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Radial and Vertical Distribution of Dissoluble Total Carbohydrate Content in the Beech (*Fagus sylvatica* L.): Relationships with Red Heartwood Formation

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ABSTRACT

Red heartwood forms in most old beech stands, which reduces the commercial value of the wood considerably. Many of the chemical and biochemical processes involved in red heartwood formation are known, but research has been limited to a single level of the stem (usually at breast height). The present study investigated the radial and vertical distribution of dissoluble carbohydrates at different height levels within a red heartwood (17 levels) and a non-red heartwood (12 levels) beech stem. The radial changes of the concentrations differ notably in beech with or without red heartwood. An increase in the transition zone is not a mandatory condition for red heartwood formation, but a decrease in concentration always occurs after the transition zone. Intense sugar metabolism at the color boundary contributes to the surplus energy required in red heartwood formation and the *in situ* synthesis of polyphenolic compounds.

TANULMÁNY INFÓ

Kulcsszavak:
Bükk
Álgesztesedés
Kioldható összcukor tartalom eloszlás

KIVONAT

A kioldható összcukor tartalom radiális és vertikális megoszlása a bükk (*Fagus sylvatica* L.) törzsben: összefüggések az álgesztesedés folyamataival. Az idős bükkállományok nagy részében álgeszt képződik, ami a faanyag kereskedelmi forgalmi értékét jelentősen csökkenti. Az álgesztesedés kémiai és biokémiai folyamatainak jelentős részét feltárták, de az eddigi kutatások csak a törzs egy adott szintjére korlátozódtak (általában a mellmagassági átmérő). Jelen munkánkban vizsgáltuk egy álgesztes és egy álgesztmentes bükk (*Fagus sylvatica* L.) kioldható összcukor tartalmának radiális és vertikális eloszlását. Mértük az álgesztes törzs 17 és az álgesztmentes törzs 12 magassági szintjén a koncentrációk sugárirányú eloszlását. Megállapítottuk, hogy a kioldható összcukrok koncentrációja, valamint radiális és vertikális megoszlása mind az álgesztes, mind az álgesztmentes törzsben magasságfüggő. A koncentrációk sugár irányú változásai szignifikánsan különböznek az álgesztes és az álgesztmentes bükkben. Az álgesztesedésnek nem kötelező feltétele a kioldható szénhidrátok koncentrációjának megemelkedése a tranzicionális zónában, de a koncentráció csökkenés a tranzicionális zóna után minden esetben bekövetkezik. Az intenzív cukor metabolizmus egyrészt az álgesztesedés folyamatait fedezheti, másrészt hozzárulhat a polifenol vegyületek *in situ* szintéziséhez az álgeszt határon.

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1 INTRODUCTION

Beech is a widespread broadleaved tree species in Europe. Its wood is of high economic, ecological, and silvicultural value and acts to stabilize forest ecosystems (Frýdl et al., 2011). Compared to conifers (Sáenz-Romero et al., 2019), beech has demonstrated higher adaptability and acclimation potential (Visi-Rajczi et al., 2021). Beech comprised 5.5 % of forested land in Hungary in 2019 (103 thousand hectares) (URL1). Red heartwood, a color and technological beech defect, forms in most old beech stands. Profound morphological and anatomical changes occur when red heartwood forms. These changes significantly affect wood properties, which differ from non-discolored ripewood in some of its properties. The moisture content drops below 60 %, and the distribution changes inside the stem. The wood cracks, warps, dries slower, is difficult to saturate, and attains poor adhesiveness (Pöhler et al., 2006; Vek et al., 2013). However, determining this color defect in standing trees is challenging (Knoke, 2002, 2003; Wernsdörfer et al., 2005, 2006). It does not show worse technological properties than non-discolored beech wood in terms of volume density, flexibility, bending, and compressive strength (Pöhler et al., 2006; Todorovic et al., 2012); however, the furniture industry seldom uses discolored beech because of its lower economic value (Molnar et al., 2001; Zell et al., 2004). Marketing efforts have done little to change this perception, and discolored timber remains a lower-value wood.

The crown base height, growth rate, defect prevalence, and the presence of forks can influence red heartwood development, which depends on forest ecosystem characteristics (Knoke, 2003). Defects and damage render the tree susceptible to oxygen, which penetrates the stem and increases microorganism activity (Sorz and Hietz, 2008). Oxygen degrades soluble carbohydrates and starch involved in the enzymatic transformation of colored phenolic substances (Koch et al., 2000, 2001; Albert et al., 2003; Hofmann et al., 2008). Chemical and biochemical processes occur in red heartwood formation, prominently in the transitional zone. Large amounts of soluble carbohydrates accumulate during these processes (Albert et al., 2002; Visi-Rajczi et al., 2002, 2003), the free and bound acid content decreases (Albert et al., 1998a, 1999), the pH increases, the buffer capacity changes (Albert et al., 1999), and the concentration of polyphenols (Koch et al., 2001; Albert et al., 2003; Hofmann et al., 2004, 2021) and the activity of phenol-oxidizing enzymes increase (Magel, 2000; Albert et al., 2000).

