Couerée et al., 2006) because sugars are supposed to act as regulators of gene expression in plants (Koch, 1996). On the other hand, such sugars as mannose and galactose are the source of AsA production through D-mannose / L-galactose pathway (Smirnoff-Wheeler pathway) with oxidation of L-galactose to L-galactono-1, 4-lactone, which is converted in turn into ascorbate by L-galactono-1, 4-lactone dehydrogenase (Baig et al., 1970; Smirnoff et al., 2001; Parsons, Fry, 2012).

The direct source of AsA can be uronic (galacturonic and glucuronic) acids themselves, which present in ethanol-soluble substances together with sugars and which change oppositely with AsA during early and late tracheid development in pine stem (Antonova et al., 2009). Galacturonic acid are supposed to be the one of main source of AsA using galactose residues eliminated from such galactose-contained carbohydrates as raffinose and stachyose (Antonova, 2012).

Cellular redox status of ascorbate in the tissues along radial and vertical directions of pine stem was estimated as AsA content and the ratio of AsA/(AsA + DHA). The data are presented in Fig. 2.

The content of AsA and AsA/(AsA + DHA) ratio within the cells of the tissues have been found to change along radial and vertical directions of the stem in the dependence on the type of forming wood. At the bottom of the tree in the radial direction ncPh cells contained certain quantity of AsA probably due to the presence of phloem parenchyma ray cells in which an accumulation or a destruction of the starch granules occured. Fulfilling of transport function Phc contained the most of AsA. Both in ncPh and in cPh AsA was more during early- than latewood formation. AsA in dXyl cells was considerably less compared with cPh cells in earlywood cells and especially in forming latewood. In late June the ratio of AsA/(AsA + DHA) was the most in cPh in both forming wood type, demonstrating some balance between ROS, produced in functioning phloem cells, and in oxidation-reduction reactions in AsA-DHA cycle. In early August, in contrast, the ratio was highest in dXyl cells, indicating enhance in AsA and relative decrease in DHA.

At consecutive developmental stages of cells AsA has been found to increase during late tracheid maturation in line with completing of lignification and to decrease with of earlywood cell development in line with the strengthening of lignification (Antonova et al., 2009, 2014). That is in agreement with observation what until AsA is available for hydrogen peroxide the processes of cross-linking and polymerization in the cell wall are retard-

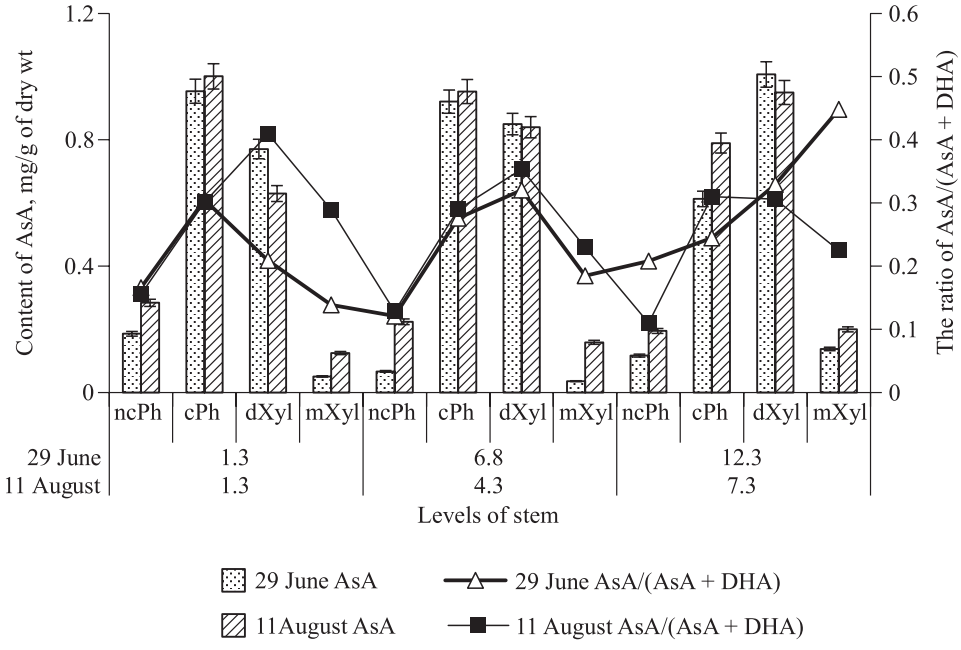

Fig. 2. The content of AsA and the ratio of AsA/(AsA + DHA) in the cells of non-conducting phloem, conducting phloem, developing xylem and mature xylem at different levels of Scots pine stem during the formation of earlywood and latewood in the season.