Carbohydrates provide the building blocks for plant structures and versatile resources for metabolic processes. Non-structural carbohydrates (NSC), mainly sugars and starch, fulfill distinct functional roles, including transport, energy metabolism, and osmoregulation. They also provide substrates for defense compound synthesis or exchange with symbionts involved in nutrient acquisition or defense. NSCs are crucial forms of tree carbon storage, mainly composed of soluble sugar and starch. NSC concentration represents a trade-off between carbon source gain via photosynthesis and carbon sink costs through metabolism and growth. It also reflects the relationship between supply and demand across plant tissues (Hartmann and Trumbore, 2016).

The soluble non-structural carbohydrate fraction of woody tissues consists primarily of sucrose, glucose, and fructose (Höll, 1997; Magel et al., 1997) but may also contain maltose or sugar alcohols (Höll, 1981; Sauter and VanCleve, 1993; Popp et al., 1997). Considerable amounts of raffinose and stachyose can also be detected in the living tissues in cold seasons (Magel et al., 1994; Sauter et al., 1989, 1998). Furthermore, disaccharide trehalose was identified in beech wood extracts (Dietrichs, 1964b; Vek et al., 2014). In all the examined trees, starch is the polymer-carbohydrate that fulfills the defining non-structural and reserve nutrient function, but very rarely, fructans are also detectable. Metabolic processes (physiological reactions) in wood tissues depend on the mobility and distribution of soluble carbohydrates and starch. These substances play a role in biochemical reactions of heartwood formation as starting and synthesis products of primary and secondary metabolic processes.

Research results indicate that dissoluble carbohydrates, polyphenols, and their oxidizing enzymes are decisive in red heartwood formation. However, most previous research focused on only one stem level (diameter at breast height). The moisture content distribution in red heartwood beech changes inside the stem (Pöhler et al. 2006; Vek et al. 2013). Within one stem, the tissue structure and stem diameters also differ vertically, so it can be assumed that the dissoluble total carbohydrate (DTC) concentrations vary at different altitude levels, and their radial and vertical distribution also varies.

The present study assessed the radial distribution of the DTC content at different height levels within a red heartwood stem (17 levels) and a non-red heartwood (12 levels) stem. The measurements also made it possible to follow the vertical distributions. We also examined whether differences in red heartwood beech processes can be detected as a function of height. The beech without red heartwood also served as a comparison basis. Results were compared to previous findings on sugar distributions in the stem of other woody species, and conclusions on the role of dissoluble sugars in the biochemical processes of red heartwood formation were made.

2 MATERIALS AND METHODS

2.1 Sample assignment and collection

The present study analyzed one red heartwood stem and one non-red heartwood stem from the TAEG (Tanulmányi Erdőgazdaság) Forestry Company, Sopron (Hungary). The trees were between 100–110 years old.

In the height tests, we extracted sample discs at every meter of the tested stems up to the first fork. *Tables 1 and 2* summarize the sampling heights. The red heartwood stem was cut into five (I-V) logs (*Figure 1*), and the logs were then split in the middle. Red heartwood diameters varied from 1 cm to 13.1 cm along the 19 m, depending on stem height. Red heartwood was absent below 1 m, above 15 m, and in the middle of logs IV and V. We cut 17 sample discs from the red heartwood stem and 12 from the non-red heartwood stem. Eight samples were taken along the radius of the red heartwood discs, while five samples were taken between the bark and the pith of the non-discolored stem (*Figure 2). *The letter f represents the sapwood; g, the heartwood (g) on each side of the transition zone (color boundary) in the red heartwood stems. The present study examined 196 samples.

The stems were taken to the laboratory immediately, where they were sectioned, rasped, and extracted within one day.

2.2 DTC content extraction and measurement

We extracted 0.25 g of wood grist fractions with 25 ml methanol:water 80:20 (v/v) solution for 6 hours using a Variomag Poly15 magnetic stirrer. The extracts were filtered through a Whatman GF/A grade glass fiber filter. The DTC content was determined by the Dubois method (Dubois et al., 1956), using glucose as standard. We mixed 1 ml of 5% aqueous phenol solution with 1 ml extract solution. After homogenization, 5.0 ml of concentrated sulfuric acid solution was carefully added to the mixture and homogenized again. After 10 minutes at room temperature, the mixture was cooled in a 25 °C water bath for 20 minutes. The sugar content was determined spectrophotometrically at 490 nm using glucose as standard. Assays were run in triplicates for each extract. Results were given in mg dissoluble total sugar/g dry weight (mg/g dry wood).

I. log (0-3 m) II. log (4-6 m) III. log (7-9 m) IV. log (10-12 m) V. log (12-15 m)

Figure 1. Red heartwood beech logs (I-V)

Table 1. Analysis by red heartwood beech height – Stem diameters of red heartwood in different sampling heights

Height (m)	*0.04*	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*12.5*	*13.5*	*14.5*	*15*
Log	*I.*				*II.*			*III.*			*IV.*			*V.*			
Stem diameter (cm)	54	46	44	42	42	43	43	38	36	38	34	28	32	32	30	32	30
Red-hw. diameter (cm)	0	7	10	13	12.5	13.1	12.8	10	8	9.3	2	6	8.5	6	1	5.6	0

Table 2. Analysis of beech without red heartwood by height – Stem diameters at different sampling heights

Height (m)	*0.05*	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11.4*
Log	*I.*				*II.*			*III.*			*IV.*	
Stem diameter (cm)	48	40	40	42	42	42	39	32	32	30	30	28

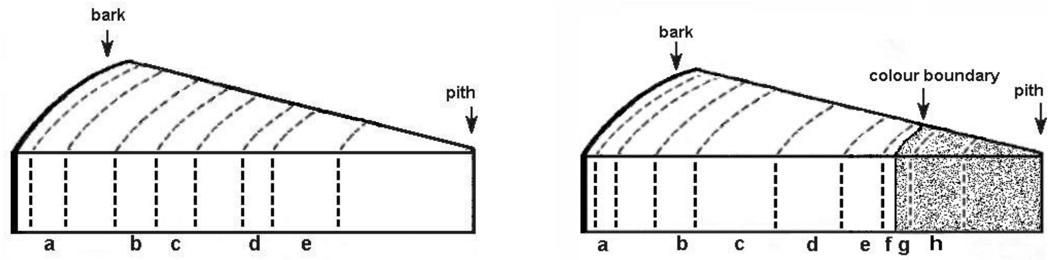

Figure 2. The graphic description of wood section assignments from sample disks; a–e: sapwood/ripewood tissues; f: red heartwood boundary white, g: red heartwood boundary red, f/g: sapwood/red heartwood transition zone; h: inner red heartwood.

3 RESULTS AND DISCUSSION

3.1 Radial distribution of DTC content at different height levels

Aligning with previous investigations, similar radial tendencies were observed in the red heartwood stem at nine levels (Albert et al., 1998b, 2002, 2003, 2005) for individual levels: a continuous radial decrease of the concentration to the inner ripewood (e) tissues, an increase in the transition zone (f) and a sharp decrease in the outer red heartwood (g) with minor or low concentrations in the inner red heartwood (h). The radial concentration distribution at the other levels deviated from this trend. *Figure 3* illustrates the characteristic changes. The general trend can be observed at 1 m: the concentration decreases up to the inner ripewood (e) tissues, increases in the transitional zone (f), and decreases dramatically in the outer red heartwood (g). At 5 m, the radial decrease is continuous; at 10 m, the decrease lasts only to the outer ripewood (d) tissues. The increase begins in the inner ripewood (e) tissues and then spikes in the transitional zone (f). At 12 m, the concentration is highest in the inner ripewood (e) tissues and decreases in the transitional zone (f). At 13.5 m, the concentration rose continuously in the radial direction. After the transition zone (f), the concentration drops sharply. The inner red heartwood tissues (h) also contain some soluble carbohydrates.

As seen in *Figure 3*, not all investigated heights experienced DTC content increases at the red heartwood boundary. This can be explained by the DTC assay being non-specific for simple sugars and measuring glycosides or by random extraction errors and the DTC assay and by deterministic trends with the heights, all of which make the vertical evaluation of the values necessary for each tissue.

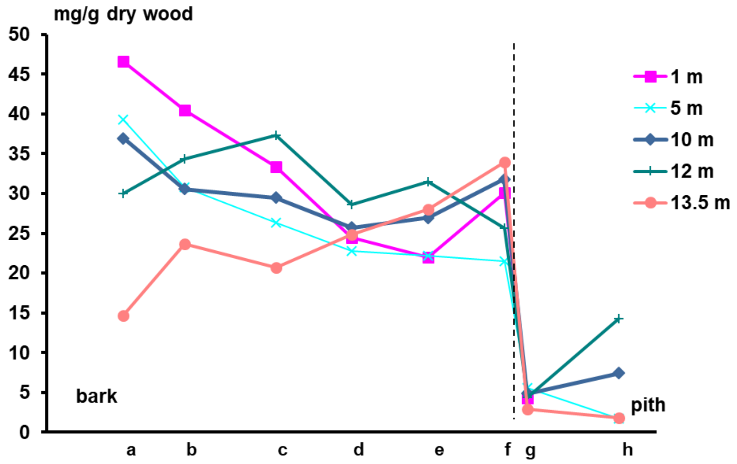

Figure 3. Radial distribution of the dissoluble total sugar content in red heartwood beech at 1, 5, 10, 12, and 13.5 m