ed (Takahama, Oniki, 1997; Zarra et al., 1999). Probably, ROS production and the changes in AsA/(AsA + DHA) ratio in early August depended on the large number of cells in D2 stage in cell wall thickening zone, where wall structural components and lignin were deposited (26–28 cells). On the contrary, in late June D2 stage contained 8–9 cells (Table).

According to literature data the redox-potential of the apoplastic AsA pool is modulated by both ascorbate oxidase (AO) and peroxidase activities (APX) and is under the influence of external and internal stimuli (Pignocchi et al., 2006). The functioning of AO, ascorbate peroxidase I and ascorbate peroxidase III, involved in AsA oxidation in the apoplast, differs in dependence on substrate available and cell developmental stage (Córdoba-Pedregosa et al., 2003; Ros Barceló et al., 2004). Peroxidase may promote the late steps of xylogenesis in the response to generated hydrogen peroxide (Sterjiades et al., 1993). The ability of apoplastic ascorbate to modulate H_2O_2 concentration has been shown in a cell culture of *Picea abies* (Kärkönen, Fry, 2006). AO was assumed to interfere in lignin deposition in both earlywood and latewood at the beginning process whereas APX at last steps of that and APX acts more in latewood than earlywood lignification (Antonova et al., 2014).

In apoplast AsA is successively oxidized to monodehydroascorbate (MDHA) and DHA. MDHA is reduced enzymatically to AsA by MDAR using both NADH and NADPH as electron donors. MDHA can also spontaneously disproportionate to AsA and dehydroascorbate (DHA) (Noctor, Foyer, 1998; Foyer, Noctor, 2003). DHA is transported into the cytosol and then in mitochondria where AsA regeneration is catalysed by dehydroascorbate reductase (DHAR) (Rautenkranz et al., 1994; Horemans et al., 2000). From the cytosol, AsA is transported into the apoplast along the concentration gradient (Arrigoni, 1994). The drought increases the activity of APX and monodehydroascorbate reductase (MDHAR) (Baisak et al., 1994) as well as DHAR and glutathione reductase (Pastori, Trippi, 1992; Sharma, Dubey, 2005). DHAR catalyzes the reduction of DHA to AsA using GSH, reduced by glutathione reductase (GR) in GSH-GSSG cycle, being thus the enzyme which consolidates the processes of reduction of AsA and oxidation of GSH in AsA-glutathione cycle. In turn GR is considered as the key enzyme in AsA-GHS cycle (Asada, 2006; Chalapathi Rao, Reddy, 2006) and the rate-limiting enzyme of this cycle (Romero-Puertas et al., 2006). The activity of APX, MDHAR, DHAR and GR can be probably different in cell compartments due to transient changes in ascorbate-glutathione cycle (Foyer, Noctor, 2011). This may be also due to the reaction of the membranes to a modification of water potential gradient and solutes inside and outside of cells.

The distinction in the interrelation of AsA and DHA in dXyl cells can be the consequence of the differences in synthesis, reduction and transport of AsA and DHA under the changes in water potential into both apoplast and inside cell compartments that influences the transport of the compounds trough the membranes. The transport of DHA has been found to be inhibited by glucose because the transport of DHA and glucose in plant mitochondria depends on the one or closely related transporter(s) (Szarka et al., 2004). On the other hand the DHA carrier through plant plasma membrane is distinct from the plant Glc transporters (Horemans et al., 2008). The pool of Glu in the carbohydrate composition has been shown to decrease to mXyl during late tracheid development (Antonova, 1999) as well as the carbohydrate pool itself (Fig. 1). This may promote to DHA transport through mitochondrial membranes in apoplast where AsA pool is restored by DHAR. However, the rate of AsA transport across the plasmalemma and tonoplast has been found to be lower than DHA (Rautenkranz et al., 1994). In addition, the AsA pool produced by DHA restoration is supposed to be probably not completely equivalent to the AsA pool produced via L-galacto-y-lactone (Paciolla et al., 2001). In the same time glutathione-independent pathway for DHA reduction has been found to exist *in vivo* and to be present together with a glutathione-driven DHA reduction (Potters et al., 2004). The possibile loss of DHA in reaction chain can't be also excluded since DHA is considered as unstable molecule and undergoes spontaneous and irreversible hydrolysis to 2, 3-diketogulonic acid and further oxidation to oxalic acid (Deutsch, 1998; Parsons, Fry, 2012). It can be assumed that the appearance of oxalic crystals in non-conducting phloem in conifers is the result of such transformation of DHA.