The dissoluble total sugar content was high in the lower and upper parts of the stem and low in the middle part of the **non-red heartwood beech** samples. In tissues (a-e), the lowest total value was measured at 8 m, the highest at 0.05 m. According to the literature, the DTC content of the sapwood tissues in non-red heartwood beech continuously decreased in the radial direction, but the decrease did not become notable in heartwood (Visi-Rajczi et al., 2002; Albert et al. 2002). The radial changes of the concentrations at the five height levels of the investigated non-red heartwood stem followed the trend described in the literature and differed at seven height levels.

The DTC content in the inner ripewood (e) tissues increased at 1 m, 9 m, and 11.4 m, where it increased or remained constant in the inner sapwood (b) and outer ripewood (d) tissues but only decreased in the inner ripewood (e) at 3 m. There was a continuous increase from the outer ripewood (d) tissues at 9 m, and this increased significantly in the inner sapwood (b) tissues, decreased in the outer ripewood (d) tissues, and increased in the inner heartwood (e) at 11.4 m. *Figure 4* shows the radial variation of the soluble total sugar content at 0.05 m, 3 m, 9 m, and 11.4 m.

The trend-like radial decrease of the concentration can be followed at 0.05 m. At 3 m, the concentration increases in the sapwood (b, c) tissues, remains constant in the outer ripewood (d) tissues, and decreases in the inner ripewood (e). At 9 m, it rises continuously after the sapwood tissues (c). At 11.4 m, it increases significantly in the sapwood (b-c) tissues, decreases in the outer ripewood (d) tissues, and increases in the inner ripewood (e).

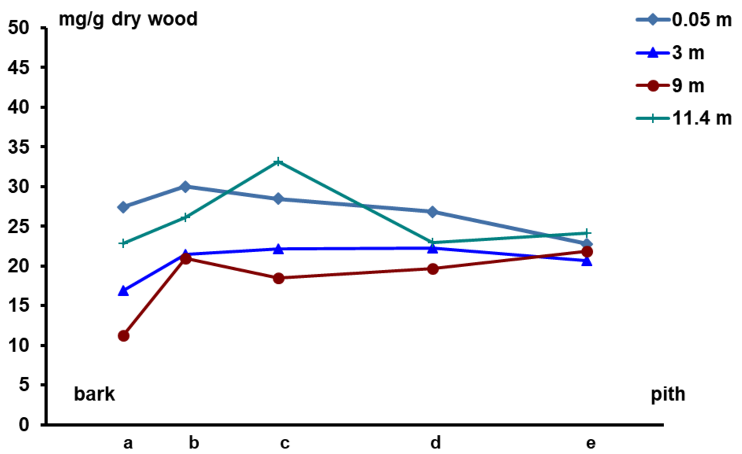

Figure 4. Radial distribution of the dissoluble total sugar content in the beech without red heartwood at 0.05, 3, 9, and 11.4 m

Dietrichs (1964b) was the first to examine the distribution of soluble carbohydrates from the cambium to the pith in beech (*Fagus sylvatica* L.), oak (*Quercus* sp.), birch (*Betula alba* L.), Norway spruce (*Picea abies* KARST.) and limba (*Terminalia superba* ENG. & DIELS.). The dominant sugars (sucrose, fructose, and glucose) are present primarily in the outer sapwood, and their amount decreases from the cambium to the pith (Dietrichs, 1964b; Höll 1985). All the non-structural carbohydrates are distributed relatively evenly within the sapwood for all species that do not have obligatory colored heartwood.

Starch and sugar concentrations continuously decrease in the sapwood tissues while moving toward the heartwood boundary. However, this decrease follows different patterns for different species: it is much more noticeable in *Robinia pseudoacacia* and less visible in the case of *Pinus sylvestris*. Interestingly, the sugar content showed the opposite trend and reached its maximum near the color boundary in *Angophora costata* tissues examined in early summer (Hillis et al., 1962).

In several investigated tree species, starch content is the highest in the inner sapwood, and values decrease inwards (Dietrichs, 1964a; Hillis, 1968) to the color boundary, where they disappear (Dietrichs, 1964a). Magel et al. (1997) confirmed these results in measurements detecting the enzymatic hydrolysis of starch in the border zone.

In most trees (conifers and hardwood species), the heartwood contains almost no non-structural carbohydrates (Magel et al., 1997; Dietrichs, 1964b; Höll, 1972), yet there are exceptions. Mannose was evidenced in spruce heartwood of spruce, while xylose and arabinose were detected in oak heartwood (Hillis, 1987).

According to Saranpää and Höll (1989), the sugars present in small amounts in Scots pine heartwood (e.g., mannose or arabinose) may originate from a hemicellulose decomposition during the sapwood/heartwood transformation. Like other coniferous species, larch sapwood (*Larix* spp.) contains only trace amounts of water-soluble polysaccharides. In contrast, the heartwood contains a large amount of arabinogalactan-type compounds, which can be dissolved in hot water and are thus loosely bound to the cell wall structure (Hillis, 1968).

Researchers attribute the appearance of arabinogalactans in the heartwood tissues to changed biosynthetic pathways during the heartwood formation processes (Ziegler, 1968). According to Magel et al. (2001), the glucose in black walnut heartwood tissues is released from the cleavage of the phenolic-glycoside precursors involved in the heartwood formation reactions.

Magel (1993) identified glucose, fructose, raffinose/stachyose, starch, and adenosine mono-di- and triphosphates from red-heartwood beech trunks using thin-layer chromatography and enzymatic determination. In general, the sugar concentrations were high in the sapwood and low in the colored wood, with the young (outer sapwood) tissues showing the highest raffinose/stachyose levels. Starch amounts decreased from the outer sapwood towards the inner sapwood and were not detectable in red heartwood. Adenine nucleotide concentrations were the highest in the outer sapwood, while inner sapwood showed very low levels, and the red heartwood contained no adenine nucleotides. The presented decrease in carbohydrate levels indicates that they are transformed and participate in active hydrolysis and syntheses.

Our previous research established that the total polyphenol concentration (Albert et al., 2003) and the amount of individual polyphenolic compounds (Hofmann et al., 2022) increased in front of the red heartwood boundary. Compared with the current measurements, it can be concluded that intense processes occur at the border zone. These involve sugar metabolism, which fuels sapwood/heartwood transformation reactions and produces substrate for the *in situ* synthesis of phenolic compounds.

As mentioned, radial tendencies of the DTC content may vary at different heights. Hence, the vertical trends of the concentrations were also investigated for each tissue to improve interpretation.

3.2 Vertical distribution of the DTC content at different height levels

Figure 5 depicts the vertical variation of the DTC contents in different tissues of a red heartwood beech stem. The highest values occurred in sapwood (a, b) tissues, especially at the stem base (0-5 m), and concentrations decreased up the stem. Similarly, as in *Figure 3*, concentrations decreased in the inner sapwood tissues (e), and an increase in front of the red heartwood boundary (f) was found only at certain height levels. Interestingly, the increase of DTC content in tissue (f) was not experienced at the heights with the highest red heartwood diameter (3-7 m), which can be explained by the fact that red heartwood formation is the most expressed in the stem at these altitudes. Consequently, the biochemical reactions of red heartwood formation consume quickly. Behind the color boundary (g, h), DTC content was very low at all height levels.

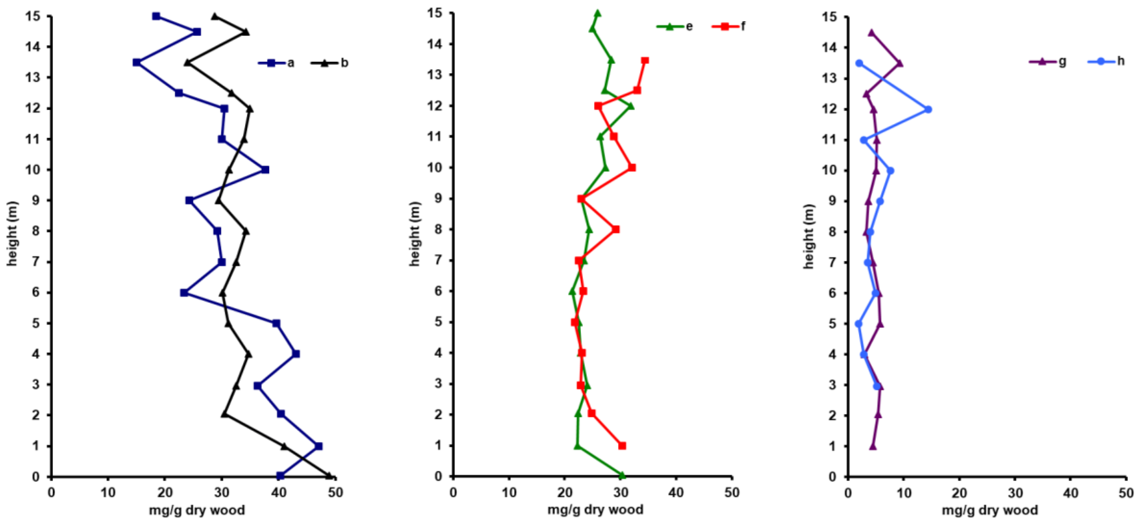

Figure 5. Vertical distribution of the dissoluble carbohydrate concentration in red heartwood beech tissues. a: outer sapwood, b: inner sapwood, e: inner heartwood, f: transition zone, g: outer red heartwood, h: inner red heartwood.