It is interesting that benzoic acid arising as the result of ß-oxidation of p-hydroxycinnamic acids enlarges the permeaility of cell membranes (Glass, Dunlop, 1974). This can promote the transfer of reduced AsA in apoplast. The pool of benzoic acid has been found to increase from the beginning to the end of latewood tracheid lignification in line with enhance of AsA pool (calculated per cell) and with the decrease of deposition lignin rate in pine and larch (Antonova, 2012; Antonova et al., 2014). All

these cellular events, taken together, can explain the increase of AsA/(AsA + DHA) ratio in dXyl in early August compared with dXyl in late June.

At the other levels of the stem along radial direction AsA and its relationship with DHA change individually that point to own redox-potential within the cells of functioning tissues. At the middle of the stem cPh cells also contained more AsA than the cells of other tissues and the ratio of the acids was practically the same in the course of two type of wood formation. Although AsA within the cells of early dXyl as well as of late dXyl was less by comparison with cPh the ratio AsA/(AsA + DHA) in dXyl cells was more compared with cPh cells and that was a little more in dXyl in late June than that in early August. This is evidence of the differences in the functioning of redox-system within the cells of conducting and developing tissues.

At the top of the tree AsA pool in cPh during early tracheid development was considerably less as compared with middle level. AsA/(AsA + DHA) ratio was also less. In this time not only conducting phloem cells take part in transport system but possibly a part of non-conductive cells. This can explain increased ratio of AsA/(AsA + DHA) in ncPh cells (Fig. 2). In early August cPh cells contained more AsA and the acid ratio was higher in 1.5 times compared with late June. It is may be that at the beginning of August all growth processes in the shoots and the formation of assimilative apparatus were completed and the transport system worked with full loading.

Along the stem the content of AsA in ncPh cells at all levels was always less during earlywood than latewood formation but it was more than in mXyl cells at the same sites. In late June the AsA pool in cPh at the bottom of the tree was practically similar to that at the middle level whereas at upper level decreased substantially compared with middle level. In early August AsA in cPh cells decreased to the top of the tree. The ratio of AsA/(AsA + DHA) decreased to top level of the stem during earlywood development and was practically the same in forming latewood. The AsA pool in dXyl cells increased from the bottom to the tope of the stem during earlywood formation whereas that in latewood cells increased to the middle level and then didn't change. At the same time the ratio of acids increased from the bottom to the middle of the tree and didn't practically change at the top.

In latewood cells the acid ratio was the highest at the bottom of the stem, decreased considerably to the middle level and lessened to the top of the tree. The cells of mXyl contained a few AsA. Nevertheless the ratio of the acids increased subsequently in early mXyl at the top of the stem, especially sharply in mature earlywood at the upper level, probably because of a large number of the cells not completed their development. In mature latewood this ratio decreased from the bottom to the middle of the stem and then was practically similar at the upper level. Such divergence in the variation of AsA content and the ratio of AsA/(AsA + DHA) along the stem points to some differences in oxidation-reduction reactions in redox-system of cells at separate stem levels leading to the distinctions in xylem cell development (Table).