The DTC content of **non-red heartwood beech** tissues was high in the lower and upper parts of the stem and low in the middle part: the lowest total concentration was measured at 8 m; the highest at 0.05 m. Unlike the red-heartwood stem, stem concentrations increased above 9 meters in the non-red heartwood. The soluble carbohydrate concentration in the vertical tissue bands corresponding to the same anatomical locations varied between 10–35 mg/g of dry wood at all height levels (*Figure 6*).

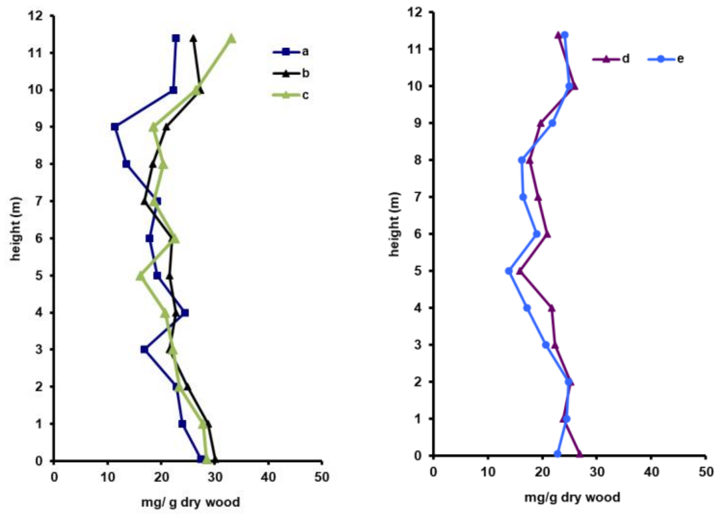

Figure 6. Vertical distribution of the dissoluble carbohydrate concentration in beech tissues without red heartwood. a, b, c: outer and inner sapwood tissues, d, e: outer and inner heartwood

Tables 3 and 4 in the Appendix show the statistical evaluation of the data.

4 CONCLUSIONS

The radial and vertical distributions and the concentration of dissoluble carbohydrates are height-dependent in both investigated beech stems with and without the red heartwood, with different radial tendencies. In accordance with previous results, the present study discovered that outer sapwood contained the highest levels of total dissoluble sugars, especially at the stem base (0–5 m), and concentrations decreased while moving up the stem. Concentrations increased above 9 meters in the non-red heartwood stem. Inner sapwood contained lower amounts of dissoluble sugars than outer sapwood. The concentration drops dramatically behind the color boundary in red heartwood beech. A non-obligatory condition for red heartwood formation is a sudden increase in the concentration of dissoluble carbohydrates in the transition zone, especially at heights between 0–2 meters and above 7 meters. Interestingly, between 2–7 meters, where red heartwood diameter is the highest, such an increase was not experienced in tissue f, which was explained by the rapid metabolism of sugars in these tissues due to expressed heartwood formation processes. In accordance with previous results, we found that sugar metabolism is especially significant in the processes of red heartwood formation in beech. Carbohydrate contents have distinct radial and vertical tendencies connected to red heartwood diameter. Increased levels of carbohydrate contents before the red heartwood boundary are responsible for fueling the metabolic pathways of red heartwood formation and for the *in-situ* production of polyphenolic compounds needed for the synthesis of the red heartwood coloring substances.

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APPENDIX

Table 3. Radial and vertical distribution of total soluble carbohydrate content (mean(std. dev)) in red heartwooded beech

h (m)	0.04	1	2.05	2.96	4	5	6	7	8
a	39,8(2,1)$_{ab}^{EF}$	46.6(3.0)$_{f}^{F}$	39.9(4,9)d^{EF}	35.8(3.5)d^{DEF}	42.7(4.3)$_{d}^{F}$	39.3(2.4)$_{d}^{EF}$	23.1(2.3)$_{b}^{ABC}$	29.6(3.4)$_{cd}^{CDE}$	28.8(1.9)$_{bc}^{BCDE}$
b	48.3(5,9)$_{b}^{D}$	40.5(3.7)$_{ef}^{CD}$	30.2(1.8)$_{bc}^{AB}$	32.2(1.3)$_{cd}^{ABC}$	34.4(4.1)$_{c}^{BC}$	30.8(0.7)$_{c}^{AB}$	29.8(1.6)$_{c}^{AB}$	32.2(2.0)$_{d}^{ABC}$	34.0(2.2)$_{c}^{BC}$
c	43.9(2,6)$_{b}^{F}$	33.3(4.6)$_{de}^{DE}$	31.9(2.5)$_{cd}^{CDE}$	27.1(1.4)$_{bc}^{ABCD}$	25.0(2.5)$_{b}^{ABC}$	26.4(0.7)$_{bc}^{ABCD}$	25.1(0.5)$_{bc}^{ABC}$	23.8(2.6)$_{bc}^{AB}$	24.8(2.8)$_{b}^{ABC}$
d	39.2(3,6)$_{ab}^{C}$	24.5(0.4)$_{bc}^{AB}$	24.5(4.7)$_{bc}^{AB}$	24.1(1.2)$_{b}^{AB}$	23.7(0.6)$_{b}^{AB}$	22.8(1.5)$_{b}^{AB}$	22.1(1.8)$_{b}^{AB}$	20.2(1.8)$_{b}^{A}$	22.8(2.0)$_{b}^{AB}$
e	29.9(3,3)$_{a}^{CD}$	22.0(0.8)$_{d}^{AB}$	22.2(0.5)$_{b}^{AB}$	23.7(0.5)$_{b}^{ABC}$	22.6(1.1)$_{b}^{ABC}$	22.2(0.6)$_{b}^{AB}$	21.1(3.2)$_{b}^{A}$	23.2(3.3)$_{b}^{ABC}$	24.1(0.6)$_{b}^{ABCD}$
f		30.1(0.7)$_{cd}^{ABCD}$	24.6(3.7)$_{bc}^{ABCD}$	22.6(1.9)$_{b}^{ABb}$	22.9(1.2)$_{b}^{AB}$	21.5(4.2)$_{b}^{A}$	23.1(1.5)$_{b}^{ABC}$	22.3(2.1)$_{b}^{AB}$	28.9(4.6)$_{bc}^{ABCD}$
g		4.3(1.9)$_{a}^{AB}$	5.2(1.4)$_{a}^{AB}$	5.6(1.1)$_{a}^{B}$	2.7(0.3)$_{a}^{A}$	5.6(0.3)$_{a}^{B}$	5.4(0.4)$_{a}^{AB}$	3.9(0.6)$_{a}^{AB}$	3.1(0.0)$_{a}^{AB}$
h				5.0(2.3)$_{a}^{AB}$	2.5(0.2)$_{a}^{A}$	1.8(0.2)$_{a}^{A}$	4.7(0.5)$_{a}^{AB}$	3.4(0.2)$_{a}^{AB}$	3.9(0.6)$_{a}^{AB}$

h (m)	9	10	11	12	12.5	13.5	14.5	15
a	24.0(1.1)$_{b}^{ABC}$	36.9(3.8)$_{c}^{EF}$	29.5(1.9)$_{b}^{CDE}$	30.0(9.9)$_{bc}^{CDE}$	22.2(4.1)$_{b}^{ABC}$	14.7(1.0)$_{b}^{A}$	25.3(1.0)$_{b}^{ABCD}$	18.2(1.5)$_{a}^{AB}$
b	29.1(1.7)$_{c}^{AB}$	30.6(4.1)$_{bc}^{AB}$	33.4(3.6)$_{b}^{BC}$	34.3(3.2)$_{bc}^{BC}$	31.1(2.0)$_{cd}^{AB}$	23.7(2.5)$_{c}^{A}$	34.0(2.1)$_{c}^{BC}$	28.4(3.0)$_{b}^{AB}$
c	24.2(1.9)$_{bc}^{AB}$	29.5(4.9)$_{bc}^{BCD}$	29.7(1.3)$_{b}^{BCD}$	37.3(1.4)$_{c}^{EF}$	25.3(2.7)$_{bc}^{ABC}$	20.7(0.4)$_{bc}^{A}$	26.8(1.4)$_{b}^{ABCD}$	28.4(1.2)$_{b}^{BCD}$
d	23.3(2.7)$_{b}^{AB}$	25.7(1.1)$_{b}^{AB}$	26.4(2.5)$_{b}^{AB}$	28.6(0.6)$_{bc}^{B}$	21.8(1.9)$_{b}^{AB}$	24.9(3.0)$_{c}^{AB}$	26.6(1.3)$_{b}^{AB}$	23.2(3.2)$_{ab}^{AB}$
e	22.7(2.9)$_{b}^{ABC}$	27.0(4.5)$_{b}^{ABCD}$	26.0(3.6)$_{b}^{ABCD}$	31.4(3.5)$_{bc}^{D}$	26.8(0.6)$_{bcd}^{ABCD}$	28.0(1.7)$_{cd}^{ABCD}$	24.7(0.7)$_{b}^{ABCD}$	28.6(3.0)$_{b}^{BCD}$
f	22.7(0.6)$_{b}^{AB}$	31.8(2.3)$_{bc}^{BCD}$	28.3(3.6)$_{b}^{ABCD}$	25.6(0.5)$_{b}^{ABCD}$	32.7(3.9)$_{d}^{CD}$	33.9(7.2)$_{d}^{D}$		
g	3.4(0.5)$_{a}^{AB}$	4.8(0.3)$_{a}^{AB}$	5.0(0.9)$_{a}^{AB}$	4.4(0.1)$_{ab}^{A}$	3.1(0.3)$_{a}^{AB}$	2.9(1.5)$_{a}^{AB}$	4.1(1.1)$_{a}^{AB}$	
h	5.6(0.1)$_{a}^{AB}$	7.4(1.2)$_{a}^{A}$	2.6(3.5)$_{a}^{A}$	14.3(1.0)$_{a}^{C}$		1.8(0.7)$_{a}^{A}$		