One of the reasons of the changes in metabolism during early and latewood formation along the stem can be distinctions in the levels of the hormones. In *Pinus contorta* the changes in indol-3-yl-acetic (IAA) and abscisic acids was considered in relation to seasonal cambium activity and xylem development (Savidge, Wareing, 1984). The substantial change in the relation of hormones has been found to occur in the period when cell expansion growth is over. The changes in the availability of water at the top of stem due to active transpiration in the period, when water reserves in soil was exhausted, provoke a modification in cellular metabolism and in particular in low content of IAA. The diminishing in IAA is resulted from the increase in IAA-oxidase. So, the activity of IAA-oxidase increased in the tissues of Scots pine seedlings under conditions of short-time water stress (artificial drought) in rhizosphere equally with the activity of peroxidase, malate dehydrogenase, ß-glucosidase (Sudachkova et al., 2012). According to Aloni et al. (2006) polar transport of IAA downward via the cambium to the root tips induces and controls wood formation. The vascular tissue continuity along the plant axis is a result of the steady polar flow of IAA from leaves to roots. Auxin is thought to act as a significant component stimulating transcriptions of a large number of genes (Hagen, Guilfoyle, 2002) and to play role of an integrator in the activities of multiple phytohormones (Jaillais, Chory, 2010). However, it should be admitted that the physical signals such as water potential and osmotic pressure are the firsts, which exert impact on apoplast and plasmalemma, and what in turn modulates biochemical and morphological processes trough electron-transport chain.

CONCLUSION

Thus, along horizontal and vertical directions of pine stem the cellular redox state of ascorbate changed in line with the functions and the devel-

opment degree of the tissues and in dependence on earlywood or latewood formation. These changes at different levels of the tree were in agreement with morphological status of the cells in the tissue and the content of soluble carbohydrates. At all levels of the stem the intensity of oxidation-reduction reactions in the cells of non-conducting phloem were higher than in mature xylem cells and less during earlywood than latewood formation. The cells of conducting phloem and forming xylem, as the principal tissues taking part in annual ring wood formation, showed the differences in the ascorbate/dehydroascorbate contents and, as the consequence, in their redox status. The content of ascorbate in conducting phloem during earlywood formation was higher at the low level of the stem and diminished to the top of the tree while in the course of latewood development it was similar at all levels. The ascorbate/dehydroascorbate ratio in the forming xylem cells increased to the top of the tree during the formation of early xylem and decreased in late xylem. Taken together, the data indicate the difference in oxidation-reduction reactions in cellular redox status of ascorbate in the stem tissues leading to the distinctions in xylem cell development and as the result in wood structure along the stem.

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ИЗМЕНЕНИЕ ОКИСЛИТЕЛЬНО-ВОССТАНОВИТЕЛЬНОГО ПОТЕНЦИАЛА АСКОРБАТА В КЛЕТКАХ ТКАНЕЙ СТВОЛА В ХОДЕ РОСТА СОСНЫ ОБЫКНОВЕННОЙ

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Изучали содержание аскорбиновой (АК) и дегидроаскорбиновой (ДАК) кислот и их отношение, показывающее уровень окислительно-восстановительного состояния АК в клетках тканей на разной высоте ствола сосны обыкновенной *Pinus sylvestris* L. в ходе образования ранней и поздней древесины. Морфологические характеристики клеток тканей и содержание растворимых углеводов изучали параллельно. Установлено, что содержание АК и отношение АК/ДАК зависят от типа ткани, степени развития ее клеток, высоты ствола, а также от типа формирующейся древесины. Содержание АК и отношение АК/ДАК в клетках непроводящей флоэмы вверху ствола были выше, чем в зрелой ксилеме, и меньше при образовании ранней, чем поздней древесины. Клетки проводящей флоэмы и формирующейся ксилемы, как основных тканей, принимающих участие в развитии годичного слоя древесины, отличаются по содержанию кислот при формировании ранней и поздней ксилемы. В клетках проводящей флоэмы содержание АК с высотой ствола уменьшалось, тогда как в клетках формирующейся ксилемы – увеличивалось при образовании как ранней, так и поздней древесины. При образовании ранней древесины АК/ДАК в клетках проводящей флоэмы было наибольшим внизу ствола и уменьшалось к вершине, а при развитии поздней ксилемы было практически одинаковым на всех уровнях ствола. В клетках формирующейся ксилемы АК/ДАК увеличивалось к вершине дерева при развитии ранней ксилемы и уменьшалось при развитии поздней, что указывает на различие окислительно-восстановительных потенциалов в клетках двух типов формирующейся ксилемы. Данные обсуждаются в связи с морфологическим развитием клеток тканей и содержанием в них углеводов.

Ключевые слова: *Pinus sylvestris L., высота ствола, непроводящая флоэма, проводящая флоэма, формирующаяся ксилема, зрелая ксилема, аскорбат / дегидроаскорбат отношение.*