Table 4. Radial and vertical distribution of total soluble carbohydrate content (mean(std. dev)) in beech without red heartwood

h (m)	0.05	1	2	3	4	5	6	7	8	9
a	27.4(4.4)$_{a}^{F}$	24.0(3.5)$_{a}^{DEF}$	22.9(2.8)$_{a}^{CDEF}$	16.9(1.9)$_{a}^{ABC}$	24.4(1.3)$_{a}^{EF}$	19.2(1.4)$_{bc}^{BCDE}$	17.7(1.1)$_{a}^{ABCD}$	19.3(2.3)$_{a}^{BCDE}$	13.4(0.4)$_{a}^{AB}$	11.2(1.0)$_{a}^{A}$
b	30.0(0.8)$_{a}^{C}$	28.8(5.3)$_{a}^{C}$	24.9(2.8)$_{a}^{ABC}$	21.5(2.0)$_{a}^{ABC}$	22.7(3.6)$_{a}^{ABC}$	21.5(1.7)$_{c}^{ABC}$	22.0(1.4)$_{bc}^{ABC}$	16.9(2.3)$_{a}^{A}$	18.4(1.5)$_{bc}^{AB}$	21.0(0.9)$_{bc}^{ABC}$
c	28.5(1.4)$_{a}^{E}$	27.8(2.5)$_{a}^{E}$	24.2(1.3)$_{a}^{CDE}$	22.2(2.6)$_{a}^{BCD}$	20.7(0.7)$_{a}^{BC}$	16.1(1.0)$_{ab}^{A}$	22.5(0.3)$_{c}^{BCD}$	18.6(1.5)$_{a}^{AB}$	20.3(1.9)$_{c}^{ABC}$	18.5(1.2)$_{b}^{AB}$
d	26.8(5.0)$_{a}^{C}$	23.9(1.8)$_{a}^{ABC}$	25.1(2.2)$_{a}^{BC}$	22.3(5.9)$_{a}^{ABC}$	21.7(3.5)$_{a}^{ABC}$	15.8(1.0)$_{a}^{A}$	20.9(1.4)$_{abc}^{ABC}$	19.3(1.3)$_{a}^{ABC}$	17.6(1.1)$_{bc}^{AB}$	19.7(0.4)$_{bc}^{ABC}$
e	22.8(1.4)$_{a}^{BC}$	24.5(3.4)$_{a}^{C}$	24.8(2.0)$_{a}^{ABC}$	20.6(2.2)$_{a}^{AB}$	17.1(3.5)$_{a}^{ABC}$	13.8(0.4)$_{a}^{A}$	18.9(1.2)$_{ab}^{ABC}$	16.4(0.5)$_{a}^{AB}$	16.1(1.4)$_{ab}^{A}$	21.8(1.9)$_{c}^{AB}$

h (m)	10	11.4
a	22.3(1.9)$_{a}^{CDEF}$	22.8(1.2)$_{a}^{CDEF}$
b	27.4(7.2)$_{a}^{BC}$	26.1(0.3)$_{a}^{ABC}$
c	26.5(0.8)$_{a}^{DE}$	33.1(0.4)$_{b}^{F}$
d	25.9(2.2)$_{a}^{C}$	22.9(1.5)$_{a}^{ABC}$
e	25.0(0.6)$_{a}^{BC}$	24.1(2.7)$_{a}^{ABC}$

Different capital letters in the same row (vertical direction) indicate a significant difference at the p = 0.05 % level. Different lowercase letters in the same column (radial direction) indicate a significant difference at the p= 0.05 % level.